Seasonal movement, winter habitat use, and population distribution of an east central Wisconsin pheasant population. No. 76 1974

Gates, John M.; Hale, James B.

Madison, Wisconsin: Wisconsin Department of Natural Resources, 1974

Technical Bulletin No. 76

SEASONAL MOVEMENT, WINTER HABITAT USE, AND POPULATION DISTRIBUTION OF AN EAST CENTRAL WISCONSIN PHEASANT POPULATION

DEPARTMENT OF NATURAL RESOURCES
Madison, Wisconsin 1974

ABSTRACT

Year-round patterns of pheasant movement and seasonal habitat requirements were studied from 1958 to 1966 in southwestern Fond du Lac County and adjacent parts of Green Lake and Dodge County, Wisconsin. This area traditionally supported some of Wisconsin's highest pheasant populations. Analysis of pheasant movements was based on 2,323 marked pheasants which provided 7,600 individual movement records following original capture and marking.

Movements in fall, as well as distance of travel to winter cover, differed prominently with sex and age. Adult cocks were the least mobile, followed in order by adult hens, juvenile cocks, and juvenile hens. Wetlands provided the major winter cover. Successive generations of hens from various parts of the study area had well-defined traditions for specific wintering areas, and persistence of family organization during the move to winter cover was one of the primary mechanisms through which tradition was passed. Movement to winter cover was jointly influenced by weather and availability of alternative cover. Traditional wintering areas attracted pheasants from summer ranges averaging 8.3 square miles in size.

Daily movements in winter between food and cover typically covered ¼ mile or less, with ½ mile the apparent upper limit of the daily cruising radius. Distribution of winter cover had a more important bearing on the distribution of winter populations than availability of food. For 7 winters, 78 to 88 percent of the winter pheasant population was associated with wetland cover, primarily shrub-carr.

Among hens, body condition at winter's end varied significantly from year to year depending on food availability and energy demands of the preceding winter. Late-winter variation in hen condition had an important bearing on subsequent rates of reproduction and survival.

Spring dispersal from winter cover showed cocks departing ahead of hens, and adult hens preceding young hens. Spring dispersal of adults was interpreted as goal-oriented homing to specific breeding areas. Because of lower reproductive success on uplands, egress of hens from wetlands predisposed higher spring populations to lower productivity, a key mechanism through which population growth might have been checked.

Habitat needs during the reproductive period could be supplied on tracts as large as ¼ to ½ square mile without exceeding the normal range of travel during reproduction. Both cocks and hens showed strong preferences for wetland cover during prenesting activity. Wetlands were the primary cover type in which brood production occurred, although adjacent uplands were preferentially used for brood rearing.

Management recommendations for the preservation of winter cover, provision of winter food, influencing hen distribution in spring, and use of wintering areas as shooting preserves are offered.

SEASONAL MOVEMENT, WINTER HABITAT USE, AND POPULATION DISTRIBUTION OF AN EAST CENTRAL WISCONSIN PHEASANT POPULATION

By
John M. Gates
and
James B. Hale

Technical Bulletin No. 76
DEPARTMENT OF NATURAL RESOURCES
Madison, Wisconsin 1974

It is with deep regret we announce the death of John M. Gates on February 2, 1974, during the time this report was being prepared for publication.

CONTENTS

NATURE OF THE INVESTIGATION

BACKGROUND

Information on the ecology of Wisconsin pheasants began with the researches 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 investigations 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.

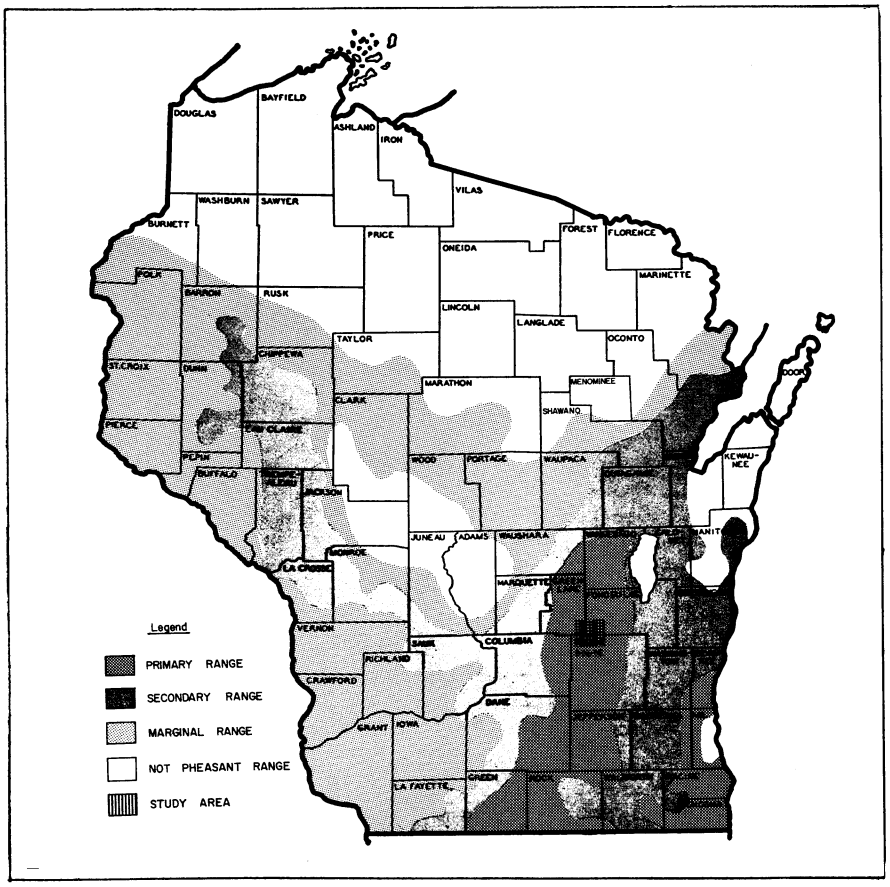
Field work on this project began in August of 1958 and was pursued as a full-time endeavor between January of 1959 and May of 1965. Certain phases of data collection were continued on a part-time schedule through May of 1966. Although 1959-1965 represented the main period of study, data collected outside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

The purpose of this report is to describe the year-round pattern of pheasant movement and to define seasonal habitat requirements of the intensively studied local pheasant population in east central Wisconsin. Major attention is centered on the

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).*



ecology of wintering and prenesting populations.

The main sections are concerned primarily with the population from October 1 through ultimate concentration in winter cover; details of wintercover selection and winter movement; spring dispersal from winter cover through final occupancy of home ranges during reproduction; and movement and cover use during the breeding season.

Analysis of pheasant movement in this study was based on 2,323 marked individuals which provided 7,600 movement records subsequent to initial capture and marking. These represented 69 percent of the 3,390 wild birds originally marked for movement and survival studies.

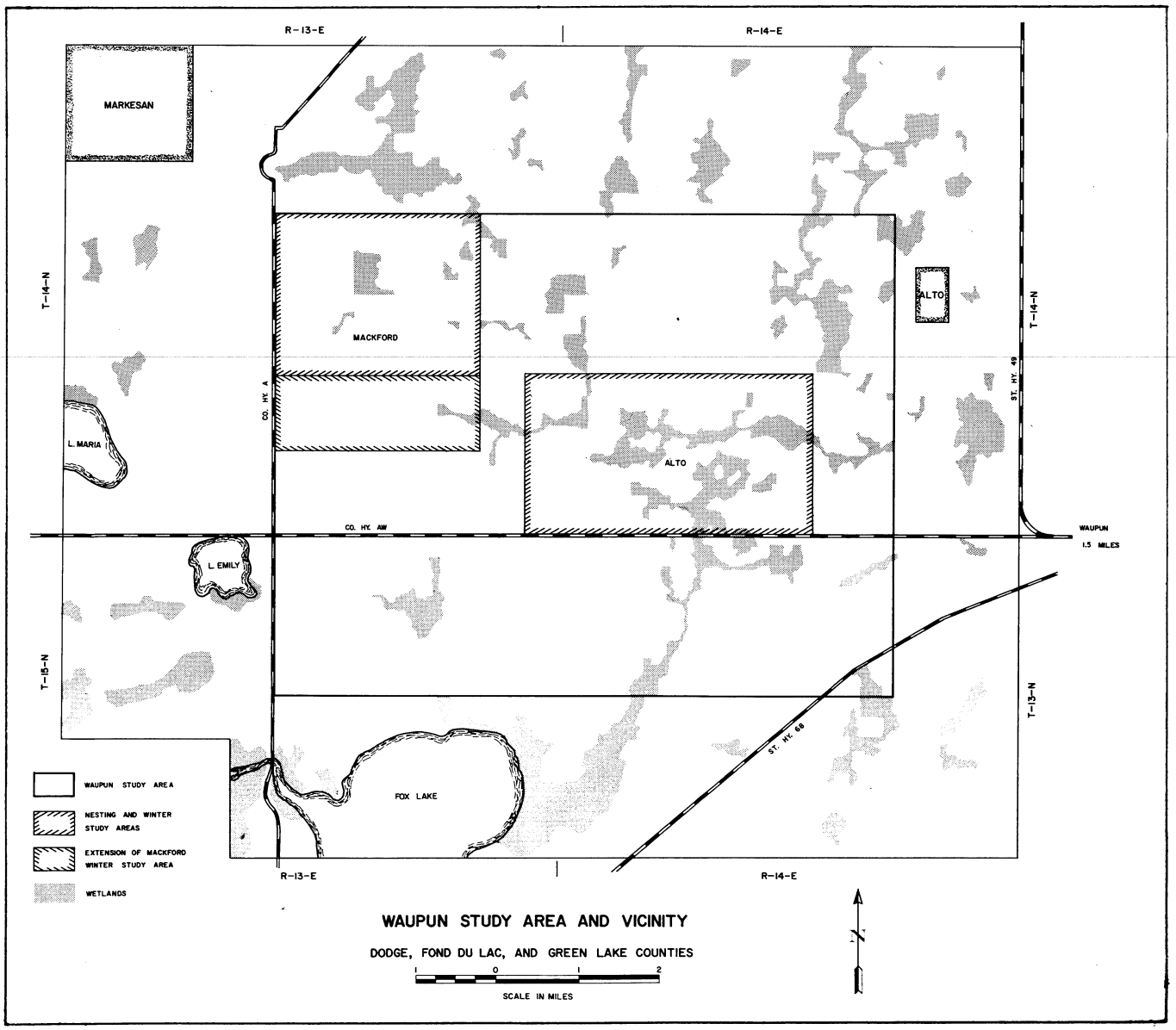
STUDY AREAS

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.

The Springvale Study Area (Fig. 3), 3 miles northeast, served as a study area in 1958 and 1959, but it proved to be an unwise choice for logistic reasons. Field work there was phased out in favor of the Waupun Study Area after the spring of 1959. Only periodic contact was maintained with the Springvale pheasant population

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



thereafter.

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 characteristically 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.

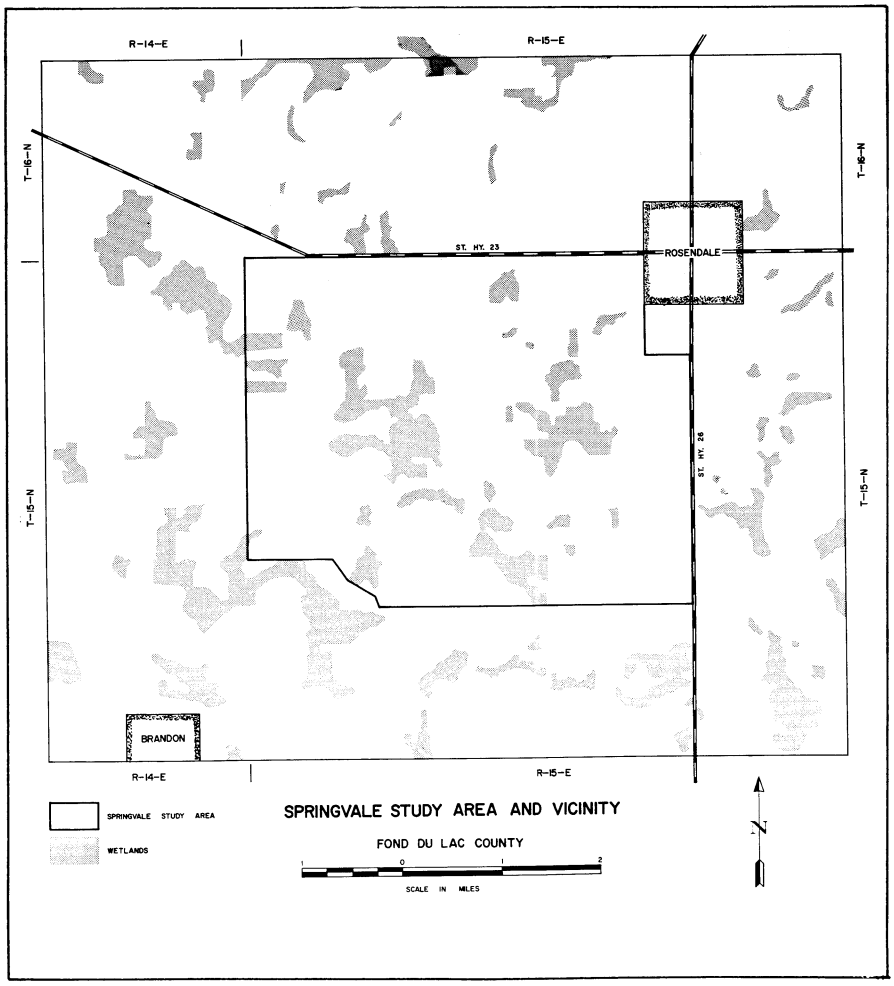
During our study, agriculture consisted mainly of dairy farming. Cash crops for canning, chiefly peas and sweet corn, provided secondary farm income. Roughly 78 percent of the land area was cultimated (Table 1). During the years 1961-65, land diverted from crop production under Federal land-retirement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

Because of the importance of winter weather to pheasant welfare, "winter hardness" indices were calculated (Table 2). These were based on minimum daily temperatures recorded at the weather station in the City of Fond du Lac and on snow depths measured by us at the Waupun Study Area. Snow depth was rated on a 5-point scale ranging from a value of 1 for depths from 0 to 5 inches, to a value of 5 for depths exceeding 20 inches. Minimum daily temperatures were also rated on a scale of 5 ranging from a value for 1 for temperatures above 30 degrees Fahrenheit to a value of 5 for temperatures below -15 degrees. The daily product of these ratings was summed between December 1 and March 31, and expressed on a scale of 1000 relative to 1961-62, the severest winter of the study according to this criterion.

A survey of weather records showed that winters as severe as 1958-59 and 1961-62 occurred in the region about 1 year out of 6. Fortunately, our period of study also included mild winters, so that composite information from all our winters probably gave a reasonable picture of average winter conditions for the area.

FIGURE 3. *Map of Springvale Study Area and vicinity, located approximately 3 miles northeast of Waupun Study Area and vicinity.*



METHODS OF CAPTURE AND MARKING

Capture and marking of pheasants was concentrated in early fall and mid- to late winter. Nightlighting was carried out with the use of a specially equipped pick-up truck as described by Labisky (1959, 1968). Trapping in winter was done with baited live-traps of the type developed by McCabe (1949). In total, 3,390 wild-reared pheasants (excluding recaptures) were caught and marked over a 7-year period for movement investigation, survival calculation, and population estimation (Tables 3 and 4).

Birds were marked with leg bands and 2 x 6-inch fabric-backed, vinyl plastic back tags of a design similar to the ones described by Blank and Ash (1956) and Labisky and Mann (1962). Observed rates of backtag loss were zero the first year, 11 percent the second, 29 percent the third, and 60 percent the fourth. Available data did not suggest that backtags had an appreciable influence on flight, social behavior, or survival.

Records of marked pheasants after release were obtained through systematic visual searches of the study areas at intervals throughout the year, observations during the course of other surveys such as brood counts, recap-

TABLE 1. Average Land Use Statistics, Waupun Study Area, 1959-1965

Cover Type	Percent of Total Area
Permanent cover	12[2]
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[1]	7
Roads, feedlots, farmsteads, etc.	3

*Roadsides, fencelines, and ditchbanks.
**Lima beans, soybeans, buckwheat, and sugar beets.
[1]Includes upland permanent pasture, exclusive of grazed woodlots, and all wetland acreages typed as heavily pastured.
[2]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.

Birds were marked with vinyl plastic back tags.

tures by nightlighting and trapping in winter, checks of birds killed by hunters, road kills, and miscellaneous random observations along roads.

MOVEMENT DATA

Observations of marked birds were daily recorded on field maps and later transferred to permanent file records by 40-acre land units, e.g., NWNE 32 A designating the northwest quarter of the northeast quarter of section 32, Alto Twp. All pheasant movement was therefore plotted and measured between centers of "forties." Admittedly this procedure introduced a certain element of error into the analysis. A bird simply crossing a "forty" line was accordingly treated as having moved 1/4 mile, whereas another moving diametrically across a "forty" was treated as sedentary. While this procedure was not entirely satisfactory for study of home ranges, it was no handicap in dealing with the more extensive seasonal and annual movements which were our principal concern.

Movement distances in this study departed from Poisson expectation at high levels of significance in virtually every instance in which sample sizes were large enough for discriminating tests. Movement was not therefore a random variable, each sex and age group containing a relative preponderance of unusually sedentary animals as well as individuals predisposed to longer-range travel. Analysis was further confounded by heterogeneous variances, not only between sex and age classes, but also between years within comparable sex and age groups. Neither the square-root nor logarithmic transformation successfully dealt with this problem, hence standard methods of analysis of variance were ruled out. Significance tests were therefore performed using Snedecor's (1956.287-289) procedure for analysis of variance in presence of nonhomogeneous variances. All statistical analyses were based on movement distances measured to the nearest 1/4 mile. Summary tables in this report have been recast by 1-mile intervals.

Many of the movement data on which this report is based could be most effectively presented on maps, but data in most instances were too voluminous for all records to be plotted. Our compromise has been to commit as much information as possible to tables and to illustrate individual movement patterns with

TABLE 2. Annual Variation in Winter Weather Conditions, December 1 Through March 31

Winter	Total Snowfall (Inches)*	Number of Days With Snow Cover 10 Inches or Greater**	Number of Days With Daily Minima Below 0 F.	Winter Hardness Index
1958-59	68	70	39	964
1959-60	34	18	13	466
1960-61	10	0	12	277
1961-62	47	92	29	1,000
1962-63	27	15	38	647
1963-64	22	0	19	334
1964-65	35	5	20	426

*Data from U. S. Weather Bureau, Fond du Lac, Wisconsin (Climatological Data for Wisconsin).
**Based on daily field notes of snow conditions on study area and depth in undrifted locations.

TABLE 3. Winter Trapping Summary, Springvale and Waupun Study Areas*

	Number of Initial Captures**		Number of Repeat Captures		
Winter	Cocks	Hens	Cocks	Hens	Total Captures
1958-59	26(0)[1]	279(0)	59	558	922
1959-60	18(0)	286(0)	13	293	610
1960-61	13(1)	89(0)	0	15	117
1961-62	44(2)	501(14)	34	306	885
1962-63	20(0)	310(19)	10	285	625
1963-64	12(0)	87(0)	5	53	157
1964-65	15(0)	164(2)	15	216	410
Totals	148(3)	1,716(35)	136	1,726	3,726

*Trapping conducted in 1958-59 on the Springvale Study Area (Fig. 3); on the Waupun Study Area (Fig. 2) in all subsequent winters.
**Includes birds recaptured from previous fall and/or winter marking periods. Also includes birds captured by winter nightlighting: 8 cocks and 32 hens in 1960-61; 6 cocks and 17 hens in 1963-64.
[1]Figures in parentheses included in initial capture totals and represent the number of pen-reared pheasants captured.

TABLE 4. Fall Nightlighting Summary, Waupun Study Area

	Number of Initial Captures*			
Year	Cocks	Hens	Unsexed Juveniles	Totals
1960	82(1)**	85(0)	6	173
1961	190(10)	202(5)	7	399
1962	184(3)	225(0)	0	409
1963	160(0)	262(1)	1	423
1964	177(0)	253(0)	5	435
Totals	793(14)	1,027(6)	19	1,839

*Includes birds recaptured from previous fall and/or winter marking periods.
**Figures in parentheses included in initial capture totals and represent the number of pen-reared pheasants captured.

selected examples. Readers are cautioned that examples chosen were not necessarily representative of all pertinent data on a given subject, but were singled out because large samples were available or because they demonstrated certain phenomena with special clarity.

Fall-to-Winter

The bulk of our movement data for cocks originated from hunting season recovery records, whereas the majority of the hen data were obtained after the move to winter cover had been completed. Fall-to-winter movement will therefore be considered in two parts--movement through the hunting season and movement between fall capture sites and winter cover. Analysis of the former will focus on the cock segment of the population, particularly juvenile cocks, and the latter on the hen segment of the population. It should be emphasized that this breakdown is purely arbitrary and is not meant to imply that movement occurred in two discrete periods. At least among hens, movement between fall and winter appeared to be a rather gradual process.

Out of 40 adult hens recaptured during fall nightlighting, the average distance between the fall capture site and the geographic center of all known spring and summer locations (May through August) was only 0.23 mile. Only two individuals were known to travel more than 1/2 mile, 34 of the 40 being recaptured in fall in the same "forty" or one adjacent to the spring-summer location. Comparable distances among 11 adult cocks averaged only 0.21 mile. Eight of the 11 were recaptured in the same or an adjacent "forty."

It was clear from these data that adult birds remained comparatively sedentary during the breeding season, suggesting (1) that nightlighting capture sites could be safely regarded as the vicinity in which adult birds had spent the nesting and brood-rearing seasons; and (2) that spring-summer locations could be relied upon as the approximate origin of fall-to-winter movement. Analysis of adult movement was accordingly based on movement records plotted from fall capture sites as well as from spring-summer locations in instances where autumn locations were not definitely known.

Nineteen marked hens identified in summer with broods were subse-

quently recaptured in fall, the average distance of travel between sites being 0.28 mile. Only two of these individuals moved more than 1/2 mile. Fifteen were recaptured in the same "forty" or one adjacent to the summer brood location. In each instance, the age of the juveniles with which they were captured corresponded with age determinations made during summer brood counts. This suggested that family organization persisted late enough that the majority of young birds encountered during nightlighting could be assumed to have been hatched and reared in the general vicinity in which they were captured. Only during the latter stages of the nightlighting season did we routinely encounter lone juveniles that had obviously severed family ties and which may have been captured at sites comparatively remote from their birthplaces. Included were 35 young cocks, as compared with 13 young hens, which suggested that young males were somewhat earlier than females in abandonment of family groups.

Winter-to-Spring

From the sedentary behavior of wintering birds, it was assumed that the location of marked individuals between January 1 and winter breakup could be relied upon as the actual site from which dispersal originated in spring. Only in 1959 and 1962 was there sufficient interchange of birds between various tracts of winter cover to seriously weaken this assumption. In these years, all dispersal records were discounted from trapping stations or other concentration sites abandoned by winter flocks wholly or in part before winter's end. In instances where two or more winter locations were known for a given bird, that record obtained latest in winter, but well in advance of winter breakup, was plotted as the origin of the spring move.

Since results of summer movement studies showed generally restricted movement of breeding birds, destination of spring dispersal was based on movement records available through September 30. Where multiple spring and/or summer records were available for a given bird, the approximate center was plotted as the endpoint of the spring move. In common with fall-to-winter movement, distance of spring dispersal was nonrandom, departing from Poisson expectation at a high level of significance among all sex and age groups each year that sample sizes were adequate for testing.

Breeding Population

Only 10 back-tagged cocks and 2 hens furnished as many as 10 movement records during a single breeding season, with a maximum of only 20 observations available per individual. Home-range size of individual birds obviously could not be delineated with this limited volume of data, hence a composite approach was relied upon in which spring and summer movement records of marked birds were combined.

Movement records were screened for marked individuals which provided at least 5 sight observations between May 1 and September 30, of which there were 45 cocks and 26 hens. Observations of each were plotted on a 1/4 x 1/4 mile grid, each square equivalent to 40 acres, this representing the basic land unit by which movement of marked birds was recorded. That "forty" which contained the largest number of records, or that "forty" nearest the center of those which contained only a single observation apiece, was designated as the center of the individual's home range. A composite was then constructed by superimposing the central "forty" of each bird on each other and by summing the number of observations which fell in each square of the grid. Results of this procedure were believed to provide a generalized picture of "average" home-range size during the period of reproduction.

SEX AND AGE RATIOS

Sex and age ratios, especially in winter, were necessary to establish the size of pheasant populations and the dimensions of population changes. In this context, we compiled winter sex ratios from field counts, which included both roadside observations and flush counts during beat-outs of winter cover units. Sex ratios were also obtained from birds trapped in winter (Table 5). However, field count data appeared most reliable.

Winter sex ratios in 1958-59 and 1961-62, which were severe winters, demonstrated a progressive decline in hens, the trend suggesting differen-

TABLE 5. Comparison of Methods of Determining Winter Sex Ratios*

Winter	Number of Hens Per Cock by Method of Observation		
	Field Counts (Primary Data)	Initial Trap Captures	Nightlighting Counts**
1958-59	11.6(2,744)[1]	10.7(305)	–
1959-60	6.9(2,246)	15.9(304)	–
1960-61	4.6(1,261)	14.3(61)	4.4(167)
1961-62	6.0(2,461)	11.6(529)	–
1962-63	6.4(1,422)	14.6(311)	–
1963-64	7.7(1,358)	10.0(66)	6.7(132)
1964-65	8.1(2,850)	10.8(177)	–
1965-66	5.9(589)	–	–

*Trapping results in 1958-59 from Springvale Study Area; field counts from Springvale and Waupun areas. Information for all subsequent years from Waupun Study Area and vicinity. Includes all winter sex-ratio data from December through March.

**Nightlighting observations conducted from February 16 to March 3 in 1961 and from February 17 to 21 in 1964.

[1]Sample size shown in parentheses.

tially high rates of hen mortality in winter (Table 6). Corroborative evidence of differential hen loss in these winters included rates of repeat capture of hens in winter traps and rates of hen observation in subsequent springs which were only about half the rates observed in less severe winters. Hens in spring were less than half as observable as cocks, but sex ratios recorded between April 15 and May 10 were strongly correlated with sex ratio trends of the preceding winter and furnished a useful check on extrapolation of winter sex ratios to the breeding population (Fig. 4). We concluded that breeding season sex ratios could be reliably inferred from December-through-March field counts, except in years of differentially high winter hen mortality when March-only data were preferable.

Methods of estimating prehunt sex ratios in fall consisted of late summer roadside counts, fall nightlighting, and hunter flush records from the opening weekend of hunting (Table 7). None were exempt from bias, but nightlighting ratios appeared most reliable. Posthunt sex ratios were based on subsequent winter field counts restricted to December and January data in winters of demonstrable sex ratio change (Table 8).

Interest centered on three specific age ratios in this study: the winter hen age ratio, the prehunt hen age ratio, and the cock age ratio in the hunting season kill. Ages of hens in winter were based on the Bursa of Fabricius, which appeared to give reliable age separation through the month of February (Table 9). Age ratios secured by winter trapping apparently were unaffected by trap selectivity. We therefore concluded that observed age composition was an unbiased estimate of age structure in the winter hen population at large.

Prehunt age ratios, based on hens captured by nightlighting, also appeared to be unbiased and agreed closely with comparable values calculated from sex and age structure (Table 10).

Cock age ratios in the kill (Table 11), usually exhibited seasonal declines, which we attributed to greater vulnerability of young cocks to the gun. Heavier non-hunting mortality among juveniles, however, apparently compensated for the bias, and cumulative age ratios in the bag at season's end closely approximated age ratios in the prehunt population in late September. Survival of young cocks

TABLE 6. Monthly Variation in Observed Sex Ratios Based on Winter Field Counts (Primary Data Only)

Winter	Number of Hens Per Cock				Chi-square Value*
	December	January	February	March	
1958-59	–	14.3(277)**	12.4(1,670)	9.5(797)	3.91(2)
1959-60	6.0(112)	6.8(567)	6.8(1,027)	7.4(540)	1.41(3)
1960-61	4.8(180)	4.2(411)	4.9(356)	4.7(314)	0.64(3)
1961-62	8.4(264)	6.3(1,044)	5.9(575)	5.2(578)	5.42(3)
1962-63	–	6.4(666)	5.9(319)	6.9(437)	0.57(2)
1963-64	7.2(397)	7.1(822)	5.9(76)	9.2(460)	2.28(3)
1964-65	–	8.3(995)	8.1(1,291)	8.0(564)	0.11(2)
1965-66	–	6.5(456)	4.3(133)	–	1.34(1)
Combined chi-square					15.38(19)[1]

*Degrees of freedom shown in parentheses. No individual chi-square values significant at the 5 percent level (reference value at 0.05 with 1 df = 3.84, with 2 df = 5.99, and with 3 df = 7.81).
**Sample size shown in parentheses.
[1]Combined chi-square nonsignificant (reference value at 0.05 with 19 df = 30.14).

TABLE 7. Comparison of Methods of Determining Prehunt Sex Ratios

Year	Number of Hens Per Cock by Method of Observation		
	August Brood Observations	Prehunt Nightlighting	Opening Weekend Hunter Flushes
1959	1.21	–	1.14(371)*
1960	1.25	1.29(161)	1.23(705)
1961	1.23	1.23(377)	0.98(489)
1962	1.19	1.26(406)	0.85(417)
1963	1.23	1.32(421)	0.86(376)
1964	1.23	1.26(430)	1.04(697)
1965	1.25	–	1.23(438)
Unweighted means	1.23	1.27	1.05

*Sample size shown in parentheses.

TABLE 8. Comparison of Methods of Determining Posthunt Sex Ratios

Year	Number of Hens Per Cock by Method of Observation	
	Final Weekend Hunter Flushes*	Subsequent Winter Field Counts**
1959	5.0(548)[1]	6.9(2,246)
1960	2.8(204)	4.6(1,261)
1961	4.2(183)	6.7(1,308)
1962	3.6(292)	6.4(1,422)
1963	10.6(313)	7.7(1,358)
1964	6.9(166)	8.1(2,850)
1965	4.4(172)	5.9(589)

*Data in 1959 and 1962 also included 2 additional days of hunting subsequent to the final weekend. Data in 1963 and 1964 included the week preceding the final weekend.
**Based on December through March sex ratios in all seasons except 1961 in which December and January data were used exclusively.
[1]Sample sizes shown in parentheses.

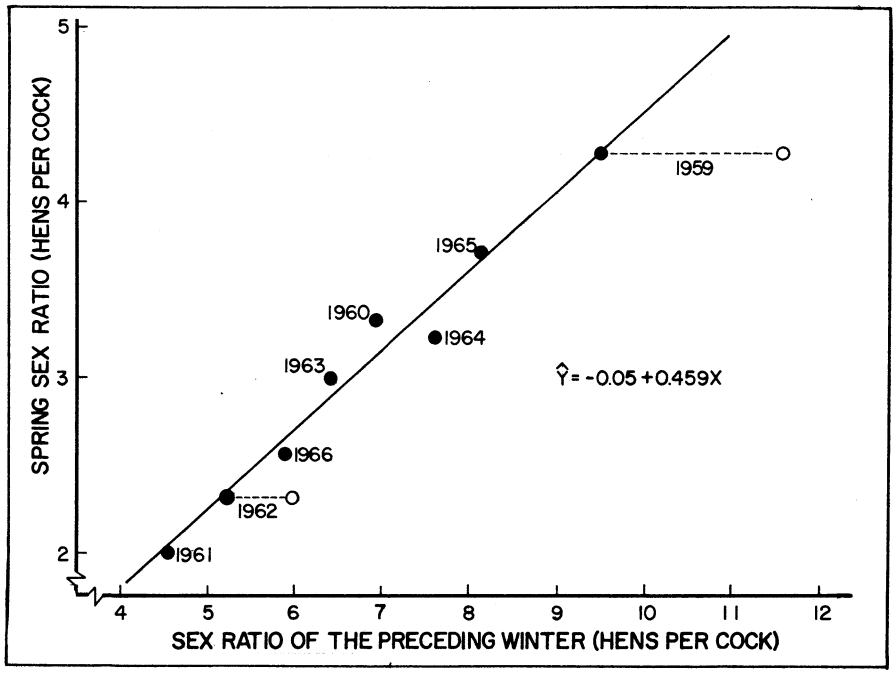


FIGURE 4. *Relationship between winter and observed spring sex ratios. Open points in 1959 and 1962 represent average of all December-through-March data; closed points represent March data only. Closed points in all other years represent December-through-March data. Regression line fitted to solid points only. Spring sex ratios based on observations between April 15 and May 10. Sample sizes for the years 1959-66 were: 588; 650; 1,159; 918; 1,156; 1,784; 1,531; and 705 respectively.*

TABLE 9. Summary of Winter Hen Age Ratios Based Largely on Results of Winter Trapping*

	Juvenile Hens Per Adult Hen				
Winter	January	February	March	Final Age Ratio Estimate**	95 Percent Confidence Limits
1958-59	1.7(51)[1]	2.1(179)	1.2(49)	2.0(230)	1.5-2.5
1959-60	2.7(41)	2.8(150)	2.4(92)	2.8(191)	2.0-3.9
1960-61	2.0(3)	3.0(24)	2.9(62)	2.9(89)	1.9-4.6
1961-62	2.1(235)	1.8(180)	1.2(53)	2.0(415)	1.6-2.4
1962-63	5.9(69)	4.5(172)	4.0(50)	4.9(241)	3.2-6.2
1963-64	–	2.7(66)	1.1(21)	2.7(66)	1.7-5.1
1964-65	3.2(47)	2.7(92)	1.3(23)	2.9(139)	2.0-4.3

*Results from Springvale Study Area in 1958-59 and Waupun Study Area in all subsequent winters. Includes data from winter nightlighting in 1960-61 and 1963-64. Total number of birds examined in individual winters does not agree in all instances with Table 3 due to inclusion of unaged hens in the latter.

**Based on January and February age data in all winters except 1960-61 when some early March age ratios were also included to enlarge the sample.

[1]Sample size shown in parentheses.

between this date and the latter stages of the hunting season averaged about 2/3 the adult rate, implying that young cocks must have been about half again as vulnerable to hunters as adults.

POPULATION ESTIMATIONS

Estimates of annual size and trends in pheasant populations were made using several indirect methods and compared to regional population trends. Estimates of the winter population were based on Lincoln Index calculations and the method of Davis et al. (1964) through which efficiency of winter trapping was determined (Table 12). Spring populations were censused by the "intersection" method of counting territorial males, the census total for cocks being multiplied by the breeding season sex ratio to estimate the size of the spring hen population (Table 13). Fall population estimates were obtained by the Lincoln Index method (Table 14).

Regional pheasant population trends for the years 1940-65 revealed that the 1959-65 period of study represented a population low for the region (Fig. 5). Decline from the most recent high in pheasant numbers (mid-1950's) was mainly precipitated by severe winter weather in 1958-59. Regional and study area populations both showed significant recovery over the period of study, but recovery was seriously hampered by recurrence of adverse winter weather in 1961-62. Study-area populations at the close of the investigation were roughly comparable to those which prevailed at its outset.

SURVIVAL AND MORTALITY RATES

Various methods of calculating annual, seasonal, and age specific trends in survival were evaluated (Gates 1971: 626-657, 871-888). Marked fluctuation in annual survival rates characterized both sexes of the population.

Among hens, annual survival ranged between 11 and 33 percent, fall-to-spring survival between 27 and 64 percent, and spring-to-fall survival between 34 and 58 percent. These rates were correlated with each other, and both were correlated with winter hardness. In the hen segment of the population, winter weather appeared

TABLE 10. Comparison of Methods of Determining Fall Hen Age Ratios, Waupun Study Area

	Captured in Fall Nightlighting		Calculated from Fall Sex and Age Structure		
Year	Juvenile Hens Per Adult Hen	95 Percent Confidence Limits	Fall Sex Ratio (Hens Per Cock)	Fall Cock Age Ratio (Juv. Per Ad.)	Juvenile Hens Per Adult Hen
1959	–	–	1.21	15.6	3.5
1960	2.7(168)*	1.9-4.0	1.29	15.1	2.7
1961	3.2(373)	2.5-3.8	1.23	10.7	3.0
1962	2.9(380)	2.2-4.1	1.26	9.2	2.5
1963	2.5(412)	1.9-3.3	1.32	16.3	2.5
1964	3.5(432)	2.6-4.9	1.26	21.3	3.1
1965	–	–	1.25	17.3	3.1

*Sample size shown in parentheses.

TABLE 11. Comparison of Methods of Determining Cock Age Ratios in the Hunting Season Kill, Waupun Study Area and Vicinity

	Juvenile Cocks Per Adult Cock			
Year	Examined in Bag Checks	Submitted by Cooperators*	Combined Sample	95 Percent Confidence Limits
1958	–	–	–	–
1959	16.5(210)**	14.6(172)	15.6(382)	10.8-23.5
1960	16.1(256)	12.7(82)	15.1(338)	9.9-24.6
1961	9.3(258)	12.0(221)	10.7(479)	7.9-15.1
1962	8.4(254)	10.5(183)	9.2(438)	5.9-13.1
1963	15.0(240)	18.3(193)	16.3(433)	10.5-25.3
1964	17.9(340)	36.8(151)	21.3(491)	13.7-34.7
1965	20.6(151)	12.8(69)	17.3(220)	11.3-26.8

*Values corrected for errors in age determination by spur appearance.
**Sample size shown in parentheses.

TABLE 12. Summary of Winter Population Estimates, Waupun Study Area*

	Number of Hens by Method of Estimation				
Winter	Lincoln Index	Trapping Efficiency	Flush Counts	Average Number of Hens by Indirect Methods**	Calculated Number of Cocks[1]
1959-60	1,220	–	–	1,220	177
1060-61	1,730	1,750	–	1,740	378
1961-62	1,910	1,780	1,590	1,845	308
1962-63	1,200	970	1,070	1,085	170
1963-64	1,010	1,210	1,040	1,110	144
1964-65	980	920	980	950	117

*Indirect estimates apply to population levels at mean dates of winter capture. Flush counts apply to variable dates depending on time of winter census.
**Average of estimates obtained by the Lincoln Index and calculated trapping efficiency.
[1]Calculated from the average winter sex ratio (Table 5).

TABLE 13. Spring Population Estimates Based on the Crowing Cock Census and the Sex Ratio of the Breeding Population*

		Alto Study Area		Mackford Study Area		Waupun Study Area		
Year	Number of Hens Per Cock**	No. Cocks	Calc. No. Hens	No. Cocks	Calc. No. Hens	No. Cocks	Calc. No. Hens	95 Percent Confidence Limits
1959	9.5(797)[1]	37	348	–	–	147	1,397	1,120–1,810
1960	6.9(2,246)	46	317	16	110	173	1,194	1,055–1,370
1961	4.6(1,261)	89	409	25	115	332	1,527	1,330–1,760
1962	5.2(758)	49	255	19	98	180	936	755–1,170
1963	6.4(1,422)	39	250	13	83	137	877	750–1,015
1964	7.7(1,358)	35	269	11	84	128	986	845–1,150
1965	8.1(2,850)	–	–	–	–	126	1,021	910–1,150
1966	5.9(589)	–	–	–	–	183	1,080	860–1,375

*Estimates apply to populations on May 1. Alto Study Area (7 square miles) and Mackford Study Area (5 square miles) are both subdivisions of the Waupun Study Area (42 square miles).
**Based on winter sex ratios in Table 6, restricted to March-only observations in 1959 and 1962.
[1]Sample size shown in parentheses.

to be the predominant cause of survival fluctuation.

Rates of cock survival varied from 3 to 14 percent per annum. Among cocks, winter weather apparently had less pronounced effect on survival, and levels of hunting harvest showed the strongest correlation with survival trends from year to year.

From 1958 to 1965, hen survival between successive autumns averaged 24 percent and cock survival averaged 7 percent. During this period of essentially stable populations, reproduction and mortality were approximately balanced. Little evidence of age-specific survival change was detected. Trends in age structures also ruled out the possibility of significant improvement in life expectancy after the first autumn of life.

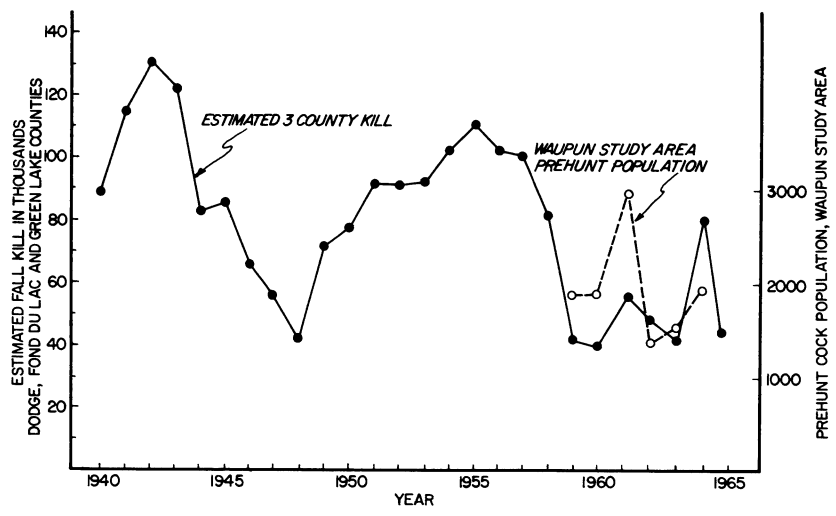
Compared with earlier Wisconsin studies (Buss 1946; McCabe 1949), notably higher rates of productivity and mortality prevailed in the present study, suggesting the possibility of a long-term change in Wisconsin pheasant demography. Review of literature from other states (Gates 1971:655) suggested that unusually rapid turnover may be a characteristic feature of Wisconsin pheasants.

TABLE 14. Summary of Prehunt Population Estimates, Waupun Study Area*

Year	Adult Cocks**	Juvenile Cocks	Adult Hens[1]	Juvenile Hens
1959	111	1,730	494	1,730
1960	114	1,730	641	1,730
1961	249	2,660	831	2,660
1962	124	1,140	393	1,140
1963	77	1,260	504	1,260
1964	83	1,770	506	1,770

*Estimates apply to populations on October 1.
**Number of adult cocks estimated from fall age structure (Table 11) and the Lincoln Index estimate of the juvenile cock population.
[1]Number of adult hens estimated from fall age structure (Table 10) and the Lincoln Index estimate of the juvenile cock population assuming a 50:50 juvenile sex ratio.

FIGURE 5. *Comparison of regional trends in fall pheasant harvests with prehunt population estimates on the Waupun Study Area.*



FALL-TO-WINTER MOVEMENT

FALL MOVEMENT

Movement by Age and Sex Class

Fall mobility differed significantly between sex and age groups, juvenile hens covering the greatest distance, followed in order by juvenile cocks, adult hens, and adult cocks (Table 15). Movement data for cocks consisted principally of hunting season recoveries, these being concentrated during the early stages of the season, whereas many of the hen records stemmed from visual observations made later in autumn. Mean distances of travel doubtless reflected this difference; however, rates of daily travel demonstrated parallel trends by sex and age in fall mobility (Table 15).

Fall movement of young cocks averaged 0.62 mile, 84 percent of this group traveling 1 mile or less. Only 3 percent of all hunting season recoveries were more than 2 miles removed from the fall capture site (Table 15). The most extensive move recorded in this study was by a juvenile cock captured at 10 weeks of age on September 12, 1964; this bird was shot 57 days later 10.3 miles from the point of capture.

From the seasonal increase in average distance between capture and recovery sites, mobility of young cocks clearly accelerated after the hunting season began. In an average year, birds shot during the initial 10 days of the hunting season had moved only 0.48 mile between the mean dates of capture (September 20) and recovery (October 23), whereas those shot in the succeeding 10-day period nearly doubled this distance to 0.86 mile. Disturbance by hunters doubtless contributed to the trend, but coincident cover destruction through corn picking and fall plowing may have been equally important stimuli to fall movement. None of the tests we performed indicated a relationship between the distance of travel and the age of individual birds at time of capture or recovery.

To explore other influences affecting fall movement, all available movement records were plotted from individual capture sites. Dispersal from selected marking sites with sufficient observations to reveal the distance and direction of egress is shown in Figure 6. Three generalizations were suggested by these and comparable examples: (1) that dispersal of young cocks was essentially random in direction; (2) that fall movement led to progressive concentration of birds in wetland cover; and (3) that distance of disperal varied geographically depending on proximity of fall capture sites to wetland cover. Each of these hypotheses were evaluated against the composite 1960-64 fall movement sample. Recovery records from all capture sites within a given section were combined and plotted from the center of that section.

(1) Ten sections provided at least 16 dispersal records apiece, the range being 16 to 46. Each array was divided into quadrants (north, east, south, and west) and tested by chi-square for correspondence to theoretical numbers per quadrant assuming random dispersal. Only one instance demonstrated significant departure from randomness, combined chi-square for all 10 sections being nonsignificant at 35.58 (reference value with 30 df at 0.05 = 43.77). From these tests, as well as from the general pattern of movement (Fig. 6), dispersal from fall capture sites appeared to be directionally

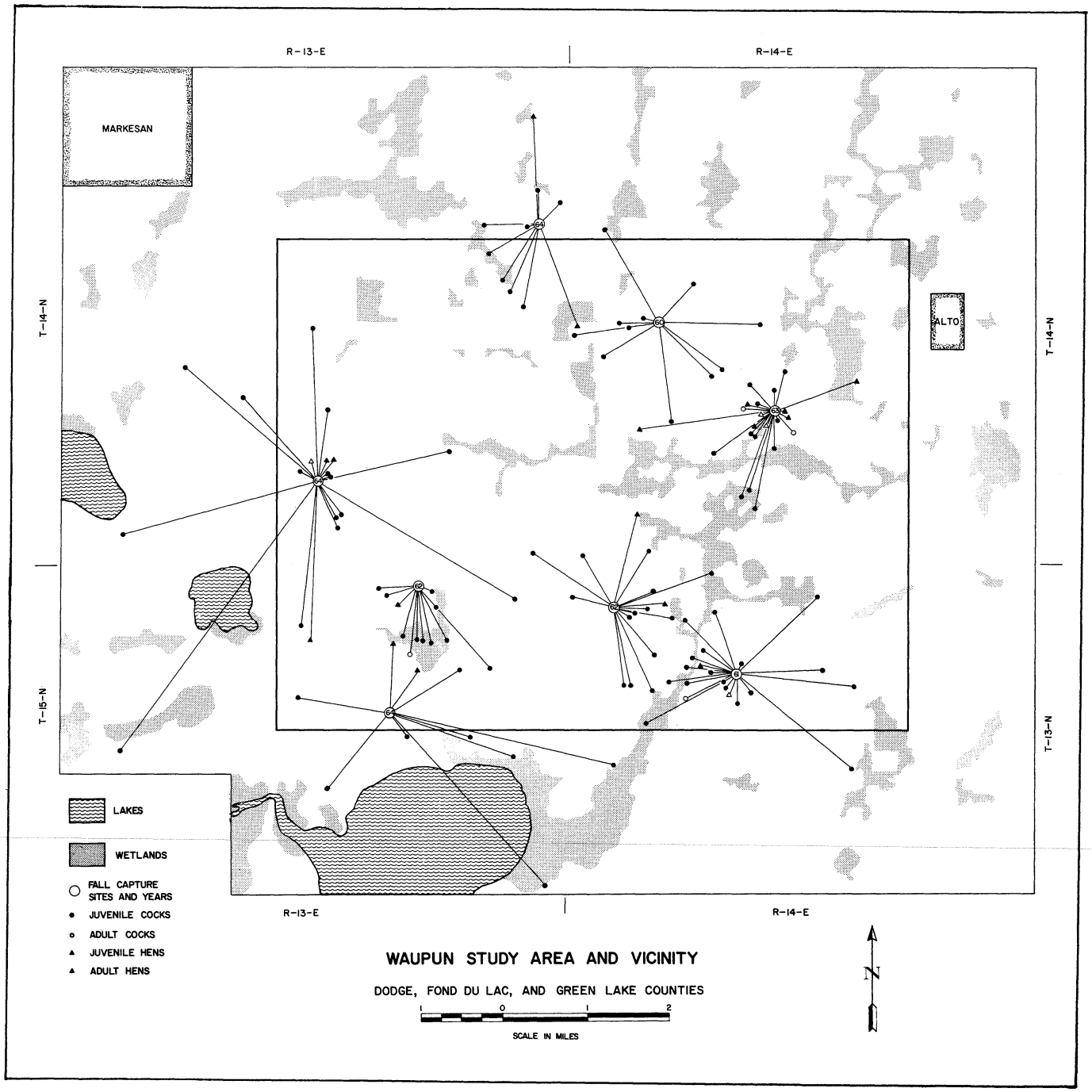
TABLE 15. Age and Sex Variation in Distance of Fall Travel Based on Hunting Season Recovery and Observation Records, Waupun Study Area and Vicinity, 1960-64

Age and Sex Class	Distance of Movement in Miles								Total	Mean and Standard Error*	Miles Per Day**
	0-1	1-2	2-3	3-4	4-5	5-6	6-7	>7			
Juvenile cocks	372	55	11	2	0	0	1	1	442	0.62 ± 0.09	0.019
Juvenile hens	47	13	3	1	1	0	0	0	65	0.77 ± 0.11	0.024
Adult cocks	40	1	0	0	0	0	0	0	41	0.34 ± 0.03	–
From fall capture sites	20	1	0	0	0	0	0	0	21	0.30 ± 0.14	0.010
From spring-summer locations	20	0	0	0	0	0	0	0	20	0.39 ± 0.04	–
Adult hens	33	3	0	0	0	0	0	0	36	0.47 ± 0.06	–
From fall capture sites	19	3	0	0	0	0	0	0	22	0.57 ± 0.08	0.012
From spring-summer locations	14	0	0	0	0	0	0	0	14	0.42 ± 0.04	–

*Means and standard errors originally calculated from movement distances measured to nearest ¼ mile. Differences in mean distance of travel between age and sex groups highly significant by analysis of variance in presence in heterogeneous variances (Snedecor 1956:287-289) (F' with 3 and 61 df = 13.48; reference value at 0.01 = 4.13).

**Distance moved divided by the interval in days between time of capture and time of recovery or observation.

FIGURE 6. *Dispersal from fall capture sites based on hunting season recovery and observation records. Heavy line designates boundary of Waupun Study Area.*



unoriented. Movement of a highly directional nature, such as the 1962 example in the southwest corner of the study area (Fig. 6), seemed to be the exception rather than the rule.

(2) Out of 427 young cocks shot and recovered by hunters, 155 (36%) were originally captured in the vicinity of wetland cover, i.e., within 1/4 mile of a wetland edge. Among those shot the initial 10 days of hunting, 46 percent were recovered in wetland vicinities, compared with 58 percent during the second 10 days of the hunt and 71 percent during the remainder of the season, the difference being significant at the 5 percent level (chi-square with 2 df = 6.18; reference value at 0.05 = 5.99). Unless cocks stationed in wetland cover became increasingly vulnerable to hunters as the season progressed, these data indicated a generalized ingress into wetland areas after the hunting season began.

(3) Finally, the average distance of dispersal from 20 sections providing at least 10 movement records was calculated and plotted against the percentage of that section consisting of wetland cover. Figure 7 shows that dispersal tended to be least from those portions of the study area characterized by larger wetland acreages, such cover apparently dampening fall egress by holding young cocks in the vicinities in which they were captured and presumably hatched and reared.

In summary, fall movement of

young cocks tended to be random in direction. Mobility apparently was unrelated to age, but obviously accelerated once the hunting season began. Stimuli triggering fall movement were unclear, although changing cover conditions, coupled with disturbance by hunting, may have been most important. Presence of wetland cover tended to restrict fall egress and apparently functioned as escape cover into which surviving birds gravitated as the hunting season wore on.

Fall movement of adult cocks averaged 0.34 mile (Table 15). Only one dispersal record exceeded 1 mile in distance, 76 percent of the total being 1/2 mile or less. Within this restricted range of travel, adult birds demonstrated certain parallels with young cocks. Movement of 14 individuals through October averaged 0.32 mile between capture and recovery sites, whereas 7 November records averaged 0.53 mile, suggesting increased mobility as the hunting season progressed. Seven of 21 adults furnishing fall movement data were originally captured in wetland vicinities, compared with 14 eventually shot in these cover types.

Young hens were the most mobile component of the population, the mean of all hunting season moves being 0.77 mile (Table 15). The longest recorded move by a young hen at this season was 4.6 miles, with 28 percent of all dispersal records exceeding 1 mile in distance. Juvenile hens also appeared to concentrate in wetland areas as autumn progressed. Among 65 individuals comprising the fall movement sample, only 17 were originally captured in wetland vicinities, compared with 43 ultimately observed or recovered at such locations.

Mobility of adult hens in fall averaged 0.47 mile (Table 15); the longest recorded move by an adult hen at this season was 1.6 miles. Eight of 22 individuals in the fall movement sample were initially captured in wetland vicinities, compared with 14 subsequently observed or recovered at such sites.

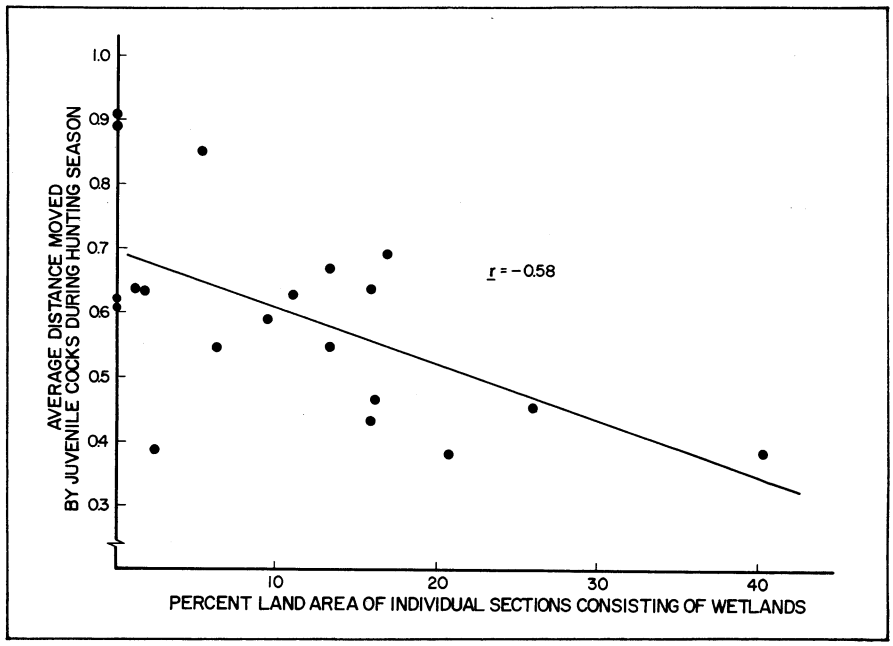
Conclusions on Fall Movement

Ingress into wetland cover typified the hunting season movement of all age and sex groups. Although wetlands constituted only about 10 percent of the study area, it was our opinion that these cover types held between 75 and 90 percent of the area's pheasant population at the conclusion of a normal hunting season. Such movement had at least three practical implications. First of all, it doubtless facilitated the high rates of cock harvest—83 percent on the average—that prevailed in this population. Concentration of cocks in only 10 percent of the landscape must have made them substantially more vulnerable to hunters toward the end of the season than would otherwise have been the case, since wetland cover also sustained a disproportionally high percentage of the area's late-season gunning pressure.

Secondly, results of this study clearly demonstrate the importance of cover lasting throughout the hunting season if an objective is to retain birds in the vicinity in which they were produced, or, alternatively, of locating management efforts intended to improve local hunting in areas where good escape cover already exists.

Thirdly, it seems obvious that wetland areas leased or otherwise regulated for private hunting may benefit importantly from pheasant productivity drawn in from adjacent lands, and that such benefits may accrue well before the close of the general pheasant season. On areas where hen shooting is permitted, as on licensed shooting preserves, a potential exists for reduction of off-preserve populations, particularly in areas where wetlands are in short supply and where the most attractive acreages are licensed for private shooting.

FIGURE 7. *Relationship between the percentage of individual sections consisting of wetland cover and the average distance of fall egress by juvenile cocks, Waupun Study Area and vicinity, 1960-64. Correlation significant at 1 percent level (reference value with 18 df at 0.01 = 0.56).*



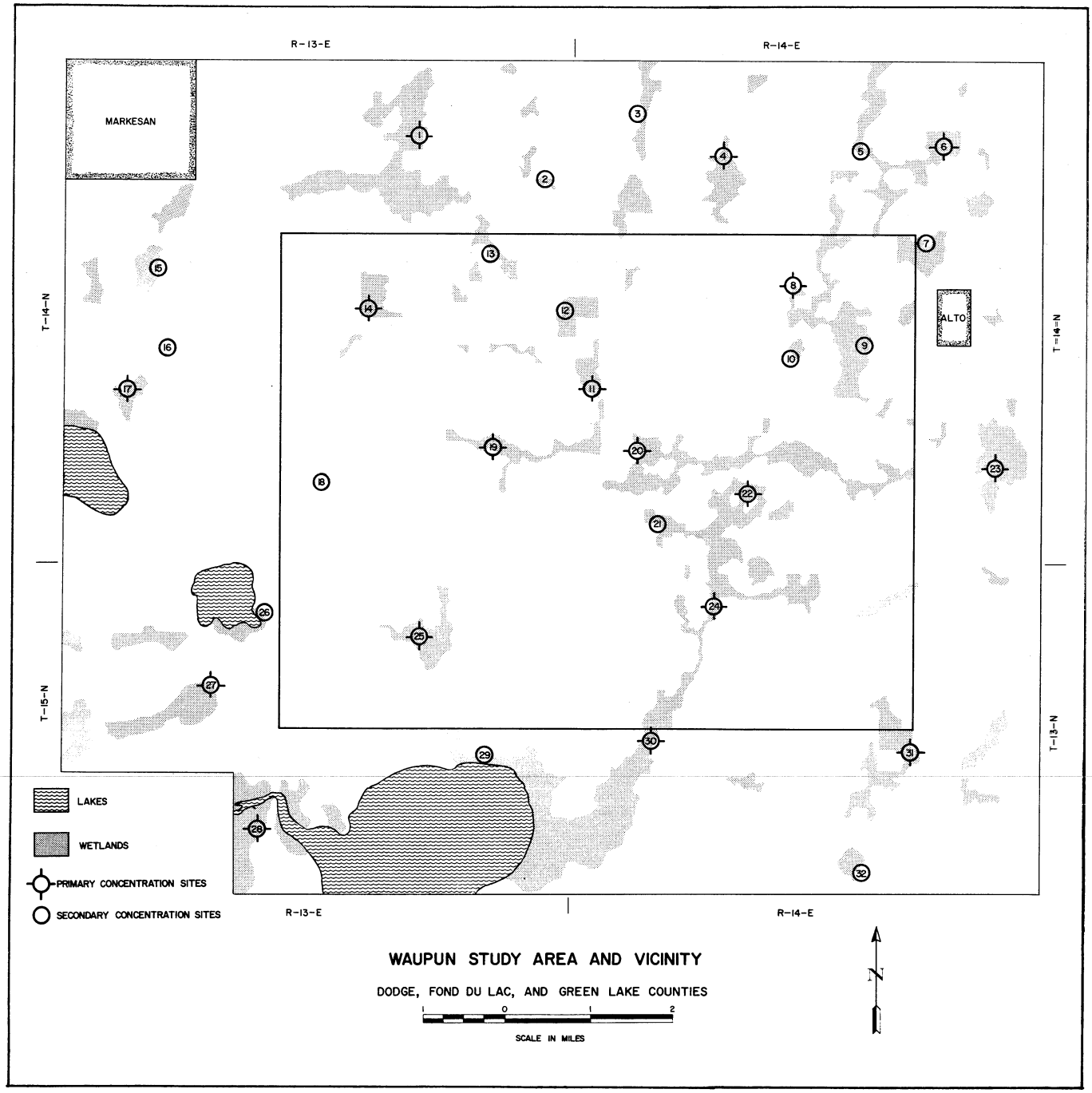
MOVEMENT TO WINTER COVER

Distribution and Classification of Winter Cover

Thirty-two sites on the Waupun Study Area and vicinity were classified as *traditional wintering areas,* these representing areas that were occupied by pheasants during each winter of study (Fig. 8). In most years over 80 percent of the winter population was concentrated at these 32 locations.

Traditional wintering areas were subdivided into *primary* and *secondary concentration sites* according to the average size of winter flocks. Except during open winters, primary sites seldom held fewer than 50 wintering birds and in most winters sheltered flocks of 100 or more. Secondary sites routinely held groups of 50 birds or fewer even when winter flocking was tightest. Excluded from Figure 8 were a number of *tertiary wintering areas,*

FIGURE 8. *Location of traditional wintering areas, 1958-1965. Definition of terms and criteria used to classify wintering areas explained in text; cover characteristics of each area listed in Table 16. Heavy line designates boundary of Waupun Study Area.*



cover used by small groups of perhaps 5 or 10 birds but consistently enough from year to year to qualify as traditionally used sites.

We also recognized two types of *nontraditional winter cover,* areas which held pheasants during some but not all winters of study. With snow cover absent or virtually so, *satellite wintering areas* were occupied throughout the winter period, but in most years were abandoned as soon as significant snow cover accumulated. Most of these sites were peripheral to traditional winter cover. *Temporary wintering areas* represented chance combinations of food and shelter, e.g., abandoned cropland adjacent to unharvested crops, which were present and utilized by pheasants during a single winter only. Such areas were most prevalent in 1960-61 and to lesser extent in 1963-64.

Table 16 briefly characterizes the cover composition of traditional wintering areas. At all but 3 of the 32 sites, some form of wetland vegetation was the principal cover on which wintering birds were dependent. Of the various wetland types, shrub-carr

Wetlands provided important escape cover during the hunting season.

TABLE 16. Cover Composition of Traditional Wintering Areas, Waupun Study Area and Vicinity, 1958-1965

Cover Type	Map Number (Figure 8)									
	Primary Concentration Sites						Secondary Concentration Sites			
Shrub-carr wetland										
Dominant**	4	8	22	25	28	30	21	26	32	
Subdominant[1]	1	17	23	24			–			
Cattail and/or river-bulrush wetland	6						2	5	29	
Aspen swamp	11						9	12		
Canary-grass, herbaceous, and/or sedge-meadow wetland	14	19	20	27	31		7	10	13	15
Farm shelterbelt	–						3	18		
Woodlot	–						16			

*For detailed description of wetland vegetation types see Gates (1970, 1971).
**Principally closed canopy shrub-carrs with nonshrub vegetation subdominant.
[1]Actually dominated by nonshrub vegetation, but with scattered pockets of shrub-carr to which wintering flocks were predominantly oriented.

was pre-eminently important, the main cover relied upon at 10 out of 17 sites sheltering the largest winter flocks from year to year. Another indication of this cover type's importance to wintering birds was the fact that no closed-canopy stand of shrub-carr on the study area failed to qualify as a primary concentration site.

Time of Movement

For the years 1960-65, only 8 movement records were available from which time of movement to winter cover could be inferred. One adult hen completed the move sometime prior to October 28 and another prior to November 9. Six juvenile hens included two individuals that completed the move before November 10, two during the second half of November, and two others during the first half of December. From limited observations, movement to winter cover thus appeared quite variable, some hens apparently arriving by early November, others not until December or perhaps early January.

Among hens, dispersal from fall capture sites tended to stabilize after January. This was particularly evident in juvenile hens and seemed to imply that movement to wintering areas was essentially finished by the first of the year. Among cocks, particularly young cocks, mobility appeared to stabilize after November, suggesting that cocks probably completed the move somewhat earlier than hens. Wintering birds remained relatively sedentary between early January and winter breakup, except under emergency conditions when food and cover availability progressively worsened during this period. Analysis of fall-to-winter movement was accordingly based on all marked birds visually identified, recovered, or recaptured between January 1 and mid–to late March, depending on time of winter breakup. In instances where marked birds were known to shift winter quarters during this period, that record obtained latest in winter was plotted as the ultimate move to winter cover.

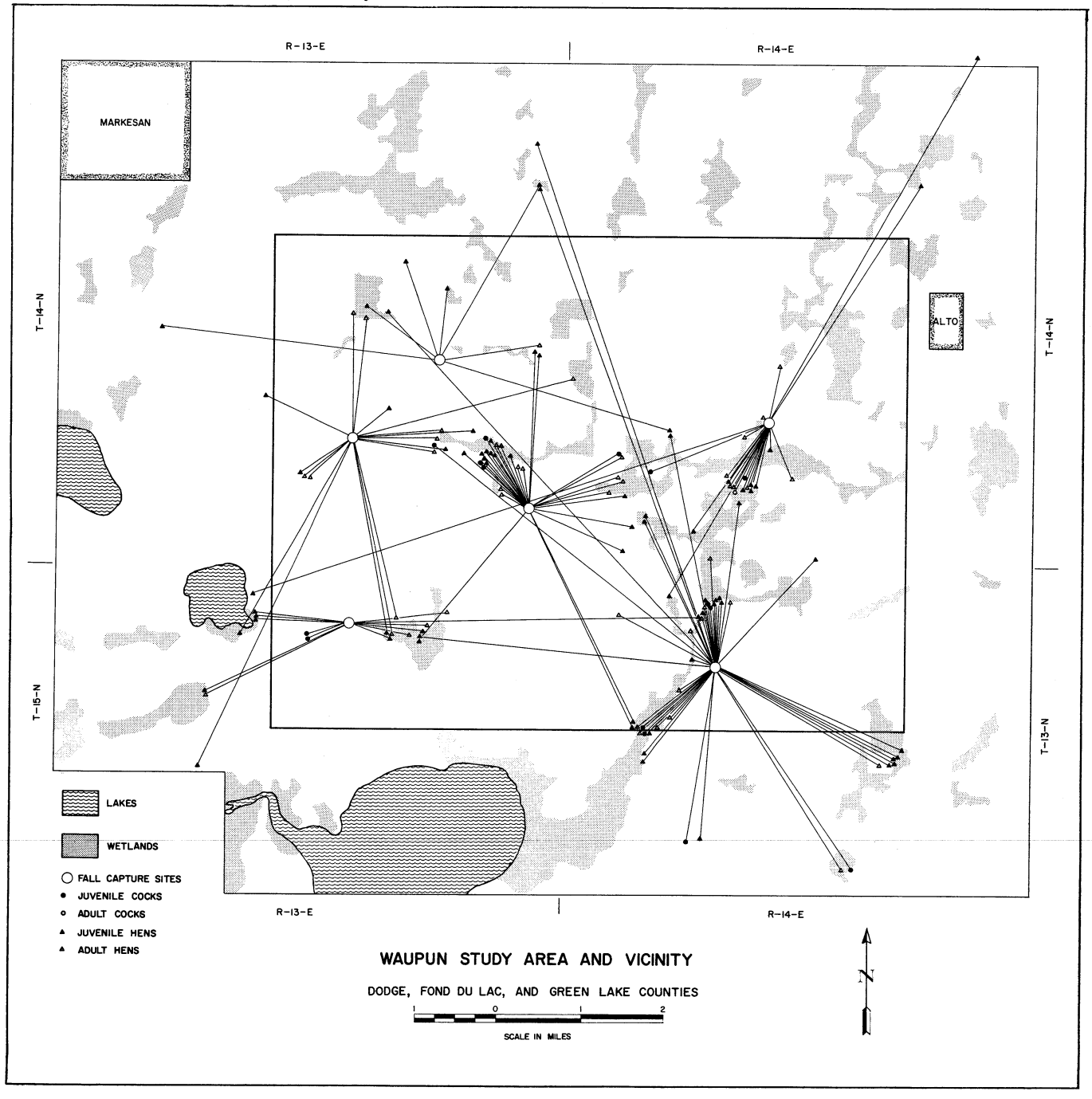
It should be noted that the phenology of winter movement described above may have been unique to our particular period of study. None of the winters during which we investigated the move to winter cover progressively increased in severity after mid-January. January weather conditions in each winter were as severe as any which prevailed throughout the winter period. Information obtained in 1958-59, based on reobservation of winter-marked birds, revealed extensive redistribution of winter flocks during late February and early March associated with increasing snow depth and progressive restriction in food and cover availability. From these and other data, it was clear that pheasants were capable of mid-winter adjustment to changing habitat conditions, hence we do not infer that the migratory urge, or whatever else motivated to move to winter cover, was necessarily confined to the early winter months.

Movement by Age and Sex Class

Distance of movement to winter cover differed significantly with sex and age and followed the same general trend as fall movement. Juvenile hens covered the greatest distance, followed in order by juvenile cocks, adult hens, and adult cocks (Table 17).

Our basic analytic procedure was to

FIGURE 9. *Movement to wintering areas from selected fall locations, 1960-65. Heavy line designates boundary of Waupun Study Area.*



plot all 1960-65 movement records originating in a given section from the center of that section, examples of which are illustrated in Figure 9. Discussion will begin with adult hen segment of the population, since knowledge of adult movement was essential to interpretation of juvenile movement.

Movement to winter cover by adult hens averaged 0.83 mile, 72 percent traveling 1 mile or less (Table 17). Among roughly half the adults, the move represented a return to winter cover used the previous year. Out of 261 hens identified in consecutive winters, 51 percent were found in the same tract of winter cover.

To uncover some of the variables affecting the rate of return, the adult sample was first subdivided by age class, yearling hens referring to hens whose winter locations were compared between the first and second winters of life, and older hens referring to those in at least their second winter of life during the initial season of record. Out of 147 yearlings, 39 percent returned, compared with 66 percent return by 114 older hens, the difference being highly significant (chi-square with 1 df = 19.23; reference value at 0.005 = 7.88).

The most apparent explanation for this difference was the fact that young hens in spring tended to disperse greater distances from winter cover, hence a longer return move was required. Comparison on this basis showed that the rate of yearling return was inverse to the distance of spring dispersal. The longest return move to

TABLE 17. Age and Sex Variation in Distance of Fall-to-Winter Travel Based on January through March Movement Records, Waupun Study Area and Vicinity, 1960-65

Age and Sex Class	Distance of Movement in Miles*								Total	Mean and Standard Error**
	0-1	1-2	2-3	3-4	4-5	5-6	6-7	7-8		
Juvenile cocks	31	19	1	2	3	0	0	0	56	1.05 ± 0.14
Juvenile hens	94	91	32	21	1	1	5	1	246	1.58 ± 0.07
Adult cocks	9	0	0	0	0	0	0	0	9	0.35 ± 0.08
From prehunt capture sites	3	0	0	0	0	0	0	0	3	0.29 ± 0.09
From spring-summer locations	6	0	0	0	0	0	0	0	6	0.38 ± 0.11
Adult hens	170	54	8	4	1	0	0	0	237	0.83 ± 0.04
From prehunt capture sites	86	30	5	2	1	0	0	0	124	0.87 ± 0.07
From spring-summer locations	84	24	3	2	0	0	0	0	113	0.79 ± 0.06

*No individual appears in tabulation more than once. In instances where two or more winter locations were available for a given bird, the record obtained latest in winter was included.

**Means and standard errors originally calculated from movement distances measured to the nearest ¼ mile. Differences in mean distance of travel between age- and sex-groups highly significant by analysis of variance in presence of heterogeneous variances (Snedecor 1956:287-289) (F' with 3 and 16 df = 37.78; reference value at 0.01 = 5.29).

winter cover by a yearling hen was 3.5 miles. Three others returned from spring-summer locations 2.1, 2.8, and 3.4 miles distant. Thus while certain individuals demonstrated unusually strong ties to the original wintering area, the majority that moved to summer range over 2 miles distant selected new winter quarters in closer proximity to where they bred. We found only one second-year hen in winter cover more remote from where she bred than the area in which she spent the first winter of life.

Winter locations were known for 23 hens over 3 consecutive winters, for 5 hens over a 4-winter period, and for 4 hens 5 winters in succession. Eighteen of these birds changed wintering areas at least once. Ten selected different winter cover between the first and second winters of record and returned to the newly adopted area thereafter. Eight hens changed wintering areas twice, relying on 3 different areas 3 years in succession. The remaining 6 were the most instructive of the group. As juvenile birds, each of the six were originally captured and marked in traditional winter cover. None returned the following winter, under near-snowless conditions, but remained instead in satellite or temporary winter shelter adjacent to or in close proximity to where they bred. In subsequent winters of normal snowfall, during which nontraditional sites were unsuited as winter shelter, all returned to the original wintering area. The distance of the return move varied from 1.4 to 2.6 miles, even though alternative tracts of apparently suitable winter cover were available within lesser distances of travel. In these particular instances, it seemed clear that variation in winter weather regulated return or nonreturn to traditional winter cover. Among these hens, it appeared that some sort of latent attachment to the original wintering persisted throughout life, but attachment to the breeding area must have been comparatively stronger, provided snow depth and cover availability did not preclude winter residence in the breeding vicinity.

In summary, return to traditional winter cover was a significant factor in the fall-to-winter movement of adults, rates of return being partly dependent on weather conditions which allowed a variable percentage to forsake traditional concentration sites in favor of winter residence near the breeding area. Among yearling hens, the percentage returning was inverse to the distance of travel required, the large majority that bred over 2 miles from where they initially wintered selecting new winter quarters in the second winter of life. On such grounds, we concluded that attachment to the breeding area was comparatively stronger than that to the wintering area, and that the inherent proclivity of most hens was to winter no greater distance from where they bred than weather and habitat conditions necessitated.

Fall-to-winter movement of juvenile hens averaged 1.58 miles, approximately 25 percent of all moves exceeding 2 miles in distance, 12 percent 3 miles in distance, and 3 percent 4 miles in distance (Table 17).

Figure 9 suggested three hypotheses concerning the move to winter cover by young hens: (1) that distance of travel varied with remoteness from winter cover; (2) that movement to wintering areas was highly directional in contrast to random dispersal; and (3) that juvenile movement was not independent of adult movement.

To evaluate these hypotheses, all sections with at least 10 adult and/or juvenile dispersal records were examined, and the mean distance from the center of these sections to the four nearest traditional wintering areas (primary and secondary concentration sites) was calculated. These distances were then plotted against the average distance of movement. Among both age classes, dispersal from fall capture sites was significantly related to nearness of winter cover. Although long-range dispersal of young hens was not necessarily restricted to capture sites remote from winter cover, such records were relatively less common

from those parts of the study area with winter cover less widely dispersed (Fig. 9). Based on 9 sections providing at least 10 movement records per age class, the correlation between the average distance of adult and juvenile travel was suggestive, but not statistically significant (r with 7 df = 0.58; reference value at 0.05 = 0.66).

We then compared the direction of movement with random dispersal based on methods previously described. Five locations provided at least 16 records of juvenile movement, the minimum set for analysis. In but a single instance chi-square was significant at the 1 percent level, combined chi-square totaling 48.53 and highly significant (reference value with 15 df at 0.005 = 32.80). Only three sites afforded a sufficient number of adult observations for analysis, combined chi-square totaling 48.86 and again highly significant (reference value with 9 df at 0.005 = 23.59). From 8 out of 9 sections with at least 10 dispersal records per age class, the predominant headings taken by both adult and juvenile hens fell in the same quadrant. From these tests, it was concluded that fall-to-winter movement of young hens did not represent random dispersal, that it was related to nearness of winter cover, and that both in terms of distance and direction of travel was not independent of adult movement.

As illustrated by Figure 9, directional movement of young hens was evident up to 2 miles from the fall capture site. Almost without exception, clustering of winter observations within this radius of travel corresponded to sites representing traditional winter cover (Fig. 8). It seems highly improbable to us that young birds in their first autumn of life would have known the location of these wintering areas, hence some other mechanism must have accounted for the highly directional nature of their movement. The possibility of random search could not be entirely ruled out, since only the origin and endpoint of movement were known; however, this did not appear to be the most plausible explanation.

It has been shown that return to traditional winter cover played a prominent role in the seasonal movement of adult hens, and that juvenile movement was somehow related to adult movement. A more likely explanation, then, was that young hens were led to traditional winter cover by returning adults.

As a test of this hypothesis, all nightlighting records were screened for probable instances in which discrete broods had been captured. For the most part, these consisted of adult hens, accompanied by juveniles of a single age class, caught at sites where juveniles of different age classes were not encountered. In all instances in which the winter location of the adult was known, the known locations of her offspring were plotted. Out of 44 such records, 23 (52%) were discovered in which one or more juvenile hens were found in the same wintering area as the adult (Fig. 10). Obviously not all young hens wintered with their parents, but the relative number known to do so, and the distance over which certain of these moves must have been accomplished, seemed far too great to be explained by chance alone. Alternatively, we infer that an appreciable fraction of young hens maintained parental ties through autumn and early winter and accordingly were led to winter cover.

Other evidence of family organization during this season was provided by the winter location of sibling hens in instances where parental location was not definitely known. Among 12 such records, 8 instances were encountered in which at least 2 members of the same brood were found in the same winter cover. One of the best examples consisted of 3 young hens nightlighted as 7-week-old chicks on September 15, 1962. On January 30, 1963, all 3 were captured in a winter trap 1 mile northeast of the fall capture site. Another example, illustrating both parental and sibling ties, involved an 8-week-old brood of 7 young hens and 3 cocks marked on September 8, 1962. The adult and 5 young hens were located during the subsequent winter. Two juveniles were found with the adult in winter cover 0.8 mile northeast, two others were caught in a winter trap 2.3 miles northeast, and one was observed in winter cover 1.5 miles southwest (Fig. 10). Again, appearance of broodmates in the same winter cover several miles removed from the fall capture site could hardly be attributed to chance, and we conclude that family bonds between hens existing in late summer and early autumn not infrequently persisted during the ensuing move to winter cover.

Parental attachment probably was an important means through which young hens found their way to traditional wintering areas; however, it may not have been the sole mechanism. Association with adults outside the family may also have contributed to oriented dispersal, but we had no way of evaluating this possibility.

In conclusion, not all young hens were led to winter cover by adults from the natal vicinity, but sufficient numbers apparently were to account for the observed degree of orientation to traditionally used wintering areas. In general, it appeared that successive generations of hens from given portions of the summer range tended to have rather well-defined traditions for specific wintering areas, and that family organization was one of the primary mechanisms through which tradition was passed. How to explain the unusually long moves undertaken by certain juveniles is mainly speculation. Perhaps these represented individuals that for one reason or another failed to benefit from adult leadership. Or perhaps they merely represented an innately dispersive segment of the juvenile age class, present in most animal populations, which for unknown reasons are unusually mobile.

Movement of adult cocks to winter cover averaged 0.35 mile (Table 17). Only 7 cocks provided information on winter cover use 2 years in succession. Four returned to the same wintering area, from spring-summer locations up to 0.7 mile distant, whereas 3 others failed to return from breeding areas 0.7, 1.8, and 2.2 miles removed. All nonreturning cocks wintered less than 1/2 mile from the area occupied in spring and summer.

Based on these relatively meager data, travel to winter cover by adults appeared to be highly localized. Once a breeding territory had been established, adult cocks appeared to occupy essentially the same home range thereafter, moving the least necessary distance between winter and summer range.

Fall-to-winter movement of young cocks averaged 1.05 miles, only 11 percent of this group traveling 2 miles or more to winter cover (Table 17). The longest recorded move by a young cock to winter cover was 4.6 miles.

Among juvenile cocks, it has been previously shown that direction of fall movement did not depart from random expectation. Although sample sizes were inadequate for statistical evaluation, the generalized pattern of movement to winter cover also sug-

gested unoriented dispersal (Fig. 9). When both sets of movement data were plotted among young cocks captured as broodmates, evidence of family ties was conspicuously lacking. No records were found in which brood members were shot together more than 1/4 mile from the fall capture site, nor were any young cocks found in the same winter cover as the adult or sibling hens.

Abandonment of family groups thus seemed to occur relatively earlier and more definitively among juvenile cocks than hens, from which it is reasonable to suppose that socialization with adults probably was less prevalent among the former. That this was associated with unoriented travel seemed to be more than just coincidence. Under little influence of adult leadership, essentially random dispersal would seem to be the expected pattern of movement.

Why the apparent difference in social behavior between young cocks and hens was not at all clear. A clue, however, was believed to exist in the pattern of fall recrudescence of the juvenile gonad, reportedly absent in hens (Hiatt and Fisher 1947) but well documented in cocks (Kirkpatrick and Andrews 1944; Hiatt and Fisher 1947;

FIGURE 10. *Examples of the winter location of adult and juvenile hens captured by fall nightlighting (principally the month of September) as members of discrete broods. Heavy line designates boundary of Waupun Study Area.*

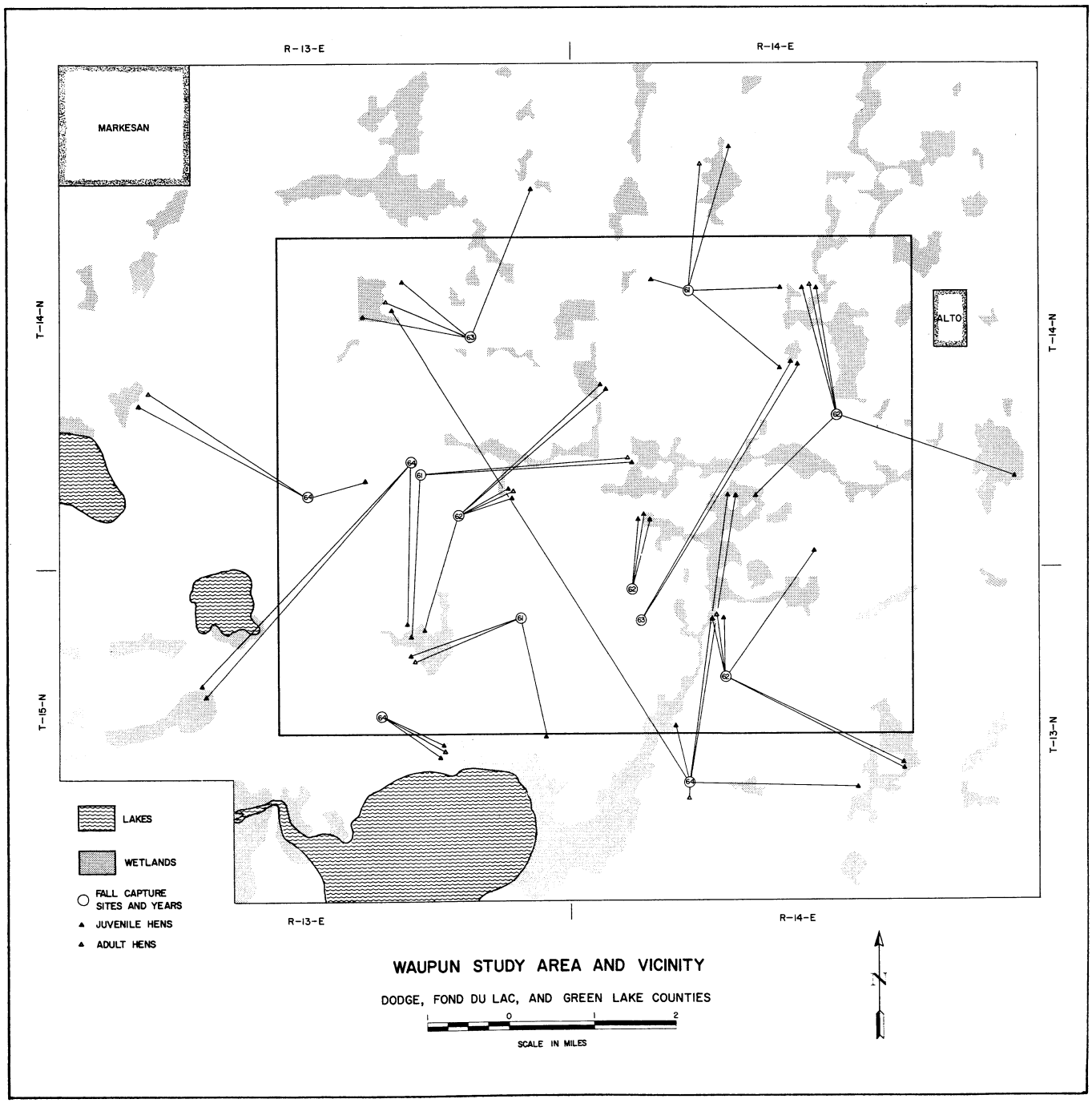


TABLE 18. Annual Variation in Movement by Sex and Age Class, Waupun Study Area and Vicinity

Year	Average Distance of Movement in Miles*			
	Juvenile Cocks	Adult Cocks	Juvenile Hens	Adult Hens
1960–61				
Through hunting season	0.57 ± 0.05(42)	0.48 ± 0.10(7)	0.38 ± 0.13(2)	0.38 ± 0.14(7)
Through January-March	1.08 ± 0.39(11)	0.38(1)	1.06 ± 0.17(23)	0.60 ± 0.03(36)
1961–62				
Through hunting season	0.50 ± 0.04(105)	0.33 ± 0.06(10)	0.63 ± 0.26(7)	0.43 ± 0.03(9)
Through January-March	1.43 ± 0.29(13)	0.43 ± 0.12(5)	1.46 ± 0.18(38)	0.80 ± 0.10(31)
1962–63				
Through hunting season	0.58 ± 0.05(109)	0.45 ± 0.05(7)	0.76 ± 0.27(16)	0.38 ± 0.06(6)
Through January-March	1.06 ± 0.15(11)	0.38(1)	1.68 ± 0.13(70)	0.84 ± 0.09(70)
1963–64				
Through hunting season	0.59 ± 0.06(87)	0.28 ± 0.07(10)	0.72 ± 0.19(22)	0.59 ± 0.14(7)
Through January-March	0.60 ± 0.24(10)	0.13(1)	1.49 ± 0.14(61)	0.79 ± 0.10(56)
1964–65				
Through hunting season	0.82 ± 0.14(99)	0.23 ± 0.05(7)	0.96 ± 0.19(17)	0.59 ± 0.19(7)
Through January-March	0.98 ± 0.40(10)	0.13(10)	1.85 ± 0.24(54)	0.95 ± 0.12(44)

*Means and standard errors with sample size in parentheses. Difference between years in distance of fall-to-winter movement by juvenile hens significant at 5 percent level (F' with 4 and 99 df = 2.61; reference value at 0.05 = 2.44). No other differences between years within sex and age classes significant at 0.05 by analysis of variance in presence of heterogeneous variances (Snedecor 1956: 287-289).

and Greeley and Meyer 1953), leading to autumnal sexual behavior in which only young males participate. While we did not personally witness courtship at this season, fall crowing was commonplace and intolerance between cocks was frequently observed. Behavior of this sort may have hastened the severance of family bonds and prevented other types of social interaction between cocks, the result being that young males were forced to lead a more solitary life than hens during the fall and early winter period.

Annual Influences on Fall-to-Winter Movement

Although the difference was not statistically significant, fall mobility of juveniles appeared at first glance to be higher than average in 1964 (Table 18). Movement to winter cover showed significant annual variation among juvenile hens and nonsignificant though strikingly parallel variation among adults. Both age classes moved unusually short distances to winter cover in 1960-61 and unusually long distances in 1964-65.

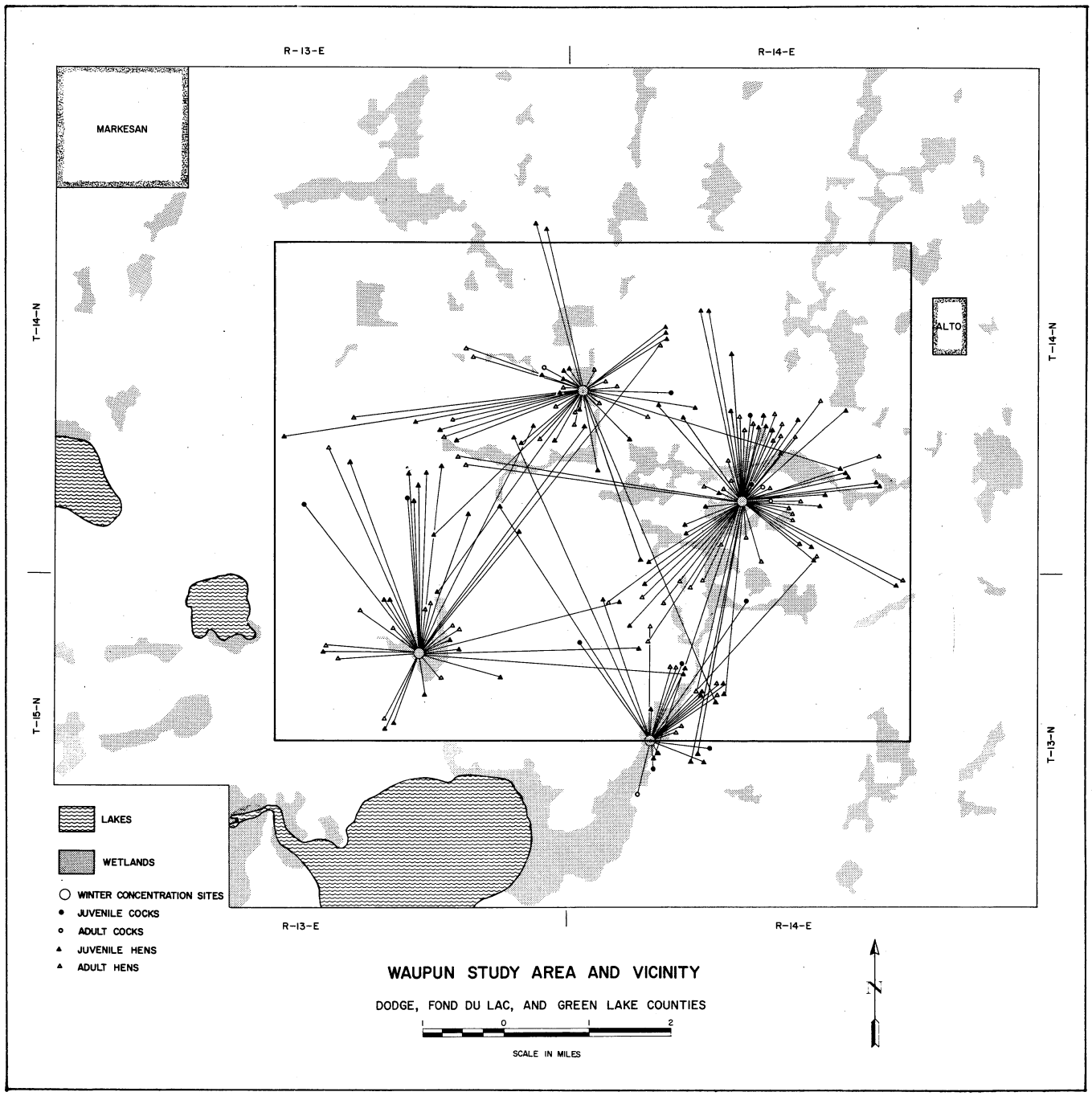
Initially these data led us to believe that the 1964 fall population was for some reason unusually mobile, but when nightlighting records were examined it became clear that an inordinately large percentage of that year's marked sample had been captured at sites comparatively remote from wetland areas. Since wetlands were the predominant source of fall and winter cover, the 1964 trend probably represented nothing more than an artifact of sampling.

The move to winter cover in 1960-61, however, clearly departed from the normal picture. Following an extremely wet growing season, substantial acreages of abandoned cropland dotted the landscape. Many of these weedy tracts were in close proximity to unharvested corn, the combination providing ideal winter habitat seldom present on the uplands. Large numbers of pheasants wintered in these temporary quarters, and among adult hens the rate of return to cover used the previous year was comparatively low. Abundant cover, coupled with virtually snow-free conditions, doubtless encouraged an unusually large percentage of adult hens to winter locally instead of returning to traditional winter cover, hence a correspondingly larger percentage of young hens also wintered in the natal vicinity.

Winter conditions were equally mild in 1963-64, yet the extent of fall-to-winter movement was not as restricted as 1960-61 (Table 18). However, return of adults to traditional winter cover was below average, in addition to which actual census data revealed a comparatively small percentage of the winter population concentrated at such sites. Hence it appeared that mean distances of travel failed to reflect heavier usage of temporary and satellite winter cover in preference to traditional wintering areas in 1963-64. This too probably stemmed from the nonsystematic distribution of the nightlighted sample. Because the distance of egress tended to vary from different parts of the study area, movement distances per se were highly imperfect grounds on which to compare annual characteristics of fall-to-winter movement.

In conclusion, fall-to-winter movement in this study appeared to represent a forced seasonal shift to winter cover, jointly regulated by weather conditions and by availability of alternative cover. Open winters and/or winters with unusual abundance of temporary cover on the uplands allowed a higher percentage of the adult hens to winter in the breeding vicinity, during which an increased proportion of young hens also spent the winter near their birthplaces. Superimposed on this picture was the fact that certain juveniles, particularly hens, moved greater distances than required to find winter cover, probably reflecting an innate tendency for dispersal. No relationship was

FIGURE 11. *Origin of birds concentrating at selected sites of traditional winter cover, 1960-65. Heavy line designates boundary of Waupun Study Area. Examples shown are wintering areas 11, 22, 25, and 30 (fig. 8).*



detected between yearly change in population level and fall-to-winter mobility, though again, annual variation in the distribution of the night-lighted sample may have precluded a very discriminating test of the possible influence of population density on pheasant movement.

Area of Summer Range Drained by Traditional Winter Cover

Attention up to this point has been focused on dispersal patterns from fall capture sites. To obtain reverse perspective of the fall-to-winter move, the origin of all birds concentrating at traditional winter cover was plotted. Eight primary and secondary concentration sites provided a sufficient amount of data to reveal the distance and direction from which wintering birds were drawn (Fig. 11). Analysis was based on 322 movement records

representing all age and sex groups combined.

The average area of summer range drained by these eight wintering areas, obtained by connecting the outermost fall locations and by measuring the circumscribed area, was approximately 5,300 acres or 8.3 square miles. Distances of ingress, however, differed markedly with sex and age. Out of 9 adult cocks, none originated from summer range more than 0.75 mile distant. Among 19 juvenile cocks, 89 percent originated from summer range within a 2-mile radius. Corresponding percentages among 128 adult and 166 juvenile hens were 81 and 62, respectively. In both age groups of the hen population combined, 70 percent of the individuals identified at traditional winter cover were from summer range up to 2 miles distant; 92 percent were from summer range within a 3-mile radius. While these results applied only to the juxtaposition of winter cover represented in the present study, it was clear that traditional wintering areas attracted birds from substantial acreages of summer range, and that events affecting pheasant survival in a given area could have had an important bearing on populations within a 2-mile radius.

DISCUSSION

For all age and sex groups combined, dispersal from fall capture sites based on hunting season recoveries and observations averaged 0.62 mile (Table 15). In south central Minnesota (Nelson 1959:63) and in California (Mallette and Bechtel 1959), comparable means were 0.37 and 1.30 miles, respectively. In South Dakota, Seubert (1956) reported that 75 percent of the hunter recoveries of banded cocks were made within 3 miles of the fall capture sites, whereas at Waupun the corresponding percentage was 99 (Table 15). In North Dakota, Oldenburg (1962) reported 3.05 miles as the average distance of travel undertaken by birds marked in fall and later captured at a winter concentration site. By comparison, the average distance from which all sexes and ages were drawn into traditionally used winter cover in the present study was approximately 1.0 mile.

From these comparisons, it appeared that fall and winter mobility at Waupun was somewhat more restricted than in most areas where pheasant movement has been investigated. If so, it seems reasonable to believe that the comparative abundance of wetland cover in our area tended to obviate the need for more extensive movement. Although other areas in Wisconsin with less abundant winter cover might show more extensive seasonal movement, we suspect that pheasant mobility in this state is generally less extensive than that which typifies the comparatively cover-deficient prairie states farther west. On the other hand, we also suspect that areas to the south, characterized by milder winter weather, may show more restricted movement than we observed.

SUMMARY

Fall movement, as well as distance of travel to winter cover, differed prominently with sex and age, adult cocks the least mobile, followed in order by adult hens, juvenile cocks, and juvenile hens. Progressive concentration in wetland cover typified the fall movement of all sex and age groups, a probable response to hunting disturbance and cover destruction through corn harvest and fall plowing. Among juvenile cocks, dispersal from fall capture sites was essentially random in direction, although distance of travel was related to proximity of wetland cover.

Movement of hens to winter cover occurred principally in November and December, cocks apparently completing the move somewhat earlier than hens. Approximately half of all adult hens returned in winter to cover used the previous year. Return rates were lowest between the first and second winters of life and among yearling birds inverse to the distance of travel required. Movement of juvenile hens to winter cover was strongly oriented to traditional winter cover and did not represent random dispersal. Several lines of evidence suggested that many young hens were led to traditionally used areas by returning adults. It was concluded that successive generations of hens from various parts of the study area had rather well-defined traditions for specific wintering areas, and that persistence of family organization during the move to winter cover was one of the primary mechanisms through which tradition was passed. Earlier dissolution of family ties, perhaps related to autumnal recrudescence and precocial sexual behavior, was suggested as a possible explanation for nondirectional fall and winter dispersal by young cocks.

Movement to winter cover appeared to be jointly influenced by weather conditions and by availability of alternative cover. Mild winters and/or winters with an unusual abundance of cover on the uplands allowed larger numbers of adults to remain in the vicinity in which they bred; correspondingly, a higher percentage of young hens also remained in the vicinity of their birthplaces over winter.

Traditional wintering areas, defined as cover sheltering pheasants each year of study, attracted pheasants from areas of summer range averaging 5,300 acres or approximately 8.3 square miles in size. Approximately 70 percent of all hens concentrating in traditional winter cover originated from summer range within a 2-mile radius.

THE WINTERING POPULATION

WINTER MOVEMENT

Daily Movement

Twelve winter flocks on the Springvale Study Area in 1958-59 were observed on a day-to-day basis for information on winter mobility and habitat selection. Observations began in late December and terminated in mid-March. Snow depths during this period increased from 3 inches to almost 3 feet, providing information on daily movement under contrasting conditions of food and cover availability.

Only one flock during this period routinely traveled as far as 1/2 mile between food and cover; 11 other groups restricted daily travel to 1/4 mile or less. One group of approximately 85 birds, quartered in canary grass and heavy ditchbank cover in early January, originally fed in an adjacent field of unharvested sweet corn. In mid-February, both cover types were completely covered with snow. Re-observation of marked individuals indicated that this flock split into three groups, moving between 0.50 and 0.85 miles to alternative cover. None of these birds returned to the original feeding location, even though food resources in the new winter quarters were far inferior. Two other flocks also abandoned standing corn for less favorable food supplies after moving barely 1/2 mile to better winter shelter.

Information on daily movement with heavy snow cover, when theoretically it should have been greatest, was next obtained in 1961-62. No flocks under near daily surveillance on the Waupun Study Area between early January and late March were known to range more than 0.40 mile between food and cover. Out of 22 fields of unharvested corn on the area, only 8 situated 1/4 mile or less from winter cover were consistently used by wintering birds. One field, just 1/2 mile from a concentration of 250 to 300 birds, showed no sign of pheasant use throughout the period.

Such examples led us to conclude that wintering birds rarely traveled more than 1/4 mile from day to day, with 1/2 mile apparently being the upper limit of the daily cruising radius. Other workers have reported essentially similar findings. In South Dakota, Kirsch (1951) reported that winter flocks typically ventured no more than 1/4 mile in search of food, and Bue (1949) observed that daily travel was ordinarily 300 yards or less. Shick (1952:21), in Michigan, also reported that winter movement was normally confined to a 1/4-mile radius.

Change in Winter Residence

The average distance of movement between January 1 and winter breakup for all sex and age groups combined was 0.40 mile (Table 19). Winter mobility, however, exhibited significant change from year to year, the two severest winters of the period (1958-59 and 1961-62) showing the greatest degree of winter movement. Only in part could this be attributed to greater range of daily travel in response to food and cover shortage, the prevalence of moves which exceeded the daily cruising radius also being higher than usual. If it is assumed that 1/2 mile represented the maximum radius of daily travel, 70 percent of the 1958-59 moves and 36 percent of those in 1961-62 apparently represented a more-or-less permanent change in winter residence. Other winters showed comparatively minor shuffle of the winter population, only 13 percent of all observed moves exceeding the limits of daily travel.

In general, winter movement led to progressively tighter concentration of birds in traditional winter cover, but once having arrived at such sites, birds tended to remain highly sedentary thereafter. In 1960-65, winter movement of 272 birds initially observed or captured at traditional winter cover averaged only 0.27 mile, compared with 0.59 mile among 50 birds first observed or captured at nontraditional sites. Even though pheasants in traditional winter cover must have been

TABLE 19. Annual Variation in Distance of Winter Movement*

Winter	Total Moves	Mean and Standard Error**	Percent of Moves Greater than 0.5 Mile
1958-59	83	0.71 ± 0.06	70
1959-60	53	0.21 ± 0.03	11
1960-61	31	0.23 ± 0.04	7
1961-62	62	0.49 ± 0.06	36
1962-63	43	0.35 ± 0.05	21
1963-64	49	0.30 ± 0.04	14
1964-65	84	0.29 ± 0.03	11
Totals and weighted means	405	0.40 ± 0.02	28

*Includes all age and sex groups combined, based principally on birds observed after winter capture but also including previously marked individuals observed twice or more during the winter period. Does not include repeat-capture records from current winter trapping. Observations from Springvale Study Area in 1958-59; from Waupun Study Area and vicinity in all subsequent winters. Based on movement records between January 1 and mid-March, depending on time of winter breakup.

**Mean distance of movement between winters highly significant by analysis of variance in presence of heterogeneous variances (Snedecor 1956:287-289) (F' with 6 and 16 df = 9.24; reference value at 0.01 = 4.24).

subject to considerable duress in winters of heavy snow, dispersal from these sites was exceedingly rare. In 1961-62, not a single movement record was obtained which indicated abandonment of a traditional concentration site.

Changes in winter residence were of particular interest in demonstrating the relative importance of food versus cover in the distribution of the winter population. In all instances in which winter flocks broke up and disbanded, the ultimate factor triggering egress appeared to be shortage of cover. Original food supplies were still available, as in the case of standing corn, or had long been covered by snow. Birds in the meantime subsisted on marginal foods, trap bait, or traveled longer-than-usual distances in search of food. We found it generally true that readily obtainable food was used only when good cover was nearby, whereas good winter cover held birds almost regardless of the quality and quantity of adjacent food. Distribution of the winter population thus depended more intimately on the stable distribution of winter cover from one year to the next than the more variable distribution of winter food.

Winter mobility in this study (Table 19) differed little from that observed elsehwere. In Iowa, 119 winter movement records reported by Grondahl (1953) averaged 0.39 mile, and 139 reported by Weston (1954) averaged 0.46 mile. We found no evidence of circuitous movement of winter flocks between several tracts of winter cover as earlier reported in Wisconsin by Leopold et al. (1938).

Wintering birds were dependent principally on wetlands for cover. Shrub-carr was preferred.

TABLE 20. Distribution of the Winter Population by Classification of Winter Cover

Winter	Study Area*	Census Total**	Percent of Census Total by Type of Wintering Area				
			Traditional			Nontraditional	
			Primary	Secondary	Tertiary	Satellite	Temporary
1959-60	A	476	71	14	3	12	0
1960-61	A	575	25	10	2	37	26
1961-62	W	1,898	68	18	6	5	3
1962-63	W	1,106	62	17	5	12	6
1963-64	W	1,184	45	10	6	26	13
1964-65	W	1,097	57	24	3	13	3

*A = Alto Study Area (7 square miles), W = Waupun Study Area (42 square miles), the former a subdivision of the latter (Fig. 2).

**Results for Alto Study Area based on March 19-23 census in 1959-60 and January 5-27 census in 1960-61. Results for Waupun Study Area based on censuses completed at various stages in winter, but generally regarded as applicable to mid-winter population levels.

COVER UTILIZATION

Winter cover preferences reflected the outcome of three basic habitat needs: (1) roosting cover for nighttime use; (2) loafing cover used between daylight periods of feeding activity; and (3) emergency cover relied upon when normal cover preferences were precluded by heavy snow conditions and severely reduced cover availability. On the whole, cover preferences for roosting were the least specific of the three. Subsequent discussion of winter cover use will therefore focus on population distribution during daylight hours, emphasizing habitat selection under emergency conditions with snow cover deepest and cover in shortest supply.

Generalized Population Distribution Related to Winter Cover

On the Waupun Study Area, 70 percent of the population was concentrated in traditional winter cover in an average year, the percentage during open winters (1960-61 and 1963-64) as low as 37 and 61, respectively, and during other winters of study ranging from 83 to 93 (Table 20). All but three traditional wintering areas consisted of some form of wetland cover (Table 16). The overall significance of wetlands as winter cover was also demonstrated by census results from winter study areas (Table 21). On the Springvale Area in 1958-59, 78 percent of the average winter population was associated with wetland cover. On the Alto and Mackford Study Areas between the winters of 1959-60 and 1964-65, 88 percent of the winter population was dependent on one or another wetland types as winter shelter.

Of the various wetland types, shrub-carr was most essential as winter cover. Less than 1 percent of the Springvale Area consisted of shrub-carr, yet nearly half of the winter population was concentrated in this cover type under the heavy snow conditions of February and March in 1959. On the Alto and Mackford areas, shrub-carr contained as high as 60 percent of the wintering birds when snow cover was maximum (March 1962), even though shrub stands constituted barely 1 percent of the landscape. Under average conditions on the

latter two areas, shrub-carr held 35 percent of the winter population, followed by herbaceous cover with 26 percent, canary grass with 10 percent, sedge-meadow with 9 percent, and cattail with 8 percent. Of the nonwetland types, retired cropland contained 5 percent of the average winter population, shelterbelts 3 percent, and woodlots and strip cover (roadsides, fencelines, and ditchbanks) 2 percent each.

Use of Individual Cover Types

To compare winter use of the various wetland types on a quantitative basis, seven sets of transects were established in traditional wintering areas. Transects were spaced approximately 100 yards apart and gridded the entire complex of winter cover known to be inhabited by wintering birds. Transect lines were mapped on aerial photos, and the intercept of each cover type was measured. Except for the aspen-swamp type, not included in the evaluation, each set of transects sampled at least three of the five wetland types listed in Table 21. Transect mileages varied from 0.62 to 1.29 per set and totaled 6.41 for all 7 sets combined.

Transects were walked at a slow pace 1 to 3 days after fresh snowfall, and all pheasant sign (roosts, tracks, and birds flushed) was recorded by cover type in which encountered. Fourteen runs were made over a 3-winter period (1959-60 to 1961-62). Results of each run were divided by the appropriate length of time that sign had accumulated and were plotted by cover type against average snow depth. The number of roosts and tracks observed per mile showed the most profound differences between vegetation types and the clearest-cut trends in relation to snow depth, results of which are summarized in Figure 12.

Assumptions on which this procedure rested were: (1) that the number of roost sites observed per mile served as a valid index to the intensity of night-time use for roosting, and (2) that the number of tracks per mile was directly related to intensity of daytime use for loafing. In point of fact, neither of these conditions may have been met. On occasion, pheasants roosted in trees or shrubs above ground, in addition to which the same roosting forms at ground level were sometimes re-used when snow was deep and heavily crusted. Birds were also less inclined to walk than fly as snow increased in depth, hence the actual relationship between track counts and loafing use probably was something other than linear. In spite of these shortcomings, results in Figure 12 were believed to provide a reasonably representative picture of the dynamics of cover selection under changing snow depths and cover availability.

Use of the various wetland types for roosting followed a sequence or more-or-less single-moded curves with increase in snow cover, canary grass and sedge-meadow at far left, followed in order by herbaceous cover, cattail, and shrub-carr at far right. Under snowless conditions, canary grass and sedge-meadow apparently were most preferred for roosting. In ungrazed condi-

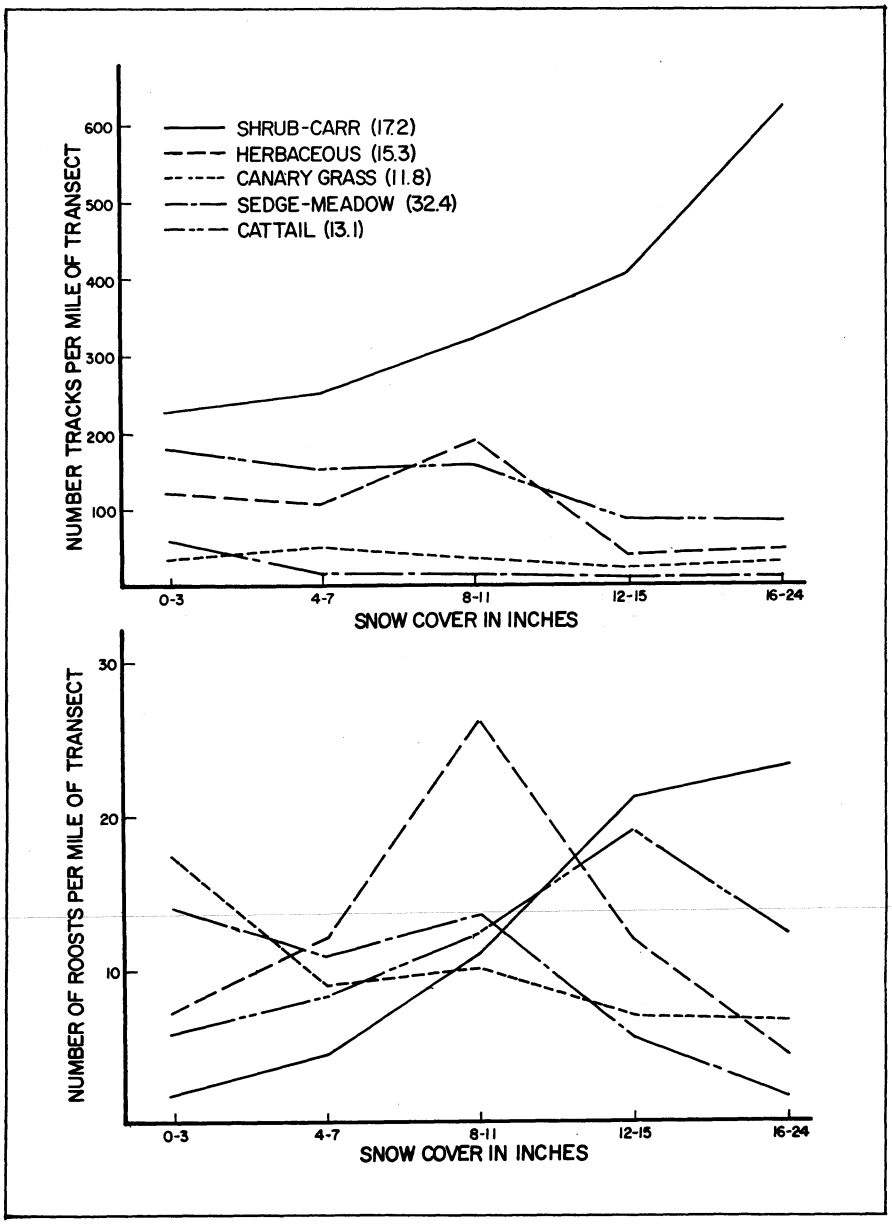
TABLE 21. Distribution of the Winter Population with Respect to Available Cover as Determined by Results of Winter Census

Winter and Study Area*	Period	Average Snow Cover (inches)	Census Total	Percent of Census Total by Cover Type**									
				Wetland Cover						Nonwetland Cover			
				Shrub-Carr	Aspen Swamp	Cat-tail	Canary Grass	Herba-ceous	Sedge Meadow	Wood-lot	Strip Cover	Retired Cropland	Shelter-belt
1958-59													
S	1/20-31	11	706	24	7	NP	15	20	21	0	13	0	NP
S	2/21-28	17	646	42	5	NP	2	26	13	8	5	0	NP
S	3/23-31	23	428	51	6	NP	0	1	0	31	11	0	NP
1959-60													
A	1/8-11	4	571	38	NP	5	9	29	18	0	1	0	0
AM	3/19-23	9	661	44	NP	0	6	40	4	0	2	0	4
1960-61													
A	1/5-27	1	575	22	NP	18	8	23	13	0	0	13	3
1961-62													
AM	12/24-1/6	10	889	31	NP	1	11	44	2	6	1	0	5
AM	3/15-21	16	590	60	NP	0	4	22	0	7	1	0	6
1962-63													
AM	12/30-1/8	4	575	39	NP	6	13	21	9	1	6	0	6
AM	3/10-21	9	452	48	NP	3	12	18	6	1	8	0	5
1963-64													
AM	12/30-1/6	4	549	23	NP	10	9	24	14	2	3	14	3
AM	3/10-19	2	441	29	NP	10	10	18	11	1	2	16	2
1964-65													
AM	1/14-19	3	478	35	NP	10	16	21	7	1	3	4	3

*Winter study areas coded as follows: S = Springvale Study Area (14.7 square miles); A = Alto Study Area (7.0 square miles); and M = Mackford Study Area (7.5 square miles). Combined results of the latter two, both subdivisions of the Waupun Study Area, designated as AM.

**Strip cover includes roadsides, fencelines, and ditchbanks. NP = cover type not present.

FIGURE 12. *Relative use of various wetland vegetation types as roosting and loafing cover in relation to increasing snow depth, Waupun Study Area and vicinity, 1959-1962. Information from amount of pheasant sign encountered on transects in traditional winter cover. Figures in parentheses are the percentages of the aggregate transect mileage consisting of individual cover types.*



tion, both of these vegetation types tended to become severely flattened by early winter and provided a dense layer of vegetative growth at ground level. Clumps of this material appeared ideal for roosting, but rapidly disappeared as snow accumulated. Roosting in these types was highly infrequent when only scattered stems protruded above the snow line. Roosting in herbaceous cover was maximum at intermediate snow depths of 8 to 11 inches. Compared with sedge-meadow and canary grass, the stiffer-stalked vegetation which comprised this type (predominantly aster and goldenrod) was taller, more resistant to flattening, and thus provided cover with considerably deeper snow. Cattail stands were still denser and taller and received maximum use with 12 to 15 inches of snow. Moderate amounts of snow seemed to improve the quality of cattail cover for roosting. Broken-over masses of this vegetation, mantled by snow, made highly attractive niches for roosting.

In absence of heavy snowfall, shrub-carr apparently was avoided for roosting. Use rapidly increased, however, as snow accumulated and alternative cover became unavailable for this purpose. The structure of a typical shrub stand in this study consisted of a shrub layer 6 to 12 feet tall with light ground cover of grasses and herbs 1 to 2 feet in height. Use of this type was therefore maximum with the understory buried and only the shrub layer furnishing concealment. This seemed to be in direct contrast to roosting preferences otherwise demonstrated, i.e., for absence of overhead concealment, suggesting that shrub-carr was definitely second choice cover into which roosting birds were forced when other wetland types were unavailable.

As loafing cover, shrub-carr far outranked all other vegetation types, but was most clearly superior at snow depths of 12 inches or greater. Cattail rated second in importance as loafing cover and herbaceous cover third. Sedge-meadow and canary grass were seldom used for loafing irrespective of snow depth, much of the pheasant sign encountered in these types probably representing travel to and from roost sites.

Stands typed as shrub-carr in this study showed at least 30 percent canopy closure, more open stands being typed according to the dominant nonshrub vegetation present. Actually, a large but unrecorded percentage of the inferred loafing use of nonshrub types consisted of tracks in the vicinity of brush clumps too small or too open in canopy to be classed as shrub-carr. In a matrix of nonwoody cover, concentration of pheasant activity around isolated shrub clumps provided one of the clearest demonstrations of the importance of shrubby vegetation as winter loafing cover.

Individual shrub-carrs in this study ranged from less than 1 acre in size to nearly 80 acres in total. Unfortunately, we cannot specify the minimum size of this cover type capable of sheltering winter flocks, but several stands no larger than 5 acres consistently held as many as 100 birds during periods of maximum snow. As a subjective evaluation, stands around 5 acres in size probably are the smallest that could be recommended as dependable sources of emergency winter cover. Stands appreciably smaller in size, depending on shape and surrounding topography, would be increasingly subject to accumulation of drifting snow.

In conclusion, wetlands were the

primary source of winter cover in this study, and shrub-carr was most important of the wetland types. At all snow depths, shrub-carr was most preferred for loafing, and under emergency conditions was increasingly relied upon for roosting. Only the cattail and herbaceous types rivaled shrub-carr in all-around importance as winter cover, but value of these cover types was largely restricted to snow depths of 12 to 15 inches or less.

Only two stands of aspen swamp occurred on the study area, both having dense understories of shrub cover. Although quantitative data were lacking, winter use of this cover type appeared comparable to shrub vegetation without an aspen overstory. Nor were any stands of tamarack available for study. Experience gained in other areas, however, leads us to believe that closed canopy tamarack would compare favorably with shurb-carr, perhaps being of even greater value as emergency winter shelter.

Use of upland cover in winter was so restricted (Table 21) that no attempt was made to quantitatively describe its use. Conclusions under this heading therefore stem from field impressions and subjective evaluations.

On the Waupun Study Area, most of the woodlot acreage was heavily pastured in summer and hence unsuited as winter cover. On the Springvale Area, ungrazed woodlots were present at 15 sites in 1958-59. Use of woodlots on this area was largely restricted to emergency situations of heavy snow (Table 21), the brushy edges in particular which were commonly used for loafing. Importance of woodlots for roosting was minimal. Ground roosts were rarely encountered in woodlots, nor did we find pheasants tree-roosting in deciduous woodlots to any appreciable extent. While woodlots have been reported as a major source of winter cover in Ohio (Leedy and Hicks 1945:105) and elsewhere, pheasants in this study seemed to avoid such sites as long as alternative cover was available.

Roadsides and fencelines were important as travel lanes, were occasionally used for loafing, but received little or no use for roosting. Hedgerows of wild plum were particularly valuable as loafing cover, but their quantity was extremely limited and therefore of slight importance in the overall picture. Of the three strip-cover types, ditchbanks were most consistently used in winter, several of which were wide enough and densely vegetated to afford protective cover despite heavy drifting. Ditchbanks routinely sheltered birds in early winter, and even during emergency situations a few small flocks persisted in such cover. Aside from ditchbanks, strip cover played an altogether minor role in meeting winter cover requirements.

Retired cropland, for the most part unharvested hay, received significant use only with snow cover absent or nearly so. Only during the open winters of 1960-61 and 1963-64 did such cover hold an appreciable number of birds throughout the winter period.

Farm shelterbelts in the region were few and far between. On the Waupun Study Area, four were occasionally used by pheasants and a fifth was classified as traditional winter cover. All five consisted of single or double rows of Norway spruce between 15 and 40 feet tall; deciduous shelterbelts of potential value to wintering pheasants were entirely lacking in the area. Shelterbelts were most important for loafing, but in emergency situations were sometimes also used for roosting. The only traditionally used cover of this type was near an outdoor feedlot and in three out of six winters contiguous with a large tract of retired cropland. From these and other observations, our general impression was that shelterbelts consistently held wintering birds only in conjunction with a readily accessible food supply, and that attractiveness to pheasants was greatly enhanced when an alternative source of roosting cover was available nearby.

Apart from feeding, little use of cultivated land was noted at Waupun. Pheasants occasionally roosted in small grain stubble and picked corn, but the overall significance of harvested cropland as winter cover was virtually nil.

Conclusions on Winter Cover Preferences

Light to moderate ground cover lacking overhead canopy was most preferred for roosting, whereas overhead concealment with minimum ground cover was preferentially sought for loafing. It is tempting to speculate on the underlying basis for differential habitat selection. One possible explanation is that both represented adaptive responses to security from predation. It is reasonable to assume that mammalian predators were the major threat at night, from which flight would be the normal escape reaction. Selective use of cover that did not interfere with the initial burst of flight from the roost may therefore have had considerable survival advantage. On the other hand, overhead cover allowing freedom of movement beneath would have provided maximum security from birds of prey, which doubtless were the more important pheasant predators during daylight hours. A second possibility was that winter cover preferences were simply related to thermoregulation. Ground cover, which seemed to be most critical for roosting, may have functioned as a windbreak which tended to conserve body heat at night. In contrast, brushy cover without ground vegetation clearly afforded better opportunity for birds to sun themselves on clear winter days. The fact that wintering birds commonly remained on the roost throughout extremely cold or stormy winter days seemed to emphasize the fact that conservation of body heat played at least a subsidiary role in winter cover selection.

It was clear that loafing cover was a more critical habitat requirement than roosting cover, the latter consisting of much greater variety of vegetation types than the former. Woody and brushy cover, in considerably shorter supply than potential roosting cover, thus emerged as the key winter cover requirement, the location of which exerted the dominant influence on the spatial and temporal distribution of the winter population. Generally speaking, other workers have reached essentially similar conclusions on the critical importance of woody cover in winter, including Randall (1939a) in Pennsylvania, Bue (1949) in South Dakota, Grondahl (1953) in Iowa, Lyon (1954) in Colorado, and Hanson and Labisky (1964) in Illinois.

WINTER FOOD

Composition of Winter Diets

Information on winter food habits was available from contents of 171 crops removed from road-killed pheasants (Table 22). While this could not be considered a representative sample of winter diets, it appeared to be an adequate basis for certain generalizations.

Cultivated grains made up the bulk of the winter diet, with corn and oats

TABLE 22. Composition of Winter Diets Based on 171 Crop Contents, 1959-1965*

Food Item	Percent Frequency of Occurrence**
Corn, *Zea mays*	85
From manure	22
From other sources	63
Oats, *Avena sativa*	45
From manure	20
From other sources	25
Burdock, seeds and seed heads, *Arctium minus*	22
Unidentified grass leaves, *Graminae*	17
Nightshade ber[illegible], *Solanum Dulcamara*	11
Rose hips, *Rosa* sp.	6
Giant ragweed seeds, *Ambrosia trifida*	5
Pigweed seeds, *Amaranthus* sp.	5
Smartweed Seeds, *Polygonum* sp.	4
Buckwheat, *Fagopyrum esculentum*	4
Milkweed seeds, *Asclepias* spp.	2
Foxtail grass seeds, *Setaria* sp.	2
Apple pulp and seeds, *Pyrus Malus*	2
Grape fruits, *Vitis riparia*	1
Barley, *Hordeum vulgare*	1
Black cherry fruits, *Prunus serotina*	1
Beans, *Phaseolus vulgaris*	1
Dock seeds, *Rumex verticillatus*	Tr.
Willow catkins, *Salix* sp.	Tr.
Arrow-head seeds, *Sagittaria* sp.	Tr.
Dandelion seeds, *Taraxacum officinale*	Tr.
Shepherd's purse seeds, *Capsella Bursa-pastoris*	Tr.
Jewelweed seeds, *Impatiens biflora*	Tr.

*Includes all sex and age classes combined. Crops from Springvale Study Area in 1958-59; from Waupun Study Area and vicinity in all subsequent winters.

**Items occurring in less than 1 percent of the crops indicated as trace amounts.

the leading staples. Aside from these two, only burdock seeds, nightshade berries, and grassy plant material occurred in as high as 10 percent of the crops examined. Actually, the relative importance of corn and oats was substantially under-rated by our analysis. Volumetric or gravimetric analysis would have demonstrated an even wider margin of cultivated grains over alternative food items, since the latter were typically consumed in smaller or near-trace amounts when included in the diet. The relative importance of corn to oats in the winter diet doubtless was also under-rated. Waste oats characteristically sprouted after harvest and hence were unavailable in winter, but substantial amounts of this grain were blown from trucks in winter and deposited on road shoulders. The source of our sample probably gave an exaggerated picture of this grain's importance to the winter population at large.

Several authors have stressed the importance of natural foods in sustaining pheasants during periods of food shortage (Hawkins 1937; Errington 1937a; Gigstead 1937; Dahlke 1943; Erickson et al. 1951:29; and Spiegel and Reynolds 1954). At Waupun, however, wild foods constituted an incidental part of the winter diet. This was true even though 61 percent of the crops examined were collected in 1958-59 and 1961-62, winters during which prolonged snow cover should have encouraged maximum exploitation of natural foods. Plants typically growing on moist or wet sites (nightshade, giant ragweed, smartweeds, dock, willow, arrowhead and jewelweed) made up such a small fraction of the collective diet that wetlands apparently furnished an insignificant amount of winter food. From these data, we conclude that nutritional welfare of wintering pheasants could be evaluated strictly in terms of access of cultivated grains, of which corn was by far the most important.

Of 171 crops analyzed, 51 (30%) included oats or corn obviously obtained from manure, suggesting that food from this source contributed significantly to winter diets.

Food Availability

Major sources of winter food were: (1) unharvested crops, primarily corn, but occasionally small grains and buckwheat; (2) waste grain from harvest operations; (3) oats and to a lesser extent corn scattered along roadsides; (4) oats and corn obtained from manure; and (5) grain stored at farmyards.

Unharvested corn was the most attractive source of winter food, but availability within normal limits of daily travel was severely restricted. On the Springvale Study Area, only 7 percent of the winter population had access to standing corn under emergency conditions that prevailed in February and March of 1959. On the Waupun Study Area, appreciable acreages of corn were left unharvested only in 1960-61 and 1961-62, but snowfall in 1960-61 was so meager that food was as readily obtainable in harvested fields. Value of standing corn was maximum under the heavy snow conditions of 1961-62, yet only 19 percent of the population wintered where such food was available. No other winter showed as high as 5 percent of the population with access to standing corn. Unharvested oats planted as cover crops on retired cropland were present and utilized by wintering birds in 1963-64. In 1961-62, one field of unharvested buckwheat was heavily used by a group of 25 to 40 pheasants until mid-February when covered by 10 inches of heavily crusted snow.

Availability of waste corn as winter food depended on three variables, viz., fall-plowing, depth of snow, and prior levels of exploitation by field-feeding Canada geese. Extent of plowing differed markedly from year to year, but only in 1962 did farmers come so close to completion of fall-plowing before freeze-up that winter food resources were seriously curtailed. Only 464 acres of unplowed corn land remained on the Waupun Study Area over the winter of 1962-63, with less than half the winter population having access to corn stubble. Further restricting the amount of waste corn available to pheasants was the intensive fall use of the area by field-feeding flocks of Canada geese. Inspection of 13 fields in mid-December of 1962 produced estimates of goose utilization that ranged between 90 and 100 percent. The only portions of most

fields from which waste grain had not been entirely consumed by geese were adjacent to farm buildings and roads. The whole of the Waupun Study Area served as an important feeding area for migrant Canada geese from Horicon Marsh (15 miles east). While large numbers of geese fed on the area each year, the problem was particularly acute in 1962 because of late autumn concentration of geese on comparatively small acreages of corn remaining unplowed. From experience gained in this study, it seems highly probable that chronic winter food shortages would exist for pheasants on wildlife areas managed principally to attract and hold large concentrations of Canada geese in fall.

Six inches of snow, especially when wind driven and heavily packed, were sufficient to cover waste corn and create food stress unless alternative food was available. In general, the 6-inch depth represented a threshold for success in winter-trapping, birds seldom coming to traps with less snow, but with daily catches mounting rapidly as snow cover accumulated. Four out of seven winters were characterized by prolonged periods of time during which waste grains were largely unavailable (Fig. 13). Sites were occasionally encountered at which pheasants had scratched through 12 inches or more of snow in search of food, but the amount of food secured in this manner could scarcely have repaid the energy expended or exposure risked to obtain it.

Grain from spread manure was a major source of winter food, but was commonly unavailable when need was greatest. Snow depths over 12 inches, particularly if crusted or accompanied by heavy drifting, usually prevented tractor travel in fields after which manure was stacked in barnyards or other sites remote from winter cover. Manure spreading was virtually impossible during February and March of 1959, between late December and mid-March of 1961-62, and during the first half of March in 1963.

Farmsteads and roadsides were the final sources of food to which pheasants resorted when snow was deepest. Although quantitative data were lacking, pheasants were commonly observed feeding at farmsteads in 1958-59 and 1961-62, occasionally observed in 1959-60 and 1962-63, but rarely observed in other winters. For the most part, birds at farmsteads fed around corncribs; few livestock were kept in outdoor feedlots where food could be obtained.

In summary, we conclude that food stress of varying length and intensity prevailed during four out of seven winters of study. Waste grains and grains from manure were for the most part unavailable over a 2 1/2-month period in 1958-59, during which only 7 percent of the population had access to unharvested corn. An even longer period of food deprivation prevailed in 1961-62, but fortunately about 19 percent of the population wintered where standing corn was available. Food conditions were considerably improved in 1959-60 and 1962-63, due in large part to manure spreading which was possible during most or all of the period that waste grains were unobtainable. In 1960-61, 1963-64, and 1964-65, waste grains were available throughout the winter or were covered by snow for such short periods that food stress must have been altogether absent.

On the whole, it was our conclusion that shortage of winter food at Waupun was a more critical habitat deficiency than shortage of winter cover.

WINTER WEIGHTS

Information on winter weights was based predominantly on pheasants examined during winter-trapping. Only 6 percent of the aggregate sample consisted of weights obtained by nightlighting or postmortem examination. Because bait was continuously present at trap sites, weights of repeat captures were excluded with two exceptions. In 1963-64 and 1964-65, so few new birds were captured during March that 18 and 29 repeat captures, respectively, were included in the sample. None of these birds had previously been retrapped and hence were regularly feeding at trap sites. With these precautions, results in Figure 14 were believed to provide an essentially unbiased picture of winter weight trends from year to year. So few cocks were examined in winter that weights among this segment of the population will receive only passing mention.

A significant decline in winter weight was exhibited by both adult and juvenile hens in 1958-59 and 1961-62 (Fig. 14). Among adults, the average weight in March was 12 and 7 percent, respectively, below the January mean. Among juveniles, the corresponding percentages were 12 and 8. No other winters were characterized by significant weight change between January and March. The lightest hen weighed in 1958-59 was a juvenile bird at 653 grams, and 19 percent of all March hen weights fell below 800 grams. In 1961-62, the smallest hen encountered was 754-gram juvenile, and the percentage of all March weights below 800 grams was 6. No hens lighter than 800 grams were handled during any other winter of study.

Although sample sizes were admittedly small in certain winters, neither

FIGURE 13. *Occurrence of snow cover at least 6 inches in depth, the approximate depth at which waste grain became largely unavailable to pheasants. Numbers at far right indicate the total number of days between December 1 and March 31 with snow cover equal to or exceeding the 6-inch depth.*

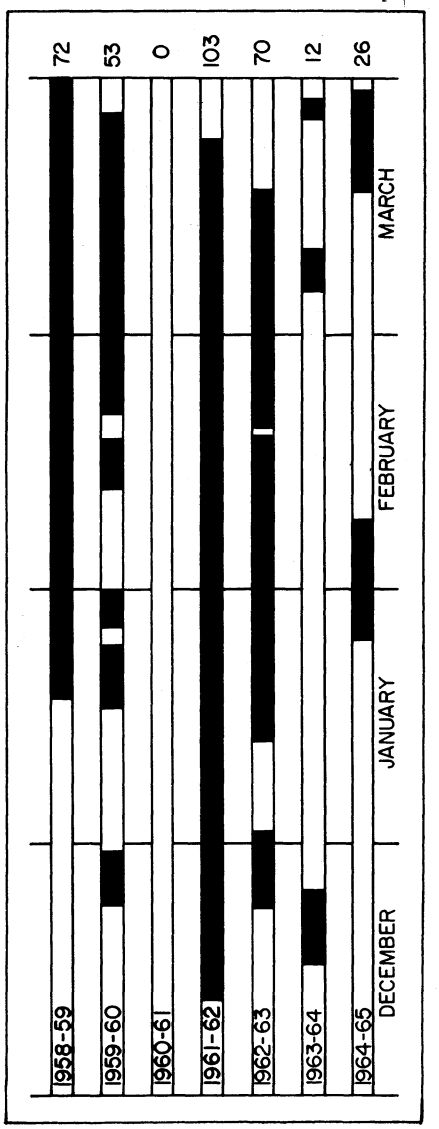
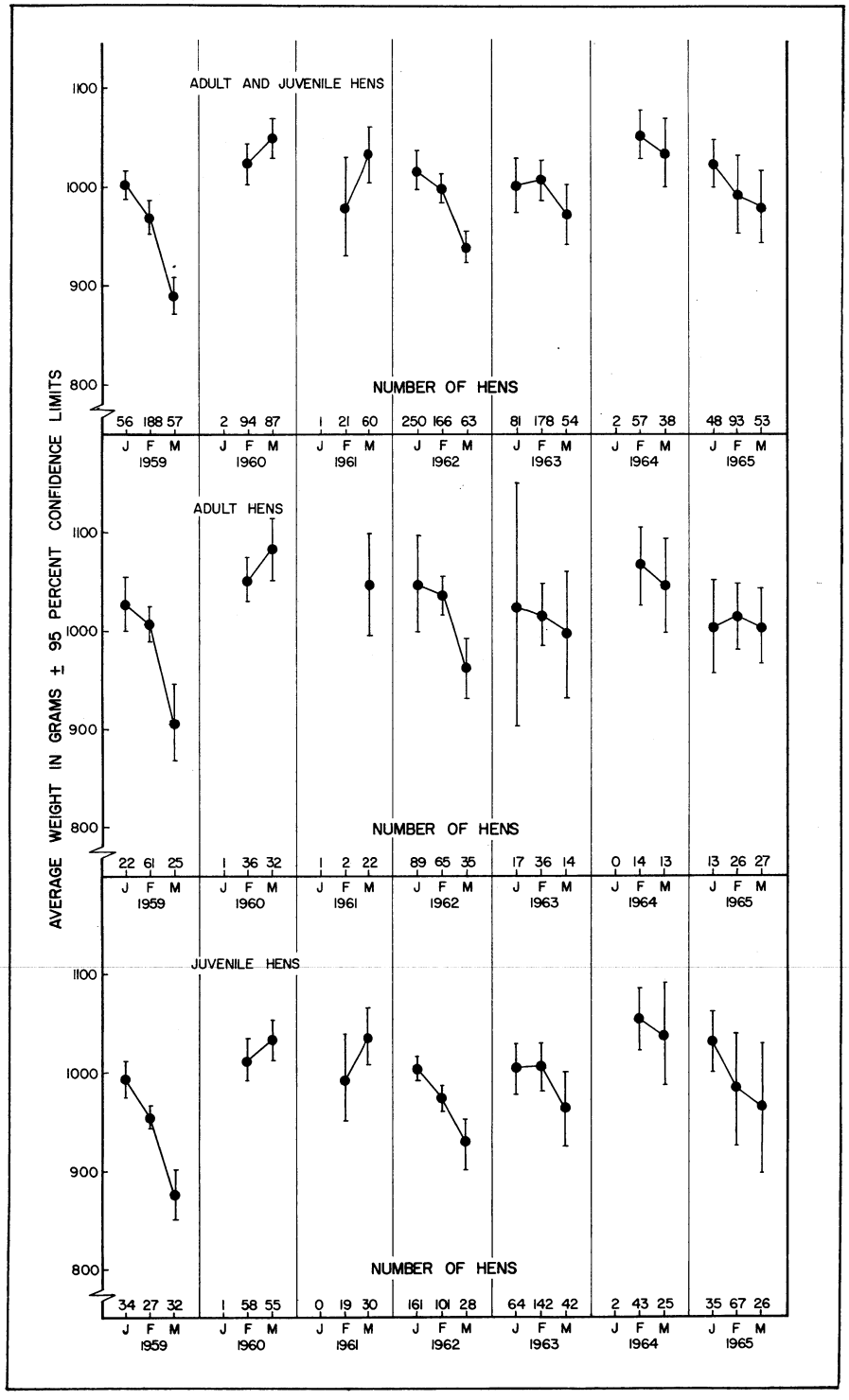


FIGURE 14. *Trends in winter hen weights by monthly periods. Information from Springvale Study Area in 1958-59; from Waupun Study Area and vicinity in all subsequent winters.*



age class of hens demonstrated much variation in January weights (Gates 1971). March weights, by contrast showed highly significant differences from winter to winter. Variation in late-winter weights thus depended on events of the winter period as opposed to weight differences that might have prevailed at the beginning. The March average for all hens combined did not produce a significant correlation with the number of days with at least 6-inch snow cover, but the correlation with winter severity (Table 2), integrating effects of both temperature and snow cover, was highly significant (r = -0.87; reference value at 0.01 with 5 df = -0.87). We uncovered no evidence of differential weight loss between adult and juvenile hens.

March pheasant weights in 1960-61 and 1963-64, the two mildest winters of the period, averaged 1.035 grams. With this as an estimate of the normal weight level at winter's end, hens in 1958-59 and 1961-62 averaged 14 and 9 percent, respectively, under-weight. The mean date to which these figures applied was March 12 and March 8, respectively, but winter breakup did not begin until the first week of April in 1959 and not until the third week of March in 1962. Weights doubtless dropped even farther, and the ultimate departure from normal was believed to be substantially greater than indicated.

Studies on captive pheasants have provided a reasonably clear picture of winter weight trends when food supply is unlimited. Kirkpatrick (1944b) observed a 9 percent drop in body weight between mid-December and early February, followed by weight increase in March. Kabat et al. (1950:25) observed essentially stationary weights through early February and rapid weight increase thereafter. Captive hens on ad libitum diets by Breitenbach et al. (1963) underwent pronounced weight gains in March culminating in an April peak in the annual weight cycle. From such studies, it is clear that the intrinsic weight rhythm, in absence of food stress, follows a more-or-less static trend until February or early March, whereupon body reserves are rapidly accumulated preparatory for reproduction. The most significant aspect of the winter weight changes we observed was that loss of body condition was most pronounced at the very time that energy stores should have been progressively accumulating.

Among wild populations, McCabe's (1949:104) 10-year study on the University of Wisconsin Arboretum demonstrated a February low in body weights, succeeded by a March peak higher than the mean observed in December and January. Roughly the same trend was observed by Stokes (1954:118) on Pelee Island, except that absolute weight loss was less, perhaps because of milder winter weather on Pelee. In the wild, it would appear that pheasants may be adapted to a period of negative energy balance in winter, modified by temperature and food availability, and to rapid weight recovery in spring provided that adequate food is available.

Studies comparable to ours, report-

ing a late winter low in body weights, have been uniformly associated with prolonged food shortage. In the Nebraska Sandhills, McClure (1948) reported a 16 percent drop in hen weights from December to March in 1942-43, during which period the population suffered heavily from starvation. In Ohio, exceptionally heavy snowfall and below normal temperatures in February and March of 1947 were associated with hen weights averaging much below normal for that season (Edwards et al. 1964). That late winter weight loss may not be unusual among Wisconsin pheasants is indicated by McCabe's (1949:107) data from the severe winter of 1942-43. Hen weights in March continued to decline from February, whereas under average winter conditions the opposite trend prevailed.

The implications of progressive winter decline in body weights seem reasonably clear cut. Hanson (1962) has collated a large body of information on condition factors affecting Canada geese in response to seasonal stresses, and has emphasized that fat deposits cannot be metabolized during periods of food shortage without concomitant breakdown in proteins. The importance of winter weight loss thus transcends simple degradation of depot fat and loss of stored energy, involving simultaneous depletion of protein reserves vital to reproduction and survival. In the present study, the physical condition of the hen at winter's end obviously varied from year to year depending on weather conditions affecting food availability and energy demands of the preceding winter. In 1959 and 1962, it was clear that body reserves had been seriously depleted by winter's end, and that breakup occurred too late for significant weight recovery before early April. Other winters were characterized by lesser weight loss and/or earlier disappearance of snow cover, both of which must have facilitated earlier build-up in fitness prior to egg-laying. It seems logical to believe that hens in 1959 and 1962 were delayed in reaching peak spring weights, or else began egg-laying at lower weight levels than was true of other seasons. Unfortunately, we do not have adequate information on spring weights to document either of these inferences, but circumstantial evidence pervading this entire study pointed to a connection between undernutrition at winter's end and delayed reproduction, lower reproductive success, and higher rates of hen mortality from spring to fall. Such matters are previewed at this point only to emphasize that winter-spring condition of nesting hens appeared to be a highly relevant factor in the dynamics of the population we studied.

WINTER MORTALITY

Contents of this section are primarily concerned with habitat use in relation to winter loss. Major mortality factors affecting winter populations in decreasing order of importance were predation, highway traffic, and winter storms. Only the latter, in addition to winter starvation are discussed here.

Influence of Wetland Availability on Winter Welfare

Over a 3-winter period (1961-62, 1962-63, and 1963-64), simultaneous early and late winter censuses were conducted on the Alto and Mackford winter study areas to determine whether mortality differed with use of wetlands as winter cover. Twenty percent of the Alto area consisted of wetlands, and only 7 percent of the population occupied nonwetland winter cover as a 3-year mean. The Mackford Area included less than 5 percent wetlands, and 36 percent of its wintering birds depended on nonwetland types. March censuses on both areas averaged 26 percent lower than January counts (Table 23), suggesting that mortality did not differ between the two.

No difference was detected in winter weights between study areas, nor between winter flocks trapped in wetland versus nonwetland winter cover throughout the area of winter trapping. Although wetlands obviously were much preferred as winter cover, and presumably contributed to population welfare, we have no quantitative data actually demonstrating that birds relying on alternative cover survived less well or suffered greater winter stress as judged by trends in winter weight.

Starvation

No instances of starvation were documented in this study, nor did an appreciable fraction of the weights we recorded near the threshold where starvation seemed imminent. In food deprivation experiments with captive birds, weights at starvation have been reported at 600 to 850 grams for cocks and 400 to 600 grams for hens, roughly 50 percent of normal (Errington 1939; Gerstell 1942: 31-39; and Tester and Olson 1959). Weights of starved pheasants in the wild reported by Nelson and Janson (1949) averaged 595 grams among cocks and 540 grams among hens. The lightest hen we examined weighed 653 grams and the lightest cock 995 grams. Even in winters of most serious weight reduction, 1958-59 and 1961-62, the percentage of hens that weighed less than 800 grams was only 19 and 6, respectively, and the percentage of cocks that weighed less than 1,200 grams was only 12 and 16. Under

TABLE 23. Rates of Winter Pheasant Mortality Compared between Study Areas of Contrasting Wetland Availability as Winter Cover*

Winter	Study Area	January Census	March Census	Percent Difference
1961-62	Alto	708	475	33
	Mackford	181	115	36
1962-63	Alto	400	324	19
	Mackford	175	128	27
1963-64	Alto	377	294	22
	Mackford	172	147	15
Totals	Alto	1,485	1,093	26
	Mackford	528	390	26

*Mackford Study Area with less than 5 percent of the land area in wetland cover; Alto Study Area with 20 percent. Census figures based on both cocks and hens combined.

conditions of the present study, food shortage was more significant through loss of body condition than as an outright cause of death.

Storm Mortality

Direct loss to winter storms was observed only in 1958-59 and 1961-62. The severest winter storm of the study occurred during a 36-hour period on March 5 and 6, 1959. Light snow began falling on the morning of the 5th. Wind velocities reached 25 to 30 mph by mid-afternoon with gusts up to 40 mph. Blizzard-like conditions prevailed all night of the 5th and during daylight hours of the 6th, finally subsiding after nightfall. Winds were initially out of the northeast, but gradually shifted to northwest as the storm center passed. Temperatures during the period were between 20 and 25 F. New snowfall was estimated at 8 to 10 inches, but drifts were piled up to 15 feet in many locations.

Access to the study area was impossible until the afternoon of the 8th. On this and the succeeding 3 days, 12 storm-killed pheasants were discovered, all hens. Two were discovered approximately 50 yards from a manure stack where they had apparently been snowed-in after taking temporary refuge in a tractor rut. Six others were found on the edge of a drifted-over shrub stand. The final four were dug out of a plum thicket. In the absence of prestorm census data, the exact magnitude of mortality was unknown; however, we estimated that 5 percent of the prestorm population may have perished as the direct result of heavy wind and snow. All intact carcasses were in reasonably good flesh, death apparently being caused by suffocation or by freezing and exposure. Losses unquestionably would have been considerably higher had not a prolonged period of deep snow already concentrated birds in the best available winter cover.

The only other documented storm loss occurred in 1962. On January 8 and 9, winds up to 30 mph caused tremendous drifting of new-fallen snow, during which temperatures dropped to -10 F. Numerous birds were observed during the 2-day period with compacted snow on the lower back and under the wings. Two hens were so badly incapacitated that flight was impossible, but rapidly recovered after several hours in a heated basement. After subsidence of the storm on January 11, several flocks were revisited which by chance had been censused immediately prior to the storm, all of which were situated in nonwetland cover where exposure to wind was maximum. Out of 69 birds in 4 groups, only 3 were missing and presumed to have succumbed. On the same day, 148 additional birds in upland cover were checked for evidence of icing. At least 14 carried various amounts of compacted snow, but none seemed to be seriously hampered. As far as known, pheasants in wetland cover, shielded from direct force of the wind, were unaffected by icing. Only 4 storm kills were actually found after this storm, but farmers reported numerous other mortalities that we were unable or did not attempt to verify. Again, the overall magnitude of the loss was unknown, but our subjective judgement was that less than 5 percent of winter population was killed. Because birds were already concentrated in emergency cover, losses probably were substantially lower than might otherwise have been experienced.

On the whole, direct mortality from winter storms appears to be unusual in Wisconsin, doubtless the result of less intense wind storms and large wetland acreages that provide relative security from such exposure. Farther west, such losses occur with much greater regularity and commonly with catastrophic effects. In South Dakota, Kimball (1948) concluded that heavy storm loss could be expected 1 year out of 6, losses as high as 90 percent having been locally recorded in that state (Kimball et al. 1956:211). Severe loss to winter storms has also been reported in Iowa (Green 1938; Scott and Baskett 1941), Minnesota (Erickson et al. 1951:33-34), North Dakota (Miller 1948), Nebraska (Mohler 1959:35-39), and Colorado (Lyon 1959).

SUMMARY

Daily movement between food and cover typically covered 1/4 mile or less, 1/2 mile apparently being the upper limit of the daily cruising radius in winter. Interchange between winter cover was common only in severe winters when flocks in satellite wintering areas were forced to break up and regroup at traditional concentration sites. Distribution of winter cover seemed to have a more important bearing on the distribution of the winter population than availability of winter food, birds concentrated in traditional winter cover typically making out as best they could on food resources within limits of daily travel.

Over a 7-winter period, 78 to 88 percent of the winter population was associated with wetland cover. Among the various wetland types, shrub-carr was most preferred as loafing cover, and as snow depth increased provided the major source of both roosting and loafing cover. Cattail and herbaceous cover ranked behind shurb-carr, but ahead of sedge-meadow and canary grass, in all-round importance as winter cover. Nonwetland cover used by wintering birds consisted predominantly of woodlots, ditchbanks, retired cropland, and farm shelterbelts. Grassy or herbaceous vegetation was preferred for roosting and woody cover with overhead canopy for loafing.

Nutritional walfare of winter birds depended almost exclusively on cultivated grains. In four out of seven winters, waste grains were unavailable for prolonged periods due to heavy snow. Shortage of winter food was associated with significant weight decline in 1958-59 and 1961-62. Among the hen segment of the population, body condition at winter's end varied significantly from year to year depending on food availability and energy demands of the preceding winter. Late-winter variation in hen condition had an important bearing on subsequent rates of reproduction and survival.

Rates of winter mortality and trends in body weight were comparable on two study areas showing contrasting percentages of the winter population dependent on nonwetland cover. No instances of outright starvation were discovered, not did winter weights fall to levels where starvation seemed imminent. Direct mortality to winter storms was observed only in 1958-59 and 1961-62, but probably affected no more than 5 percent of the winter population in either instance.

WINTER-TO-SPRING MOVEMENT

PHENOLOGY OF SPRING DISPERSAL

Onset of spring dispersal differed notably with sex and age (Table 24). Among cocks, the average distance of dispersal from the origin of movement tended to stabilize after mid-April, but among hens the mean showed progressive increase through the month of May. In a phenologically "normal" year, cocks tended to disperse from wintering areas and establish breeding territories in late March or early April, whereas hens typically waited until mid-April before vacating winter cover. The major period of hen dispersal usually extended from mid-April to early May. Young hens, on the average, departed after the adults.

Earlier spring dispersal by cocks was also reported by Weston (1954) in Iowa and by Shick (1952:28) in Michigan. Doubtless the fact that cocks come into breeding condition ahead of hens (Hiatt and Fisher 1947; Taber 1949) is the basic reason for this difference. Observations in the present study clearly suggested that cocks were physiologically and psychologically primed for reproduction by mid-March, but that final exodus from winter cover and establishment of territories was triggered by winter breakup. First evidence of territorial behavior and widespread cock crowing coincided each spring with final disappearance of snow cover, even though this event occurred as early as March 15-20 in 1961 and as late as April 1-10 in 1959. Spring dispersal of cocks thus showed as much as 3 weeks' annual variation.

To determine whether hen dispersal also differed phenologically between years, the mean distance of travel from the origin of movement (both age groups combined) was graphed each year by semi-monthly periods. The 1961 curve leveled off after April 15; the 1960 and 1963 curves after May 1; and the 1962, 1964, and 1965 curves after May 15. In contrast to cocks, the time of winter breakup appeared to be of comparatively minor consequence in regulating the spring move of hens.

These dates will be regarded as terminal dates of hen dispersal, with ultimate distances of winter-to-spring travel based only on movement records obtained subsequent thereto. Among cocks, April 10 each year will be regarded as the terminal date of the spring move.

TABLE 24. Phenology of Winter-to-Spring Movement Based on Mean Distances of Dispersal from Winter Capture or Observation Sites, Waupun Study Area and Vicinity, 1960-65*

Period of Observation or Recovery	Distance in Miles from Site of Winter Capture						Mean and Standard Error**
	0–1	1–2	2–3	3–4	4–5	Total	
Juvenile cocks							
April 1–15	55	7	0	0	0	62	0.53 ± 0.06
April 16–30	87	17	0	0	0	104	0.50 ± 0.04
May 1–15	70	20	2	0	0	92	0.63 ± 0.06
May 16–31	22	12	0	0	0	34	0.65 ± 0.09
June 1–Sept. 30	29	17	2	1	0	49	0.64 ± 0.08
Juvenile hens							
April 1–15	190	26	5	1	1	223	0.53 ± 0.04
April 16–30	243	65	10	5	0	323	0.64 ± 0.04
May 1–15	192	74	22	10	0	298	0.89 ± 0.05
May 16–31	78	42	16	9	2	147	1.21 ± 0.08
June 1–Sept. 30	90	32	28	8	4	162	1.28 ± 0.07
Adult cocks							
April 1–15	15	1	0	0	0	16	0.39 ± 0.10
April 16–30	21	2	0	0	0	23	0.41 ± 0.09
May 1–15	27	3	0	0	0	30	0.47 ± 0.09
May 16–31	9	2	0	0	0	11	0.42 ± 0.20
June 1–Sept. 30	23	3	0	0	0	26	0.45 ± 0.09
Adult hens							
April 1–15	116	12	1	0	0	129	0.38 ± 0.04
April 16–30	150	18	8	4	0	180	0.59 ± 0.05
May 1–15	102	30	5	2	0	139	0.73 ± 0.06
May 16–31	44	17	5	1	0	67	0.81 ± 0.09
June 1–Sept. 30	82	16	4	4	0	106	0.78 ± 0.08

*Based on spring and summer location of marked birds plotted in relation to observation or capture sites of the preceding winter. Individuals located in more than one period appear in the tabulation more than once, as do individuals located twice or more in the same period.

**Means and standard errors originally calculated from movement distances measured to nearest 1/4 mile.

MOVEMENT BY AGE AND SEX CLASS

As with fall and winter movement, distance of spring dispersal also varied with sex and age, hens being more mobile than cocks and juveniles more mobile than adults (Table 25). Spring dispersal was somewhat less extensive than the corresponding move to winter cover, suggesting that autumn and early winter was the more important period of population shuffle. This applied particularly to the juvenile component of the population, where 58 percent of the moves between fall and winter exceeded 1 mile in distance (Table 17), compared with 49 percent between winter and spring (Table 25).

TABLE 25. Age and Sex Variation in Distance of Spring Dispersal from Winter Cover, Waupun Study Area and Vicinity, 1960-65

Age and Sex Class	Distance of Dispersal in Miles* 0–1	1–2	2–3	3–4	4–5	Total	Mean and Standard Error**
Juvenile cocks	62	10	4	1	0	77	0.67 ± 0.08
Juvenile hens	193	154	52	23	6	428	1.31 ± 0.04
Adult cocks	16	2	0	0	0	18	0.42 ± 0.09
Adult hens	156	52	4	3	1	216	0.75 ± 0.04

*No individual appears in the tabulation more than once. Based on dispersal distances measured between winter and spring-to-summer locations.

**Means and standard errors originally calculated from movement distances measured to nearest 1/4 mile. Mean distances of travel between age and sex groups highly significant by analysis of variance in presence of heterogeneity (Snedecor 1956:287-289) (F' with 3 and 81 df = 43.94; reference value at 0.005 = 5.79).

Comparative Explosiveness of Spring Dispersal

Twenty-one marked cocks, including 5 adults and 16 juveniles, furnished a total of 87 movement records during the major period of dispersal from winter cover (the first half of April). None of these birds were identified other than where they wintered or where they ultimately established territories and bred, suggesting that spring dispersal was a comparatively explosive phenomenon rather than a leisurely move between winter and summer range. In like fashion, 43 observations of 19 adult hens between mid-April and mid-May also were confined to the immediate vicinity of the wintering area or to where these birds eventually nested or were found with broods. Some of these individuals dispersed up to 4 miles from winter cover, the absence of intermediate records again suggesting that spring movement was rapidly completed once begun.

By comparison, certain juvenile hens exhibited less oriented spring dispersal. Among 47 individuals observed between mid-April and mid-May, 9 were identified at one or more sites in addition to the vicinity in which they ultimately bred. A good example of such behavior was *Yellow 6X*. This bird, trapped as a juvenile in February of 1963, was last seen in the vicinity of winter cover on April 6. By May 3 she had traveled 0.8 mile southwest, then 0.3 mile northwest, 1.1 mile northeast, and 0.6 mile east, finally nesting about 0.8 mile from where dispersal originated. Three other juveniles were observed in spring in two widely separated localities before finally nesting in a third. Such examples, though few in number, seemed to imply that spring dispersal of young hens was a relatively unoriented process compared with adults. As shown later, adults almost invariably returned in spring to where they formerly bred. Spring dispersal by this group apparently was a goal-oriented move analogous to the migrational homing (Hickey 1943:38-41) of migratory species. Without previous breeding experience, young hens obviously lacked comparable ties to specific breeding areas, and perhaps in certain instances made one or more tentative selections before finally settling down.

Why the same phenomenon was not observed among juvenile cocks was obscure. One possibility is that reproductive behavior in cocks was so far advanced by winter breakup that spring dispersal and establishment of territories was consummated with greater urgency than was the spring move of young hens.

Generalized Movement Patterns

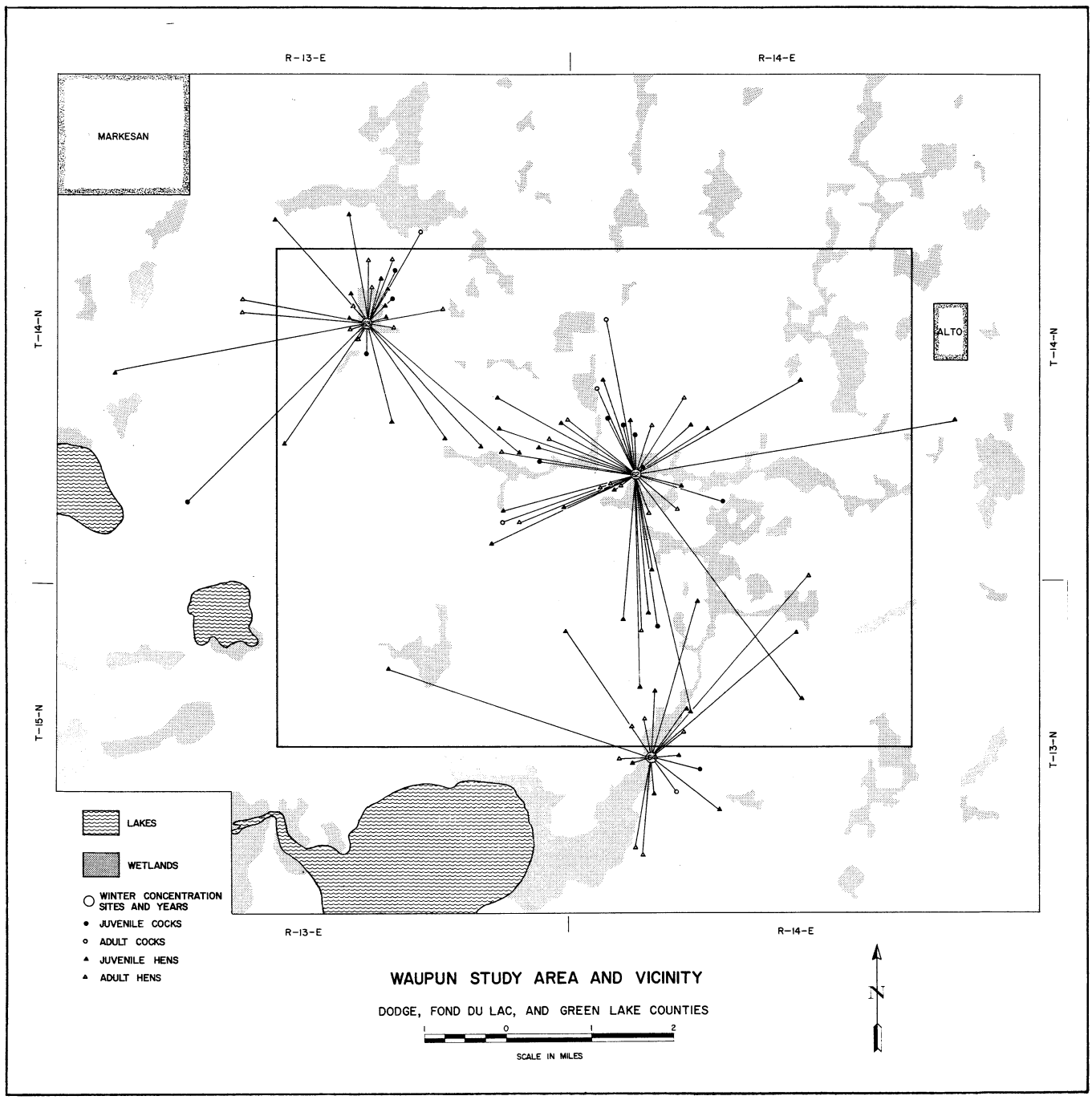
Spring movement of adult cocks averaged 0.42 mile (Table 25). The longest recorded move was 1.8 miles, and 89 percent of all movement records were 1 mile or less.

Home-range locations of 8 marked cocks were known during 2 consecutive breeding seasons, as were those of 2 cocks 3 years in succession. In all instances, the center of all available spring and summer observations from one year to the next was less than 1/2 mile apart, the average being 0.23 mile (Table 26). Six cocks that also provided information on the intervening move to winter cover returned in spring from wintering areas between 0.2 and 0.3 mile distant.

From these and other data it was clear that cock pheasants remained faithful throughout their adult lives to the area in which they first bred. The clearest example of such behavior was *Gray 16I*. This bird was trapped as a juvenile in February 1963 and later established a territory about 3 miles from the point of capture. Subsequent observations produced a virtually complete inventory of this bird's seasonal movements through the autumn of 1965. Not one of 34 records over this 2 1/2-year period fell outside the observed range of travel during the 1963 breeding season. Winter cover relied upon consisted solely of fencelines and ditchbanks, even though two tracts of obviously superior winter cover were available less than 1 mile distant.

Not all cocks demonstrated equally restricted movement outside the breeding season; however, it was clear that the location of the breeding area

a



WAUPUN STUDY AREA AND VICINITY

DODGE, FOND DU LAC, AND GREEN LAKE COUNTIES

exerted a dominant influence on the movement of cock pheasants after the first spring of life. In general, it could be said that male birds occupied the same home range year-round or moved the least necessary distance to winter cover.

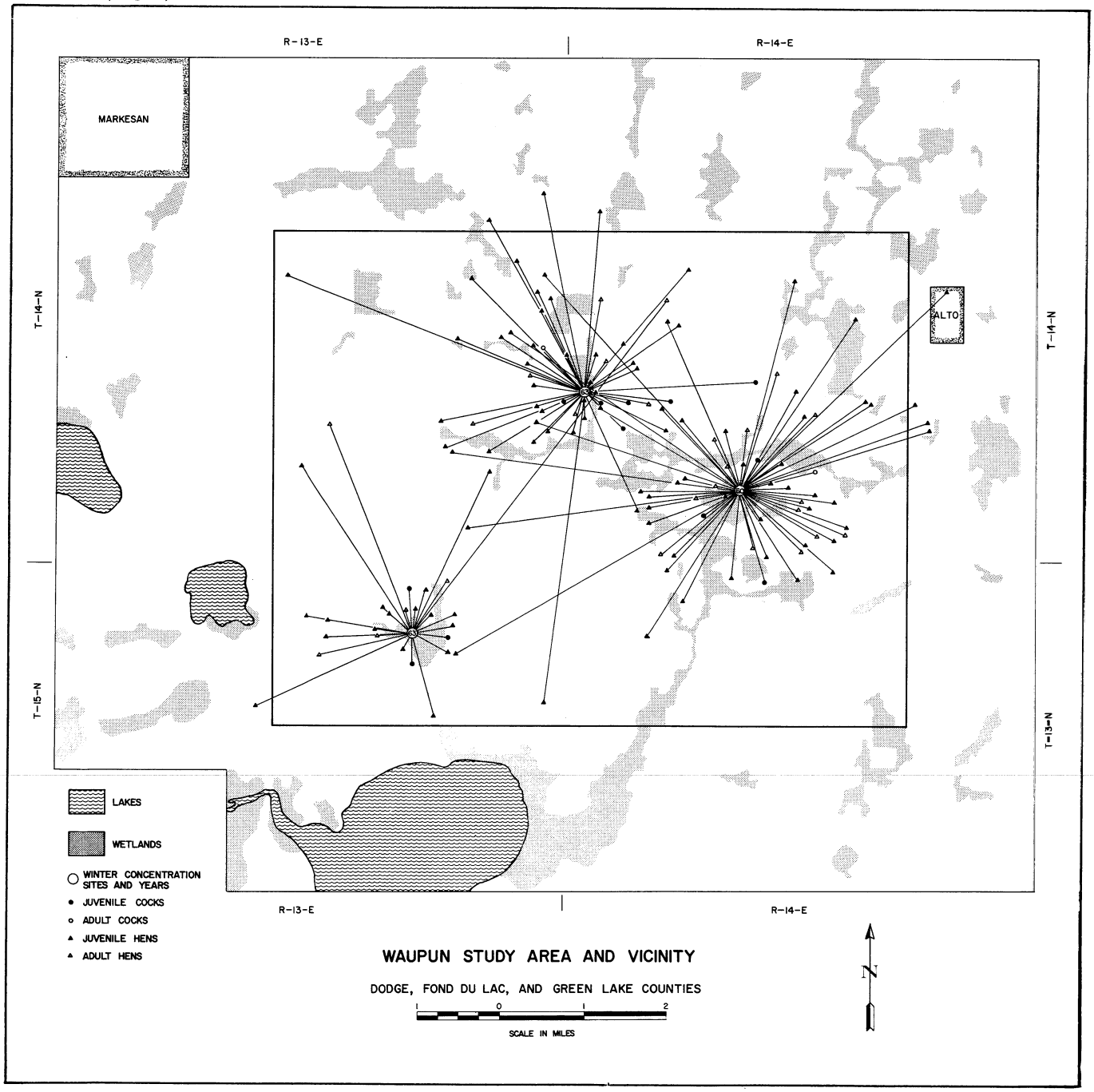
Spring dispersal of young cocks averaged 0.67 mile, with the longest recorded move 3.4 miles. Eighty percent of all winter-to-spring moves measured 1 mile or less (Table 25).

Although sample sizes were inadequate for statistical evaluation, spring dispersal of young cocks did not appear to be directionally oriented. Egress from individual wintering areas, based on individual years (Fig. 15), as well as all years of study combined, failed to suggest any departure from random scatter.

To determine whether young cocks tended to return in spring to the vicinity of their birthplaces, spring and summer observations were plotted in relation to capture sites of the preceding autumn. It was assumed that any bird whose breeding season locations centered within 1/2 mile of the fall capture site must have occupied a home range which overlapped in part, or at any rate was not far removed from, the area in which it had been

FIGURE 15. *Spring dispersal from selected tracts of traditional winter cover. Heavy line designates boundary of Waupun Study Area. (a) Examples illustrated are wintering areas 14, 20, and 30 (Fig. 8). (b) Examples illustrated are wintering areas 11, 22, and 25 (Fig. 8).*

b



hatched and reared. While this distance was somewhat arbitrary, it seemed a reasonable criterion based on knowledge of home-range size in breeding birds and provided an objective basis for comparing rates of return from one year to the next and from one sex and age group to another.

For all years of study combined, 53 percent of the young cocks bred within 1/2 mile of where they were captured the preceding autumn as young of the year (Table 26). The true test of homing, however, was whether this percentage exceeded the expected rate of return assuming random dispersal. To approximate such a value, we began with a point representing the fall capture site, i.e., the supposed origin of fall-to-winter movement. From this point two concentric circles were drawn. The radius of the first was 1/2 mile and the second was scaled to the average distance of fall-to-winter movement—1.05 miles in the case of juvenile cocks (Table 17). From a random point on the second, tangents were drawn to the first, the angle between the two (58 degrees) equaling 16 percent of 360 degrees. This percentage was regarded as the probability that the average juvenile cock would have headed in direction of the

natal area assuming random spring dispersal. (In reality, of course, the true rate of return expected would have been substantially lower than 16 percent, since no allowance was made for the requisite distance rather than direction of travel.) The 53 percent observed rate of return clearly implied that the direction of spring dispersal by young cocks was not independent of their birthplace. A significant fraction of juvenile cocks did in fact appear to return to the natal vicinity to breed.

Eight out of 16 young cocks returned from winter cover up to 1 mile from the fall capture site, while only 4 out of 11 returned from more distant winter locations. Young hens showed this trend even move conclusively from which it was clear that juvenile homing tended to be inverse to the distance of travel required. In general, this seemed to argue against the ability of young birds to "navigate" homeward, suggesting instead that homing was accomplished by means of direct search or by chance encounter with familiar terrain providing the necessary orientation to home.

At least one other factor also played a role in spring dispersal of cocks. A strong preference was shown for home ranges and/or breeding territories which included some form of wetland cover (r = 0.92, significant at 1% level). Figure 16 suggests that the percentage of cocks established in these areas was inverse to population density. While the observed range of population fluctuation was not large, if one excludes 1961, the clear implication was that higher spring densities tended to force a progressively larger fraction of the cock population onto less favored upland sites for territorial establishment. Because of the heavy preponderance of juveniles in the population, the phenomenon obviously depended on the behavior and habitat selection of young cocks. Adult cocks demonstrated such profound homing tendencies that presumably they would have been little if at all deterred by population pressures.

In summary, we conclude that winter-to-spring dispersal of juvenile cocks was jointly regulated by homing and by intraspecific competition through preferential selection of wetland habitat for territorial establishment.

Spring dispersal of adult hens averaged 0.75 mile, 72 percent of all dispersal records measuring 1 mile or less (Table 25). The longest recorded move by an adult hen between winter and summer range was 4.9 miles.

Spring dispersal of adult hens almost exclusively represented return to specific nesting areas. Out of 208 hens whose summer locations were compared from one year to the next, only 15 percent occupied different breeding areas according to our earlier criterion (Table 26). Out of 18 hens that provided comparable information 3 breeding seasons in succession, only 2 showed an evident shift in home range location. The year-to-year location of one hen, *Coral X4,* was especially well known to us over a 4-year span. Single nests belonging to

FIGURE 16. *Relationship between population density and the distribution of crowing cocks with respect to wetland edge, Waupun Study Area, 1959-1966. Correlation significant at 1 percent level (reference value with 6 df = 0.83).*

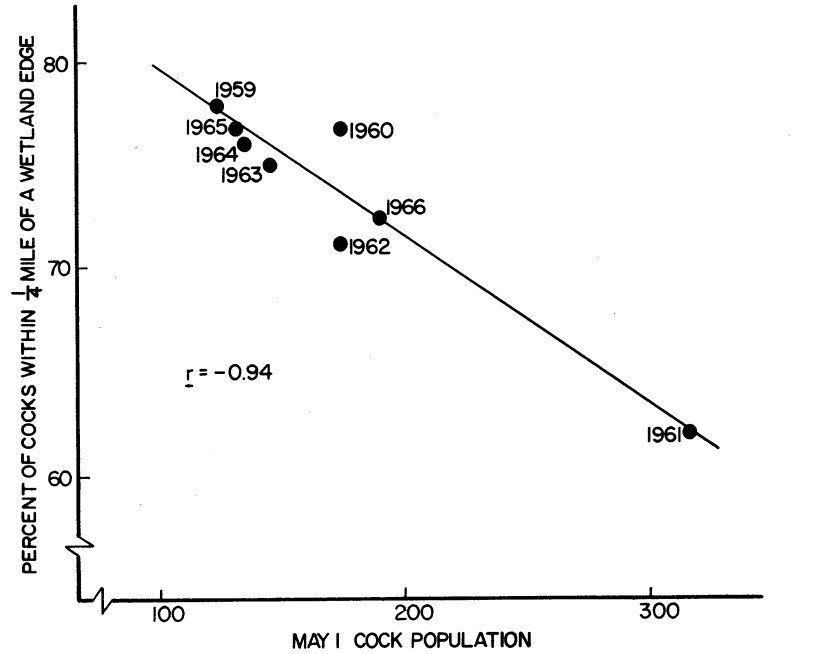
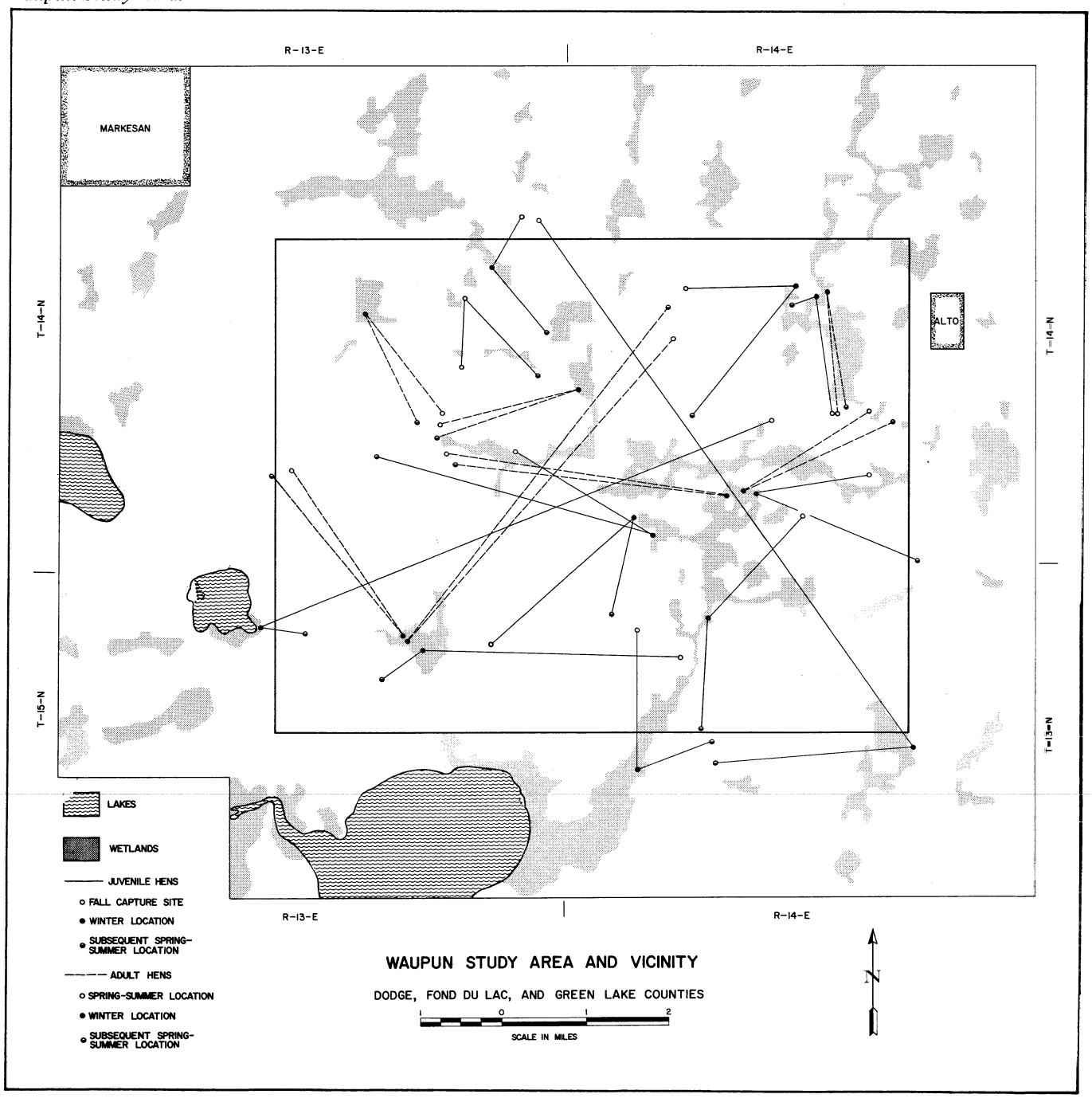


TABLE 26. Ultimate Destination of Spring Dispersal Related to the Birthplace of Juveniles or the Breeding Area of Adults in Preceding Years, Waupun Study Area and Vicinity, 1960-65*

Age and Sex Class	Total	Mean and Standard Error	Percent Returning Within 0.5 Mile
Juvenile cocks	32	0.68 ± 0.10	53
Juvenile hens	152	1.43 ± 0.11	26
Adult cocks	10	0.23 ± 0.05	100
Adult hens	208	0.33 ± 0.02	85

*Based on the location of juvenile birds in their first breeding season related to fall capture sites of the preceding autumn. Adult information based on locations in successive breeding seasons only.

FIGURE 17. *Selected examples of the return of juvenile hens to the vicinity of their birthplaces and the return of adult hens to where they previously bred, 1960-1965. Heavy line designates boundary of Waupun Study Area.*



this bird were found in 1960 and 1962, and two nests were discovered in 1963. All four were situated within a 300-yard radius. No nests belonging to *Coral X4* were found in 1961, but four visual observations confirmed her presence in the vicinity during the 1961 breeding season. Information of this sort led us to conclude that nesting hens typically returned each year to the same home range at the start of reproduction.

The distance of the return move from winter cover was known for 136 hens, examples of which are shown in Figure 17. In contrast to juveniles, adult homing appeared to be unrelated to the distance of travel required. Ninety-two percent of all adults returned in spring from winter cover less than 1 mile distant, compared with 88 percent return from wintering areas up to 5 miles removed. Based on the high overall rate of return (Table 26), and the comparatively long distances over which certain of these moves were made (Fig. 17), spring dispersal of adult hens obviously represented highly oriented movement to familiar terrain. At least in general terms, the spring move of adults appeared to be an example of purposive or appetitive behavior (Tinbergen 1951:104-107) for a specific nesting area.

That adult homing did not vary with the distance of travel required

suggested that something other than exploration or random search must have been relied upon. Whether guided by some sort of navigational sense or by memory alone, the facility for homing—or perhaps the motivation to return—obviously intensified after a hen had nested in an area. Higher rates of adult homing as compared with juvenile return have also been reported in numerous migratory species, for example song sparrows (Nice 1937:185), robins (Farner 1945) and several species of surface-feeding ducks (Sowls 1955:37).

Many hens also returned each year to the same winter cover, with certain individuals in the population occupying more-or-less discrete winter and summer range between which they traveled considerable distances. Such behavior was best exemplified by *Yellow 64.* Captured as a young hen in the winter of 1962-63, this bird subsequently nested and reared a brood 3 1/2 miles from where she wintered. Observations through the spring of 1965 revealed that she regularly traveled between these two sites, having completed at least three round trips when last observed. Two other hens were known to alternate between winter and summer range 2.5 to 3.0 miles apart, as were numerous other birds over somewhat shorter distances. As a general rule, however, much greater fidelity was demonstrated for the nesting area than for winter cover. Rates of return to winter cover averaged only 51 percent, compared with 85 percent return from one breeding season to the next (Table 26). In addition, return to winter cover was inverse to distance of travel required, whereas return to breeding areas was not.

In an attempt to understand the homing failures of certain hens, movement records of nonreturnees were screened for possible clues to their unseemly behavior. Among 31 individuals whose spring and summer locations centered more than 1/2 mile apart, 9 covered distances as great as 1 mile (Table 26), indicating home-range shifts of considerable magnitude. One of these birds, *Gold B4,* nested and reared a brood in 1962 in 10 acres of temporarily abandoned cropland. In the spring of 1963, from winter cover 1.3 miles southwest, she returned to this site and was observed in the vicinity seven times between April 9 and May 13. Shortly thereafter the field was disced and plowed, and contact with *Gold B4* was lost. On June 20, however, she was recovered as a hay-mowing casualty with newly hatched chicks approximately 1.8 miles northeast. At least outwardly, it seemed that destruction of cover to which this bird had an obvious attachment caused her to abandon the site entirely and move to a different area. In like manner, shifts in home range by two other hens were also associated with destruction of cover in which these birds had been known to nest or rear broods. One instance was precipitated by burning of wetland cover, the other by wetland drainage.

Records of six other nonreturnees were inconclusive, but from available evidence it appeared that cover destruction, particularly cover relied upon for nesting, was an important factor evicting hens from areas in which they had previously bred. In summary, it could be said that pheasant hens returned each spring to the same vicinity as long as they survived and the areas themselves remained suitable for nesting. Although hens seemed to demonstrate equally firm attachment to the breeding area as cocks, hen movement outside the breeding season was more extensive, perhaps reflecting lesser hardiness of hens and correspondingly greater motivation to find favorable combinations of winter food and shelter.

Winter-to-spring movement of young hens averaged 1.31 miles. The longest recorded move was 4.7 miles, and 55 percent of all spring moves exceeded 1 mile in distance (Table 25).

The return of juvenile hens to the natal vicinity was first evaluated. The 26 percent observed rate of return (Table 26), though clearly exceeding random expectation, was the lowest observed among all sex and age groups, and indicated that homing was of comparatively minor importance in the juvenile hen segment of the population. Return of young hens was only half as high as young cocks, doubtless a function of the correspondingly greater distance of fall-to-winter travel by the former (Table 17).

Figure 15 suggested that juvenile hens scattered more-or-less at random in spring. This was tested by plotting all 1960-65 dispersal records originating from individual trap sites and by comparing the observed number per quadrant with theoretical values assuming nondirectional dispersal. Eight sites provided between 16 and 135 movement records, the bottom of the range being the minimum selected for analysis. In all but one test the resultant chi-square value was nonsignificant, the combined chi-square for all 8 sites also being nonsignificant (chi-square = 26.76; reference value with 24 df at 0.05 = 36.42). On these grounds, spring dispersal of young hens appeared to be directionally unoriented, in sharp contrast to fall-to-winter movement in which egress from fall capture sites was highly directional. Among the majority of juvenile hens, spring dispersal appeared to be independent of the natal area.

Other lines of evidence, based on distance rather than direction of travel, also confirmed this conclusion. When the distance of travel to winter cover was plotted against the subsequent distance of spring dispersal, results showed no evidence of a relationship among juvenile hens ($r = 0.01$ with 98 df), but a highly significant one among adults ($r = 0.97$; reference value with 134 df at 0.01 = 0.22). Obviously this stemmed from age-related differences in homing. Influence of adult leadership on juvenile movement appeared to be entirely absent in spring, suggesting that final breakdown in family organization must have occurred in winter or at any rate well before the spring move was completed.

The distance of juvenile dispersal was significantly related to the size of winter flocks from which movement originated. In general, the larger the number of hens concentrated at a given tract of winter cover, the greater the distance of juvenile egress. This suggested that dispersal of young hens was somehow influenced by intensity of population pressures in the vicinity of winter cover.

As a test of this hypothesis, winter census data were examined, and the size of winter flocks with a minimum of 10 juvenile dispersal records was classified according to the midwinder estimate of the total number of hens present. Twelve flocks were classified as small (35 to 100 hens), 6 as intermediate (101 to 200 hens), and 8 as large (201 to 300 hens). From the hen age ratio observed in winter trapping, estimates of the juvenile hen population at each site were obtained and averaged by size class. A frequency distribution was then constructed, by 1/2 mile intervals, of the combined juvenile dispersal records originating from each size class, which as a final step was applied to the juvenile population estimate to calcu-

late the average density of juvenile hens breeding within concentric radii of dispersal from the origin of movement.

Results suggested that young hens tended to reach rather uniform population densities in the immediate vicinity of winter cover (Table 27). Despite wide variation in the size of winter flocks, the density of young hens which remained to breed within 1/2 mile of winter cover averaged surprisingly constant at about 5 to 6 per 100 acres. Accordingly, it appeared that saturation densities tended to prevail around winter concentration sites, and that the larger the winter flock the greater the spillage of juvenile birds into outlying areas. In the vicinity of the largest concentration sites, saturation may well have extended considerably farther, the calculated density of young hens averaging 5.6 per 100 acres for the first 1/2 mile of dispersal and nearly as high—4.7 per 100 acres—for the next 1/2 mile. Although evidence was not conclusive, it did in fact suggest that population pressures were operating in the vicinity of winter cover which appeared to be a significant factor in juvenile movement.

In common with cocks, both old and young hens demonstrated preferential use of wetland cover after completing the spring move. Among juvenile hens, the percentage of marked individuals associated with wetland cover was inverse to the overall size of the spring hen population, suggesting that population pressures in the vicinity of these cover types also played a role in juvenile dispersal. Most wintering areas in this study consisted of some form of wetland cover (Table 16) and were adjacent to, or contiguous with, substantial acreages of wetland habitat highly attractive in the spring of the year (Fig. 8). Hence it appeared that population pressures in the vicinity of winter cover could ultimately be explained by preferential use of wetland areas as winter flocks disbanded and began filtering outward, which in summary we conclude was the key factor influencing the spring movement of young hens and their eventual distribution over the summer range.

Actual mechanisms through which population pressures were brought to bear were not clearly understood. We suspect, however, that social interaction in the harem probably played a prominent role. Overt antagonism and intimidation display have been frequently reported between hens in harems (Dustman 1949:66-67; Taber 1949; Ball 1950; and Collias and Taber 1951) and were also evident from the casual observations of harem behavior undertaken in the present study. Collias and Taber (1951) showed that age is a factor facilitating dominance, and it is reasonable to suppose that aggressive encounters between hens were most often won by adults. Adults preceded young hens in spring dispersal were among the first to enter harems in spring, and succeeded better than juveniles in competing for space around wetland cover. As young birds dispersed from wintering areas, they must therefore have encountered older, more dominant individuals already established in preferred locations. The harem, by concentrating hens in space and time, doubtless led to intensified social interaction and seemed to be the most likely means through which young hens would have perceived and responded to population pressures.

Observation of marked birds around several large wintering areas were generally consistent with this interpretation. Between winter breakup and onset of hen dispersal, roughly the first half of April in a normal year, cocks stationed on wetland territories peripheral to winter cover often attracted large numbers of hens that had wintered nearby. On one occasion in early April, 24 hens were observed with a territorial cock, and counts of 10 to 15 hens with a single cock were not uncommon at this season in the vicinity of large hen flocks. Composition of these early spring groups appeared to be highly unstable, which may have represented the initial stages of harem formation. Among juvenile hens, movement records were available which showed frequent interchange from one territory to another, in some instances followed by dispersal and more regular appearance in territories farther removed from winter cover. Under the high hen densities which prevailed near large concentration sites, our definite impression was that many young birds were being buffeted from territory to territory through

TABLE 27. Relationship between the Size of Winter Flocks and the Calculated Postdispersal Population Density of Juvenile Hens Within Concentric Radii of Dispersal from Origin of Movement, Waupun Study Area, 1960-65

Distance in Miles of Spring Dispersal	Acreage Included Within This Range of Travel	Calculated Average Density of Juvenile Hens Per 100 Acres by Size of Winter Flocks from Which Dispersal Originated*		
		Small (35–100)	Intermediate (101–200)	Large (201–300)
0.0–0.5	502	5.1	5.7	5.6
0.5–1.0	1,503	0.9	2.3	4.7
1.0–1.5	2,513	0.3	0.8	1.8
1.5–2.0	3,518	0.1	0.3	0.7
2.0–2.5	4,524	0.1	0.2	0.3
2.5–3.0	5,529	–	0.1	0.1

*Size of Winter flocks based on adult and juvenile age classes combined.

harem interactions from which they ultimately escaped by egress into less crowded areas.

ANNUAL VARIATION IN SPRING DISPERSAL

Juvenile hens and cocks both showed significant yearly variation in distance of spring dispersal. Among adult hens, the degree of annual variation was nonsignificant, but generally parallel in trend (Table 28). Since the bulk of our data on spring dispersal originated with birds captured in winter traps, and since trapping was generally conducted at the same sites each winter, trends in Table 28 were believed to represent real annual differences in population mobility.

Except for adult cocks, all sex and age groups appeared to be unusually sedentary in 1961 and 1964, these particular springs also being characterized by above average return of juvenile hens to the natal vicinity. Winters preceding these springs were generally mild and near snowless, during which it was earlier concluded that unusually large numbers of young and old hens wintered locally instead of concentrating in traditional winter cover. Doubtless this facilitated higher rates of juvenile homing and also accounted for reduced mobility of adult hens in spring.

Despite the role that we have ascribed to population pressures in juvenile movement, distance of spring dispersal showed no consistent relationship with yearly trends in overall population size. Spring populations were highest in 1961, yet spring mobility of hens was less than normal. And in 1963, with spring populations at their lowest ebb, movement was near average. Actually, the major factor influencing the distance of dispersal appeared to be tightness of winter flocking. Wintering birds in 1960-61 were so loosely concentrated that comparatively little spring shuffle was required for the population to respace itself. In 1962-63, by contrast, virtually the entire population was concentrated at traditional winter cover, which necessitated more extensive redistribution in spring. Yearly variation in spring dispersal was therefore wholly consistent with the hypothesis that juvenile movement depended on the size of winter flocks and the intensity of population pressures in the vicinity of winter cover.

INFLUENCE OF TERRITORIAL COCKS ON THE DISTRIBUTION OF HENS

Because cocks were already established on breeding territories before the major exodus of hens from winter cover began, it was logical to inquire whether the spatial distribution of cocks influenced the spring dispersal of hens.

Spring sex ratios were subdivided into observations obtained within 1/4 mile of wetland cover and observations obtained beyond this distance. The number of hens per cock in the former was divided by the latter, giving a quantitative expression of the relative abundance of hens per cock in wetland versus upland habitats. Because sex ratios ran consistently higher to hens near wetlands, all values were greater than unity.

Correlation analyses did not reveal a

TABLE 28. Annual Variation in Distance of Spring Dispersal and Rates of Homing by Sex and Age Class, Waupun Study Area and Vicinity

Year	Juvenile Cocks*	Adult Cocks	Juvenile Hens**	Adult Hens
1960				
Avg. disp. dist.[1]	1.10 ± 0.23(17)[2]	0.25 ± 0.13(2)	1.69 ± 0.10(86)	0.75 ± 0.09(24)
Percent homing	No data	No data	No data	No data
1961				
Avg. disp. dist.	0.39 ± 0.08(12)	0.75 ± 0.62(2)	0.92 ± 0.12(38)	0.62 ± 0.08(35)
Percent homing	45 (9)	100 (2)	47 (15)	84 (32)
1962				
Avg. disp. dist.	0.63 ± 0.12(15)	0.53 ± 0.14(8)	1.45 ± 0.09(100)	0.90 ± 0.10(59)
Percent homing	50 (10)	100 (3)	21 (19)	76 (37)
1963				
Avg. disp. dist	0.68 ± 0.19(12)	0.21 ± 0.09(3)	1.46 ± 0.08(110)	0.80 ± 0.11(39)
Percent homing	40 (5)	100 (1)	20 (40)	89 (56)
1964				
Avg. disp. dist.	0.35 ± 0.08(9)	0.25 ± 0.13(2)	0.86 ± 0.12(42)	0.58 ± 0.10(35)
Percent homing	67 (6)	100 (2)	36 (53)	82 (49)
1965				
Avg. disp. dist.	0.65 ± 0.22(12)	0.38(1)	1.08 ± 0.08(52)	0.73 ± 0.16(24)
Percent homing	100 (2)	100 (2)	8 (25)	82 (34)

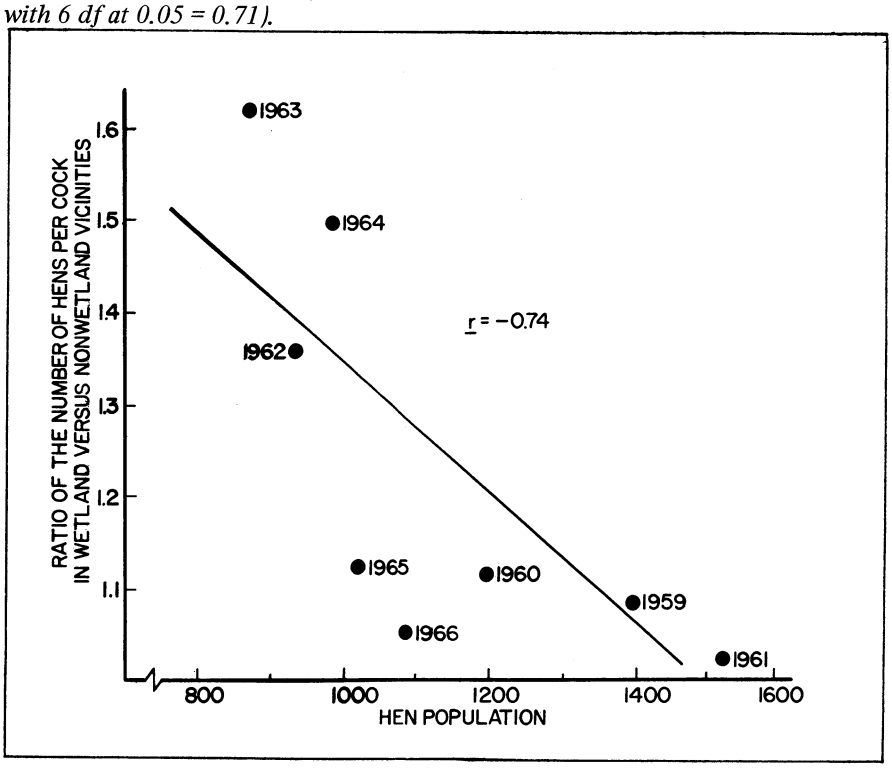
*Difference between years in distance of spring dispersal by juvenile cocks significant at 1 percent level by analysis of variance in presence of heterogeneity (Snedecor 1956:287-289) (F' with 5 and 32 df = 26.19; reference value at 0.01 = 3.66).

**Difference between years in distance of spring dispersal by juvenile hens significant at 1 percent level by analysis of variance in presence of heterogeneity (Snedecor 1956:287-289) (F' with 5 and 155 df = 7.71; reference value at 0.01 = 3.14).

[1]Miles

[2]Means and standard errors with sample size shown in parentheses.

FIGURE 18. *Relationship between the size of the spring hen population and homogeneity of observed sex ratios between wetland and nonwetland localities, Waupun Study Area, 1959-1966. Correlation significant at 5 percent level (reference value with 6 df at 0.05 = 0.71).*



significant linear relationship between these values and the size of the spring cock population (r = -0.15), but the correlation with hen density was significant (Fig. 18). As hen populations increased, sex ratios between wetland and upland habitats showed progressively greater homogeneity, whereas higher cock populations, associated with a density dependent increase in upland territories (Fig. 16), failed to elicit a corresponding change. Our conclusion from these tests was that increased numbers of cocks stationed on the uplands failed to attract proportionate numbers of hens, but that higher hen populations, by forcing more hens into less preferred upland areas, resulted in a more uniform sex ratio. Gross patterns of hen distribution thus appeared to be more critically related to their own population pressures than to the distribution of territorial cocks which were encountered during the spring move. Because juveniles were the more fluid component of the population, presumably this phenomenon depended principally on the behavior of young birds.

Actually, the relationship suggested by Figure 18 appeared to be curvilinear in trend, hence the influence of cock distribution on hen movement probably was nonuniform over the observed range of hen density. At low hen populations, with wetlands still unsaturated with hens, upland territories must have been largely unattractive regardless of their relative number. But as higher hen populations evoked progressively greater competition in wetland harems, hens apparently distributed themselves with progressively greater uniformity between available territories. Under higher hen densities in spring, the absolute number of hens moving onto the uplands may well have been determined in part by the number of upland territories that were present.

Obviously these conclusions should be regarded as provisional and subject to future revision. Tentatively, however, we conclude that the distribution of hens in spring, particularly young hens, is relatively independent of the distribution of cocks until their own population pressures in preferred locations progressively force them to distribute their numbers more-or-less uniformly between available territories.

AREAS OF SPREAD FROM TRADITIONAL WINTER COVER

Dispersal records from eight traditional wintering areas were sufficiently numerous to reveal the area of summer range to which wintering birds ultimately scattered. Areas of spread were delineated by connecting the outermost movement records originating from each site and by measuring the enclosed area.

On the average, pheasants wintering at these eight sites eventually dispersed to 10,800 acres of summer range, roughly 17 square miles. This was somewhat larger than the observed acreage of summer range from which these same sites attracted wintering birds, a consequence of the larger sample of spring dispersal data which gave a correspondingly larger number of more remote summer records. Based on 595 winter-to-spring moves, 87 percent of all birds at these sites moved to summer range within a 2-mile radius, the percentage averaging 96 among adult hens and 83 among juvenile hens. In general, fall-to-winter ingress was of similar magnitude, with 80 percent of the winter population at these sites immigrating from summer range within a 2-mile radius.

Under the particular distribution of winter cover to which these results applied, it seems reasonable to conclude that breeding populations within 2 miles of traditional winter cover would be significantly influenced by events in that area affecting pheasant survival during the period of winter concentration.

NATURE OF SEASONAL PHEASANT MOVEMENTS

All animal populations include some phase of the life cycle which is devoted to dispersal or spread of the species. Andrewartha and Birch (1954:86-125) have reviewed a large number of studies from which certain generalizations can be made: (1) that the tendency for dispersal is innate, although the instinct is more strongly developed in certain individuals than others; (2) that dispersal occurs at all ranges of population density and is not necessarily the outcome of overcrowding; and (3) that typically one of the immature stages is most active in

dispersive behavior.

Most extensive movement of pheasants occurred at two seasons of the year in the present study—coincident with the autumn move to winter cover and again in spring after breakup of winter flocks. Our objective at this point is to examine these seasonal movements in light of traditional concepts concerning animal dispersal and to gather together under one heading our final interpretation concerning their cause and function.

To begin with, adults could be characterized as a highly conservative element in the collective mobility of the population. For the most part, adult movement was confined between specific breeding areas and the nearest suitable winter cover. In the absence of habitat destruction, the seasonal movement of adult birds appeared to be highly constrained by the psychological bond that apparently existed for the area in which they first bred.

At both seasons of major population shuffle, mobility of young birds exceeded adults, and for reasons that were obscure, mobility of young hens also exceeded young cocks. Whatever the explanation, it was clear that juvenile hens were mainly responsible for long-range dispersal and would have been the most important element of the population colonizing new or vacant habitats. In most pheasant populations, pioneering instincts of such sort probably would be favored by natural selection and might contribute significantly to population maintenance. The inherent instability of most agricultural landscapes inevitably leads to favorable combinations of food and cover that arise by chance, persist for perhaps a few years, and then disappear. Exploitation of these temporary habitats, particularly for reproduction, would largely depend on young birds that lacked either the facility or the tradition to return to their birthplace to breed.

If indeed there was an innate tendency for dispersal in the population we studied, several lines of evidence suggested that it was most strongly developed in autumn. First of all, juvenile movement was more extensive at this season. Secondly, the relative frequency of unusually long-distance moves was higher in autumn. Finally, fall-to-winter movement appeared to be independent of population pressure, whereas this same factor played a key role in spring dispersal. Fall movement thus exhibited more of the characteristics of instinctive dispersal, perhaps in broad outline comparable to the "fall shuffle" alluded to in other galliforms, e.g., ruffed grouse (Chambers and Sharp 1958; Hale and Dorney 1963), bobwhite quail (Lehmann 1946; Murphy and Baskett 1952), and perhaps prairie chickens as well (Hamerstrom and Hamerstrom 1949).

While characteristics of long-range dispersal may be of critical importance in rates of population spread to vacant habitats and genetic transfer between areas, it is the movement of the average segment of the population which chiefly concerns the wildlife manager attempting to understand the habitat requirements and population regulation of a species.

Aside from a small segment of the juvenile age class, fall-to-winter movement in this study appeared to represent a forced seasonal shift to winter cover from summer range with inadequate winter shelter. The degree of population concentration in traditional wintering areas varied with presence of alternative cover and with weather conditions affecting food and cover availability. As a result, the distribution of the population showed important differences from year to year by winter's end. Population pressures were apparently nonexistent among wintering birds, or if they did exist, they were clearly ineffective in regulating the size or spacing of winter flocks.

It was the spring move through which the population annually respaced itself. Among adults, this was accomplished by return to specific breeding areas, and among juveniles through competition for space which developed in winter flocks as winter gregariousness was replaced by breeding intolerance. The average distance of spring dispersal was unrelated to overall population size, but depended instead on tightness of winter flocking which regulated the size of winter flocks and therefore the intensity of population pressures arising in spring in the vicinity of winter cover. As the pattern of winter distribution varied from year to year, so too the extent of spring dispersal.

It was also the spring move through which the population annually adjusted its numbers to the availability of preferred habitat. This was brought about by density dependent variation in the percentage of young cocks and hens successfully competing for space in wetland areas. As breeding populations increased, progressively more young birds were forced into less preferred upland habitats for breeding.

This phenomenon emerged as the clearest-cut example of density dependence affecting reproduction that we were able to identify in the population we studied, one that might conceivably have played a central role in the ultimate ceiling placed on population growth. We have found that the reproductive success of hens nesting on the uplands was consistently lower than those nesting in wetlands (Gates 1971), hence higher breeding populations were predisposed to lower productivity. From the standpoint of reproduction, wetland areas represented secure habitat niches into which lower populations tended to retreat and gain advantage of higher reproductive success. Conversely, higher populations tended to spill over into the less productive uplands and thereby experience increased environmental resistence to population growth.

COMPARISON WITH OTHER AREAS

Earlier studies in Wisconsin by Buss (1946:114) reported spring dispersal up to 2 miles from the University of Wisconsin Arboretum. From the nearby Fish Hatchery Marsh, Taber (1949) observed maximum spring movement up to 1 1/2 miles in radius. By comparison, our data show regular dispersal of pheasants up to 4 miles from winter cover (Table 25), from which it is clear that more extensive seasonal movement occurs in Wisconsin pheasants than has previously been recognized.

Elsewhere, Weston (1954) reported on spring egress from two large concentrations of wintering birds in northwest Iowa. The mean distance of dispersal by all sex and age groups combined was 1.4 miles from the Grass Lake Area in 1949-50 and 2.1 miles from the Birge Lake Area in 1949. The comparable mean observed by us was 1.1 miles, suggesting that Weston's population was considerably more mobile than ours. Also in Iowa, Grondahl (1953) reported on spring dispersal from what appears to have been scattered pockets of winter cover which sheltered comparatively small groups of wintering birds. Dispersal in this instance averaged 0.55 mile. Much

greater seasonal movement was inferred by Kimball (1949) in South Dakota from crowing counts which extended outward from winter cover. Results suggested that some birds traveled as far as 10 miles between river bottom winter cover and summer range more-or-less devoid of winter shelter.

Pheasant mobility at Waupun appeared to be somewhat less than in most areas where similar studies have been carried out. As earlier suggested, the relative abundance of wetland cover on our study area probably accounted for less extensive movement. If this is true, and we are correct that juveniel homing depends on the distance of fall-to-winter travel, then rates of juvenile homing observed by us may have been higher than might be expected in many other areas. How rates of adult homing might compare with other areas is obscure, though presumably it would exceed the juvenile rate in most other areas also.

Whether population pressures elsewhere influence spring distribution as we have inferred also is problematic. Weston (1954) has provided the only pertinent data known to us on this subject. Winter populations on the Birge Lake Area in 1948-50 varied from 120 to 240, yet subsequent spring populations varied only from 39 to 44. On the Grass Lake Area over the same period, winter numbers fluctuated between 170 and 522, but the number of birds remaining to breed showed maximum variation of only 72 to 92. The fact that these areas retained rather constant spring populations despite rather wide fluctuation in the number of wintering birds present suggests that some sort of density dependent phenomenon may have been limiting the number of breeding birds these areas were capable of accommodating. Whatever the mechanism, Weston's data were wholly consistent with ours, suggesting that population pressures may be of critical importance in the spatial distribution of breeding pheasants.

SUMMARY

Phenology of spring dispersal showed important differences with sex and age, cocks departing from winter cover ahead of hens and adult hens preceding the young. Distance of movement likewise varied; hens covered greater distances than cocks and juveniles greater distances than adults.

Spring dispersal of adults was interpreted as goal-oriented homing to specific breeding areas, both sexes returning to the area in which they first bred as long as they survived and the areas remained suitable for reproduction. Return of young birds to the vicinity of their birthplaces, though greater than random expectation, averaged significantly lower than adult homing-53 percent among juvenile cocks and 26 percent among juvenile hens.

Juvenile movement from winter to spring was importantly regulated by population pressures. All sex and age groups exhibited strong preferences for wetland cover, and higher spring populations were associated with density dependent increase in the percentage of young birds which bred on the less preferred uplands. Territorial intolerance between cocks and interaction between hens in harems were believed to be the most important mechanisms through which population pressures were exerted. Annual variation in spring mobility was unrelated to population size, but depended on tightness of winter flocking which regulated the size of winter flocks and the intensity of competition which arose in spring in the vicinity of winter cover. We concluded that the distribution of hens in spring, particularly young hens, was independent of the distribution of territorial cocks until population pressures in preferred locations encouraged more uniform spacing of hens between available territories.

Review of seasonal movements suggested that the innate tendency for dispersal was most strongly developed in autumn, especially among juvenile birds. Among the major segment of the population, however, fall movement was interpreted as a forced seasonal shift to winter cover. The ultimate distribution of the winter population was highly variable from year to year depending on weather conditions and availability of winter food and cover. Spring movement was interpreted as redistribution back to summer range, depending on winter patterns of population concentration and the degree of mobility required for the population to respace itself.

Because of lower reproductive success on the uplands, density dependent egress of hens from wetland habitats appeared to be an important mechanism predisposing higher spring populations to lower productivity. Such a phenomenon was believed to be one of the key mechanisms through which population growth might ultimately have been checked.

THE BREEDING POPULATION

MOVEMENT AND HOME–RANGE SIZE

Movement of Cocks

Ninety-two percent of all cock observations between May 1 and September 30 fell within ¼ mile of a central 40-acre unit (Fig. 19). Movement during the period was therefore largely confined to areas which averaged 9 "forties" or approximately 360 acres in size, about 0.56 square mile.

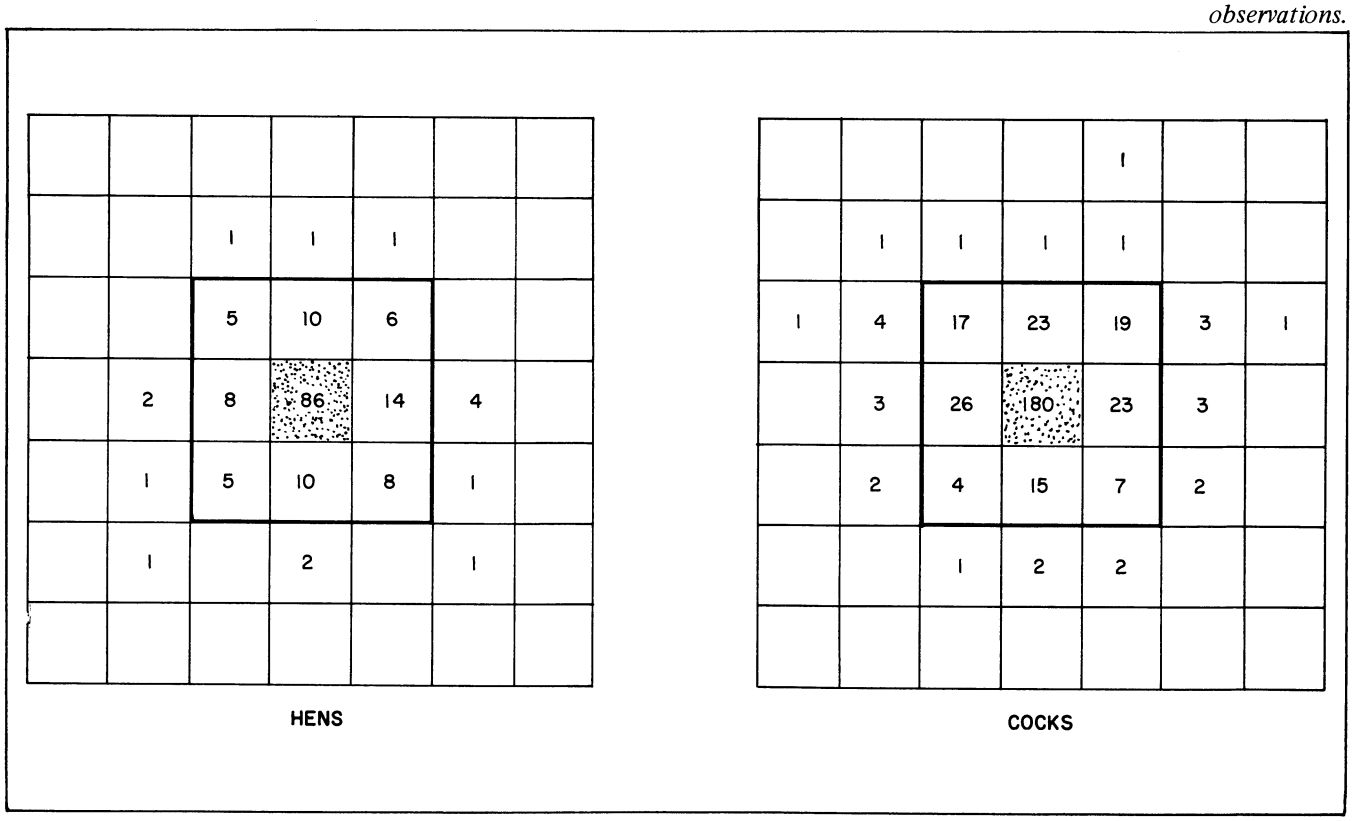
Nearly 87 percent of all cock observations in Figure 19 were obtained during the month of May. When separate analysis was repeated for this month, 94 percent of all observations were similarly arrayed, which suggested that a more or less stable pattern of home-range occupancy prevailed from May onward. Essentially the same conclusion was reached by comparing successive monthly distances of travel from the site of first observation recorded for the month of May (Table 29). No consistent increase in the mean of these distances was noted through the end of September, indicating little tendency for home-range expansion or relocation as the breeding season progressed.

From these results, movement of breeding males appeared to be typically confined to areas of about ½ square mile in size, essentially the same area being occupied between the end of spring dispersal and early autumn. Other authors have reported similar stability in spring and summer movement of cocks (Baskett 1947:8; Taber 1949).

Movement of Hens

Home-range size among hens differed little from that of cocks; 91 percent of all May to September moves fell within ¼ mile of a central 40-acre unit (Fig. 19). Information on hens was too limited for seasonal comparison of home-range behavior, but data in Table 29 suggested that some sort of expansion or perhaps a shift in home-range location occurred between the months of May and June. As a rule, May observations consisted of harem records, whereas June observations consisted of nest locations. Home-range adjustment thus seemed to coincide with next establishment and may have reflected a tendency by hens to disperse from the center of harem activity at the onset of egg-laying. As with cocks, the aggregate spring-summer mobility of hens was confined to tracts averaging about ½ square mile. This does not imply, of course, that all portions of areas this large were used with equal intensity throughout the breeding season. Doubtless certain parts received prefer-

FIGURE 19. *Composite patterns of home-range use from May 1 to September 30 based on observation of back-tagged pheasants, Waupun Study Area and vicinity, 1960-1965. Based on 343 observations of 45 cocks and 167 observations of 26 hens. Each square of the grid is equivalent to ¼ x ¼ mile, i.e., 40 acres. Stippled square represents that "forty" which included the largest number of spring and summer observations of individual birds. Area enclosed by heavy line includes 91 percent of all hen observations and 92 percent of all cock observations.*



entially heavier use at various stages of reproduction than others, with day-to-day travel almost certainly being restricted to substantially smaller acreages.

Most workers have concluded, or at least have implied, that the hen nests in the territory of the cock, or that the territory of the male is adjusted to include the nest site of the hen (Randall 1940; Leedy and Hicks 1945:65; Wight 1945:173; Baskett 1947:9; Kozlowa 1947; and Taber 1949). In the present study, cock home ranges were large and overlapping and territories were at best ill-defined. This made it impossible to associate a given nesting attempt with the territory of a specific cock. Notwithstanding, we have earlier suggested that the distribution of juvenile hens in spring, particularly at higher hen densities, was determined in part by the distribution of territorial cocks, and it is important to know whether the eventual distribution of nests might have been similarly affected. To explore this matter we plotted the nest sites of marked juveniles in relation to sites at which they had been previously observed in the harems of territorial males.

Out of 122 clutches of marked hens observed in this study, 10 belonged to juvenile birds which furnished 5 or more harem observations after completion of spring dispersal. Comparison between nest and harem locations was restricted to these 10 individuals.

Only 6 (10%) of 59 harem observations among this group occurred in the same "forty" in which the nest was located. Thirty harem observations (50%) fell more than ¼ mile from the nest site and 22 (37%) more than ½ mile. In only a single instance was the "forty" in which the nest was situated the same "forty" in which the majority of the harem observations were obtained. Eight out of 10 hens nested in "forties" in which they had not been previously observed during the prenesting period.

One's immediate impression from these observations was that nesting hens were purposefully avoiding the center of harem activity. A reasonably clear example of such behavior seemed to characterize *Yellow 7X.* As a juvenile bird in 1963, this hen was observed on 8 dates between April 2 and May 14 in the harems of two different cocks, one with a territory on wetland edge adjacent to the trap site and the other *(White 32)* in retired cropland 0.35 mile southeast. The nest of *Yellow 7X,* started on May 6, was concealed in roadside vegetation 0.41 mile from the activity center of the unmarked cock and 0.55 mile from the back-tagged cock. No previous observations of this bird were recorded in the nest-site vicinity. In like manner, *Red 5X,* a juvenile hen in 1964, was consistently observed between April 16 and May 14 in the harem of an unmarked cock. The earliest known nest of this bird, in which egg-laying began May 14, was situated 0.40 mile from the nearest harem observation.

More detailed information than we were able to obtain on a strictly incidental basis obviously would be required to clarify the relationship between the nest site and the center of harem affairs. Provisionally, however, it appeared that a minor reshuffle of hens may have coincided with nest initiation, motivated perhaps by search for suitable nesting cover and/or desire for seclusion from harem activities. Such behavior would not be inconsistent with the apparent adjustment in home-range location between May and June which was previously mentioned.

As far as available data go, they do not suggest a very precise relationship between the site chosen for nesting and the center of prenesting activity. If in fact there is genuine avoidance of the harem vicinity, then the relationship between the distribution of hens in spring and the ultimate distribution of nests might be a fairly loose one. It seems improbable, however, that the extent of movement would be great enough to invalidate our earlier conclusion that higher hen populations, through density dependent increase in use of nonwetland habitats, were subject to lower reproductive success because of greater reliance on upland cover for nesting.

Because little time could be spared from nest-searching activities by project personnel, movement studies were all but suspended during the nesting season. A previous paper on renesting behavior has already reported on the distance between successive nesting attempts of marked hens (Gates 1966c). Eleven such distances averaged 0.23 mile, ranging from 0.09 to 0.54 mile. From these data there was little reason to doubt that unsuccessful hens routinely remained in the same home range for renesting.

Only four posthatching observations were secured of marked hens whose nest locations were also known. One hen was found 0.30 mile from the nest site with a 12-week-old brood, a second was identified 0.52 mile from the nest 9 weeks after hatching, and a third was seen 0.10 mile from the nest when the young were 7 weeks of age. A fourth hen and her chicks were still within 100 yards of the nest site on the 11th day after hatching.

Records of marked hens with broods were also examined for instances in which a minimum of 5 prenesting observations were available. Among 11 such birds, all prenesting and brood records of 9 fell within a 2 x 2 area of four contiguous "forties." Observations of 2 others were contained within contiguous blocks of five and seven "forties."

Out of 89 records of brood movement obtained between July 15 and September 30, the distance between successive observations averaged 0.27 mile. Only five moves exceeded ½ mile in distance. The longest recorded move by a marked hen with a brood was 1.36 miles, undertaken when the

TABLE 29. Monthly Trend in Distance of Travel from the Site of First Observation Recorded for the Month of May, Waupun Study Area and Vicinity, 1960-65

Sex Class	Average Distance in Miles*				
	May	June	July	August	September
Hens	0.25 ± 0.02 (143)	0.37 ± 0.09 (36)	0.36 ± 0.08 (18)	0.31 ± 0.05 (34)	0.42 ± 0.10 (22)
Cocks	0.25 ± 0.02 (99)	0.25 ± 0.12 (6)	0.29 ± 0.08 (6)	0.24 ± 0.06 (11)	0.17 ± 0.13 (6)

*Means and standard errors with sample size shown in parentheses.

chicks were somewhere between the ages of 9 and 13 weeks. Aside from this single record, brood rearing appeared to be confined to rather restricted acreages coincident with, or at least overlapping, the home range occupied by the hen during prenesting and nesting activities.

In summary, home-range size of hens between the end of spring dispersal and early autumn averaged approximately ½ square mile. Although much is still to be learned of the details of daily movement, it would tentatively appear that habitat needs during reproduction could be successfully met on areas as large as a ¼ to ½ square mile without exceeding the normal range of travel during the nesting and brood rearing seasons.

BREEDING BEHAVIOR

Territorial Behavior of Cocks

Many authors have described the breeding behavior of cock pheasants. Agreement is general that the species is highly territorial, or at any rate that the cocks are highly combative, but opinion is divided on whether specific areas are the object of aggression and how rigidly territorial boundaries are defended. Leffingwell (1928:11-12) implied that cock pheasants established more-or-less fixed territories inside which crowing was confined, the purpose of crowing being to announce the cock's presence to potential mates and to competing territory holders. In Tadjikistan, Kozlowa (1947) spoke of strictly defined "cruising routes" traveled by cocks in which they fed and mated, and in which their mates nested and later spent the early stages of brood rearing. Other writers calling attention to the discreteness of the territory include Randall (1940), Sharp and McClure (1945:206), and Burger (1966).

Another group of authors has placed stronger emphasis on the plasticity of the defended area (Leedy and Hicks 1945:64; Taber 1949; Ball 1950; and Robertson 1958:34). Baskett (1947:8) concluded that "...there probably was a tendency toward the establishment of crowing areas or territories by the male pheasants, but that these territories were very plastic and subject to frequent readjustments..." As pointed out by Burger (1966), population density appears to be a critical variable in the apparent discreteness of the defended area. In the unusually dense population Burger studied, boundaries were so rigidly enforced by frequent conflict between cocks that territories could be mapped with relative ease.

Most previous studies have not adhered to precise definition of terms in discussing territorial and related behavior. Wight (1945) and Baskett (1947), along with most other workers, clearly synonomized the territory and the crowing area, but left unmentioned the possibility of daily travel outside this area. On the other hand, Taber's (1949) and Burger's (1966) remarks carry the clear implication that the defended area embraced the entire range of daily travel. To clarify subsequent discussion, we define the home range as that area encompassing the normal range of daily travel during the breeding season and the territory as the defended portion thereof. The crowing area is defined as that part of the home range occupied by the cock during periods of most intense crowing activity, viz., the early morning and evening twilight. It was this site at which the harem normally assembled and where display and courtship were most in evidence. On the whole, it could be said that the crowing area constituted the cock's mating station and represented that component of the home range around which daily activity centered at the height of breeding activity.

Under conditions of the present study, cock home ranges were large (Fig. 19) and overlapping, and daily movement was not confined to a defended area. In a purely technical sense, no portion of the home range actually qualified as a territory, since it did not appear that fixed units of space were being contested. Crowing areas came closest to such definition, but even where cock densities were highest, these seldom had a common boundary along which neighboring cocks routinely met in combat. Instead, fighting was most common on shared portions of home ranges, typically when one cock ventured upon another in following hens off the crowing area or in course of mid-day travel within the home range. From such behavior, it seemed that aggression must have been ultimately concerned with defense of "individual distance" (Conder 1949), or at best a moving zone of intolerance. Crowing not uncommonly occurred outside the crowing area. Advertisement of presence was not therefore restricted to a particular site, but shifted according to movement within the home range. Some marked cocks were observed crowing during off-peak hours up to ½ mile from their regular activity centers.

Our conclusion, then, was that cocks generally fought over infringement of individual distance rather than fixed or indefinite areas of space. The crowing area seemed less significant as an area of eminent domain than as a meeting place where the harem routinely gathered for display, courtship, and ultimately for mating. Although we have used the terms "territory" and "territorial behavior" in preceding pages, and will continue this usage hereafter, it should be emphasized that the real issue at stake appeared to be individual distance. Whether the outcome was basically different from that in which specific areas were the object of defense may have been a rather subtle distinction, but one which seemed clearly evident.

This interpretation may not be as seriously at odds with other investigators as appears at first glance. Most previous studies have been concerned with much higher cock densities than we observed. With increasing competition at higher population levels, it seems reasonable to suppose that movement of individual birds would become more closely restricted to the crowing area. Ultimately, the home range and the crowing area might coincide, at which point space itself might appear to be the object of aggression. Cock densities in the present study averaged only 0.7 per 100 acres. By comparison, authors such as Taber (1949) and Burger (1966), discussing territorial behavior in terms of more rigid defense, dealt with cock populations of 5.0 and 5.8 per 100 acres, respectively. Population differences of this magnitude would doubtless have a profound influence on aggressive tendencies and extent of uncontested movement, seemingly an important factor in the large home ranges occupied by cocks at Waupun.

Both Taber and Burger also reported noncrowing or nonterritorial males in the population. Such birds neither crowed nor defended territories, but mated with hens as opportunity arose. Incidence of noncrowing was reportedly a function of population density. In the comparatively low density population we studied, no wild-hatched males were identified as

noncrowing or nonterritorial (Gates 1966b).

Harem Behavior of Hens

A harem is any aggregation of pheasants in spring which consisted of a single cock and one or more hens. Undoubtedly the reproductive status of individual hens making up the harem was highly variable at a given observation, some having recently entered the harem, others in regular daily attendance, and still others already egg-laying and about to abandon harem affairs for duties at the nest. Notwithstanding, the percentage of hens observed in harems, as opposed to lone hens or hen-only groups, appeared to be a useful gauge to the progress of breeding activity among the hen segment of the population.

From such data it appeared that breeding activity by adults preceded the young, older hens being among the first to enter harems in spring and the earliest to disappear therefrom (Table 30). Similar results were reported by Taber (1949) in Wisconsin and by Robertson (1958:44-48) in Illinois.

Harem formation in this study was most advanced in 1961 and considerably delayed in 1959 and 1962 (Table 31). During the 1959-1964 period that information on nesting phenology was available, significant correlations existed between the percentage of hens which began clutch production by May 10 and the percentage of hens observed in harems during the initial ($r = 0.89$) and middle ($r = 0.81$; reference value with 4 df at $0.05 = 0.81$) thirds of April. Yearly variation in time of nesting was accordingly foreshadowed by parallel trends in harem formation. This we regarded as one of the most critical lines of evidence that variation in nesting phenology under conditions of the present study ultimately depended on events which transpired well before actual onset of egg-laying.

Movement records revealed considerable interchange of hens between harems. Out of 155 marked birds identified twice or more in harems, at least 29 (19%) were noted with two different cocks. In each instance, proof of interchange depended on the fact that one or both cocks were also marked, hence the indicated percentage was minimal. Young hens in early spring often shifted between territorial males before dispersing from winter cover, but interchange was not necessarily restricted to these circumstances. Likewise, some adult hens were observed in more than one harem, and out of 69 hens which furnished two or more harem records after conclusion of spring dispersal, at least 10 percent were observed with at least two different cocks.

Additional information of harem interchange was also available from the cumulative number of marked hens observed in company of marked cocks. The 1965 harem of *Yellow-green E6* comprised no more than 8 hens on 11 counts made between April 14 and May 27, yet no fewer than 10 marked hens were noted with this cock at various dates within this period. Among 21 marked cocks whose harems were observed on at least three different occasions, the total number of marked hens present at one time or another averaged 4.2. Because the spring population of hens during the period (1960-65) never contained more than 25 percent marked individuals and sex ratios did not exceed 8 hens per cock, these data demonstrated that movement of hens between harems must have been commonplace.

Such observations did not, of course, imply a polyandrous mating

TABLE 30. Variation Between Marked Adult and Juvenile Hens in Time of Appearance in Harems, Waupun Study Area and Vicinity, 1960-65

Period	Percent of Known Age Hens Observed in Harems*	
	Adults	Juveniles
April 1–10	62 (84)**	50 (135)
11–20	74 (93)	53 (154)
21–30	73 (112)	68 (167)
May 1–10	63 (60)	78 (138)
11–20	68 (53)	76 (129)

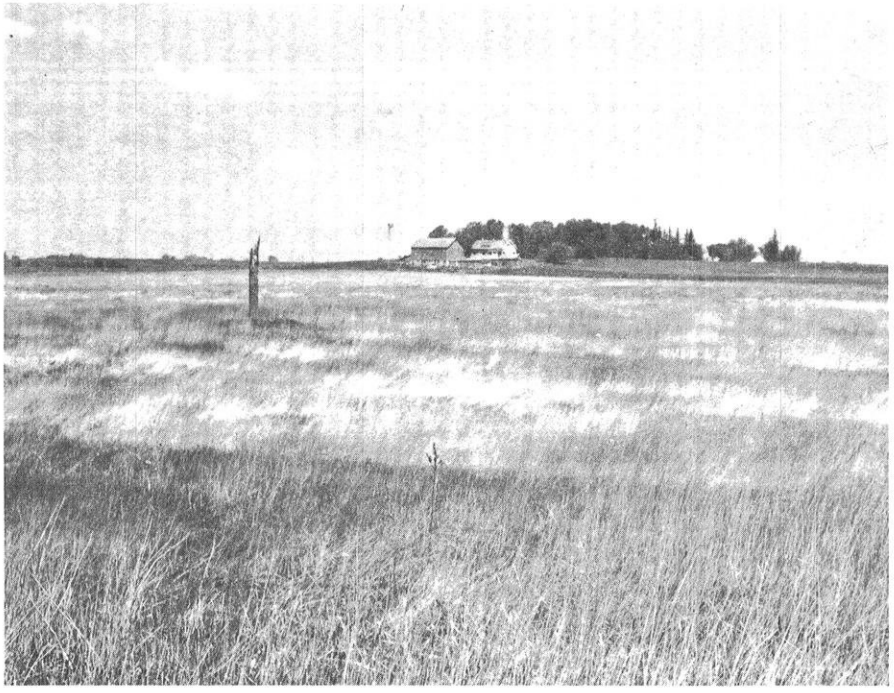
*Combined chi-square = 21.05. Required for significance with 5 df = 15.09 at 1 percent level.
**Sample size shown in parentheses.

TABLE 31. Annual Variation in Seasonal Percentage of Hens Observed in Harems, Waupun Study Area and Vicinity

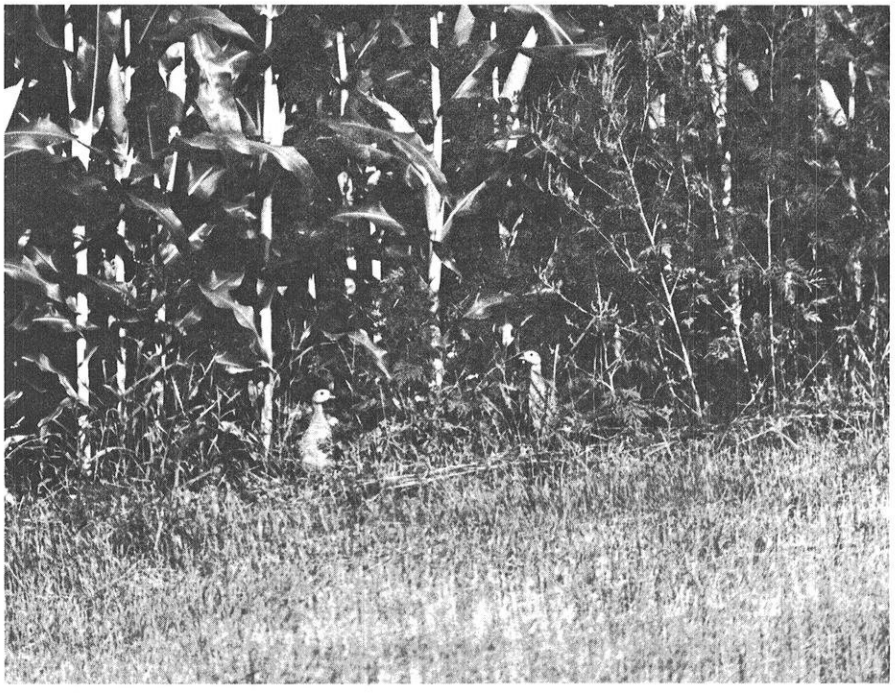
Period	Percent of Hens Observed in Harems*						
	1959	1960	1961	1962	1963	1964	1965
April 1–10	39 (190)**	55 (116)	66 (251)	50 (102)	65 (423)	63 (160)	46 (104)
11–20	57 (142)	66 (233)	73 (207)	61 (211)	66 (266)	68 (342)	67 (241)
21–30	77 (167)	68 (204)	90 (293)	76 (212)	75 (312)	64 (359)	72 (455)
May 1–10	–	–	74 (192)	85 (172)	79 (236)	75 (358)	80 (406)
11–20	–	74 (211)	–	89 (104)	82 (218)	81 (324)	86 (361)

*Percentages shown only for those periods with minimum samples of 100.
**Sample size shown in parentheses.

Retired croplands, with residual herbaceous growth, was the only type that rivalled wetlands as spring cover.



Broods appeared to move from the wetland sites of hatching to adjacent uplands for rearing.



system. Much of the exchange of hens between harems may have been highly perfunctory. More detailed observations than ours might have revealed a tendency for hens to orient to specific males while making occasional appearances on other crowing areas, or to visit several males during the early stages of harem formation before a final choice was made. It is conceivable that some hens visited at one time or another most if not all of the territorial males whose crowing areas were located within the range of daily travel. If such behavior is typical, then the relationship of the nest site to the location of the cock would be doubly difficult to establish without intimate daily knowledge of the hen's prenesting behavior and movement.

COVER SELECTION

Spring

Preferential spring use of wetland areas by both cocks and hens has already been mentioned. In 1959-1966, 72 percent of the study area's cock population was concentrated in the immediate vicinity of wetlands, even though these cover types constituted less than 10 percent of the landscape. These results pertained to the distribution of crowing males observed during early morning census periods and hence to the relationship of the crowing area to wetland cover. Because open ground or sparse vegetation is generally sought for crowing (Taber 1949), association of breeding males with wetlands obviously stemmed from habitat preferences at times of day not devoted to crowing and display. This was hardly surprising considering the barrenness of the early spring landscape. Apart from scattered tracts of retired cropland and the odd fenceline or ditchbank, wetlands constituted the only attractive roosting and escape cover available during spring dispersal and establishment of crowing areas. Contrary to Wight (1945:146), but consistent with most subsequent investigators (Baskett 1947:9; Dustman 1949:72; Taber 1949; and Robertson 1958:24), brushy cover did not emerge as a critical habitat requirement of breeding cocks at Waupun. Wetlands dominated by shrub-carr or with scattered clumps of brush appeared no more attractive than pure stands of canary grass, aster-goldenrod, or ungrazed sedge meadow.

The only cover type which rivalled wetlands from the standpoint of spring cover was retired cropland, particularly unharvested hayfields which retained a dense stand of residual plant material from one growing season to the next. During the post-1961 period when such acreages were largest, this cover type made up only 0.7 percent of the study area, yet held 7 percent of the breeding cock population. Hens also appeared to demonstrate preferential use of unharvested hayfields in spring.

Summer

Approximately 63 percent of all brood production occurred in wetlands (Gates 1971), yet wetland areas were generally less productive places

for brood observation than adjacent agricultural lands. Two marked hens produced successful clutches in wetlands and were later seen with broods. One dispersed 0.52 mile and the other 0.30 mile from lowland cover for brood rearing. During nest searches in wetlands, brood sign was conspicuous by its absence, whereas cropland searched for nests, particularly oats, peas, and hayfields, showed disproportionally heavy sign of brood use in early to mid-summer.

On strength of these observations, the net movement of broods appeared to be from wetland sites of hatching to adjacent uplands for rearing. Factors accounting for the move were obscure, although the extremely dense cover of most wetland types by mid-summer impressed us as less favorable for young chicks than the more diversified and less dense cover available on the uplands. Food supply may also have been a factor, but information on this point was totally lacking.

Cover selection in early autumn, at least for roosting, was revealed by nightlighting. Two vegetation types consistently held the highest density of roosting birds—wetlands and retired cropland. Other potential roosting cover (small-grain stubble, harvested peafields, and second- or third-growth hayfields) clearly were second-rate choices for roosting. Preferred roosting sites at this season thus consisted of the densest cover available. Resurgence in wetland use at this season may have been related to cover depletion on the uplands, particularly after the small-grain harvest, or may have reflected an increase in the daily cruising radius as young birds approached maturity and exercised cover preferences over an expanded range of daily travel. In any event, stronger orientation to wetland cover seemed to exist in late summer and early autumn than characterized the earlier stages of brood rearing.

SUMMARY

Home-range size of breeding birds averaged approximately ½ square mile between the end of spring dispersal and early autumn. Among cocks, essentially the same home range was occupied throughout the period. Among hens, adjustment or expansion in home-range location appeared to coincide with nest establishment, possibly the result of hens seeking isolation from harem activity. Home ranges during brood rearing were largely coincident with those occupied during prenesting and nesting activities. It was concluded that habitat needs during reproduction could be supplied on tracts as large as ¼ to ½ square mile without exceeding the normal range of travel during reproduction.

Observation of territorial cocks suggested that aggressive behavior was concerned with defense of individual distance, or at best a moving territory, rather than a fixed unit of space. At least in part, this interpretation may have stemmed from the low density population that was studied, and from the fact that aggressive encounters between cocks were few enough that territorial boundaries did not require rigid enforcement.

Adult hens were among the first to enter harems in spring and the first to abandon harem affairs for duty at the nest. Year-to-year trends in the percentage of hens observed in harems in early to mid-April foreshadowed corresponding variation in onset of egg-laying. Sufficient interchange of marked hens were demonstrable between harems to suggest that at one time or another hens probably visited most if not all of the crowing males established within their limits of daily travel.

Both cocks and hens showed strong preferences for wetland cover during prenesting activity. Wetlands were the primary cover types in which brood production occurred, but adjacent uplands appeared to be preferentially used for brood rearing. Resurgence in wetland use in late summer coincided with cover depletion on the uplands and may have reflected an increased preference for heavy cover as young birds approached maturity.

MANAGEMENT RECOMMENDATIONS

PRESERVATION OF WINTER COVER

Spatial Distribution

Management of pheasant winter cover in Wisconsin is mainly a matter of preserving existing tracts rather than critical need for additional cover. Population levels in the primary pheasant range of the state are strongly associated with wetland acreages. This relationship is basically the outcome of wetland importance as nesting cover (Gates 1971). Wetlands also provide the major source of winter cover, but dependence is on more specific vegetation types and much smaller acreages than are required for nesting. We do not infer that existing populations in this state are seriously disadvantaged by shortage of winter cover. Nor do we believe that provision of winter cover along would materially aid pheasants in areas more-or-less devoid of wetlands and characterized by low pheasant densities. In such areas, deficiencies in nesting cover must first be corrected before additional winter cover would provide significant benefit.

Over 80 percent of the hens moving into traditional winter cover in this study originated from summer range within a 2-mile radius. Spring dispersal from these areas was roughly comparable in magnitude, suggesting that the basic unit of pheasant management might be considered an area approximately 4 miles in diameter centering on traditionally used winter cover. In our opinion, pheasants could not be successfully managed on areas appreciably smaller than this without substantial egress into unmanaged areas.

An important management problem is the minimum spacing of winter cover necessary to fulfill winter cover requirements over an extensive unit of summer range. Results from the present study pertained to an area where

availability of winter cover appeared to be adequate, but whether it exceeded or fell short of the optimum cannot be said. Nonetheless, certain guidelines may be established which suggest the goal to which management should strive to preserve or develop a proper distribution of winter cover.

In our opinion, availability of winter cover would be adequate under circumstances where: (1) the majority of adult hens, particularly yearlings, were returning each year to traditional winter cover instead of relying on potentially less favorable cover in closer proximity to where they bred; and (2) the distance of juvenile egress from fall to winter was sufficiently restricted to favor subsequent return of these birds to the vicinities in which they were hatched and reared.

Among adult hens, 63 percent returned to where they previously wintered from summer range within 2-mile radius. Among yearling hens, 55 percent returned from breeding areas within this distance, but less than half this percentage returned from more remote summer locations. Return of juvenile hens to the vicinity of their birthplaces seldom occurred after fall-to-winter moves greater than 2 miles, whereas 20 percent returned in spring over shorter distances. On the whole, it would appear that the objectives we have specified would be adequately met if at least one suitable tract of winter cover was present near the center of each 9-section block, equivalent to 4 wintering areas per township. Under such conditions, no bird would be obliged to travel more than 2 miles to winter cover.

Recommendations for a program of scattered wetlands preservation incorporating findings of this chapter have been spelled out in a previous report (Gates 1970). In brief, the broad aim of this program is to preserve both nesting and winter cover in planned management units meeting year-round habitat requirements of local populations. Specific recommendations call for wetland preservation units approximately 4 miles in diameter centering on traditionally used winter cover. In areas of the state with winter cover well distributed, so that management units overlap, nesting cover should be preserved throughout the summer range. In areas where management units do not overlap, preservation of nesting cover should be concentrated within 2 miles of preserved winter cover.

Cover Composition

A dependable source of emergency winter cover should be recognized as the most critical habitat need in the long-term view. Accordingly, highest priority in preservation of wetland winter cover should be given to shrub-carr or tamarack stands. Tracts as large as possible should ideally be acquired, but units between 5 and 10 acres in size may be adequate if larger acreages are unavailable or if scattered pockets of winter cover are to be preserved over the landscape. Some form of preferred roosting cover should also be present, such as cattail or ungrazed stands of canary grass and sedge meadow vegetation. An ideal wintering area consists of a closed-canopy shrub-carr or tamarack stand contiguous with grassy or herbaceous vegetation, the whole occupying an area of perhaps 20 to 30 acres. If woody cover is absent, first priority should be given to herbaceous or cattail stands, both of which serve as roosting and loafing cover under a wider range of snow conditions than other wetland types.

In many wetland areas it also may be possible to improve winter cover through management. Shrub-carr ordinarily follows sedge meadow as a normal successional stage on undisturbed wetland sites (Curtis 1959:374; White 1965). Where such cover is lacking, disturbance might be relieved or methods developed to hasten conversion of small tracts of sedge meadow to shrub-carr. In much of southeast Wisconsin, shrub acreages are larger than optimum in view of their second-rate importance for nesting, and shrub development more commonly requires control than encouragement. Yet local areas do exist where additional shrub cover, interspersed with nonwoody types, would constitute a net improvement in the quality of the winter range.

On upland sites, the best opportunity for creating permanent winter cover would be to encourage farm shelterbelts, particularly coniferous plantings of Norway spruce, white spruce, and Douglas fir. While the few shelterbelts at Waupun did not provide all-round winter cover, they did appear locally important as emergency cover during periods of heavy snow, especially where alternative woody vegetation was absent or in short supply. Again, if pheasants are to be successfully managed in areas devoid of wetlands, nesting cover requirements must be concurrently met, with shelterbelts filling only one aspect of annual cover requirements. While shrub plantings may be of some value to pheasants, their usefulness as winter cover rapidly deteriorates with even moderate snowfall and ever-present drifting.

PROVISION OF WINTER FOOD

One of the clearest implications of this study was that winter food tended to be in chronically shorter supply than winter cover. In four out of seven winters, prolonged periods of food stress led to progressive reduction in body condition and presumably greater risk of direct mortality associated with search for food. Provision of winter food should therefore rate as high as provision of winter cover in pheasant management. Preservation of winter cover according to earlier recommendations would be greatly enhanced if each concentration site also provided a reliable source of winter food. Under Wisconsin conditions, corn generally supplies the most dependable source of winter food with heavy snow, although certain varieties of sorghum and sorghum-sudan grass hybrids may be equally valuable food-patch materials (Frank and Woehler 1969). In leasing or purchasing wetland areas as winter cover, each management unit should ideally contain an acre or two of cropland on which food patches can be grown. Alternative means of food-patch production include custom establishment by local farmers or reliance on game management personnel and equipment. One of the major disadvantages of a food-patch program is that it requires an annual or alternate-year expenditure, and in some winters snowfall is so light that need for emergency food does not exist. The obvious recourse is for artificial feeding, but this might be even more expensive in the long run.

Comments on the winter-feeding program of the Department of Natural Resources are also pertinent in this context. As snow conditions warrant, limited-scale winter feeding is carried out and corn is furnished to private individuals and sportsmen's clubs for distribution. The overall significance of these practices would be difficult or impossible to evaluate, but we find no grounds on which to categorically deny their possible value. Feeding stations operated by lay personnel are sometimes ill-chosen and left unat-

tended after a winter flock has been attracted; however, these are shortcomings easily subject to correction by closer supervision.

The pros and cons of artificial feeding have been thoroughly debated elsewhere (Gerstell 1942:107-114). Arguments against the practice have largely centered on the ability of captive pheasants to withstand 2 weeks or more of complete food deprivation before starvation (Tester and Olson 1959). We agree with Kabat et al. (1956:37-38), however, that indirect effects of prolonged food shortage, though nonfatal, may be almost as inimical in the long run as outright death from starvation. An effective winter-feeding program in locally hard-hit areas might alleviate direct mortality and help avert serious weight losses. When emergency conditions develop, a legitimate management function in our view would be to encourage artificial feeding by farmers and sportsmen through news releases and other means of mass communication. Although game management personnel and equipment are obviously inadequate to provide a significant fraction of a statewide population with emergency food, private interests might well accomplish something significant along this line.

INFLUENCING HEN DISTRIBUTION IN SPRING

With higher hen populations in this study, it was concluded that the number of hens breeding on the uplands tended to be determined in part by the number of upland territories that were present. In turn, the number of cocks stationed on the uplands was inversely related to cock density. Because of generally poor nest success in most upland cover, high removal of cocks by hunting may be of considerable advantage in minimizing the number of upland territories potentially attractive to breeding hens. Granted that we know comparatively little about the actual placement of nests in relation to the territory, it seems reasonable to conclude that less nesting would occur in the uplands with fewer cocks present. The point is that high rates of cock harvest which presently prevail in Wisconsin do not appear from present knowledge to be inimical to reproduction and indeed are more likely an advantage. Unless future research demonstrates otherwise, hunting regulations which permit 80 to 90 percent removal of cocks, as was true at Waupun, probably are not excessive and should be retained in the interest of providing maximum opportunity for the hunter.

Other methods of controlling hen distribution in spring should also be investigated, the objective being to retain the maximum number of breeding birds near the most productive nesting cover. One possibility might be to increase the number of territorial cocks that can be accommodated in wetland areas. Perhaps by increasing the amount of wetland edge, or by breaking up large wetland monotypes, more cocks could be induced to establish wetland territories instead of dispersing to the uplands.

Since the vicinity of winter cover tended to become saturated with juvenile hens before overflow began into outlying areas, the density of nesting birds was typically higher in the vicinity of winter concentration sites than prevailed over the summer range as a whole. On this basis, attempts to manage small areas for improved pheasant production would be most effective if carried out near winter cover, or, alternatively, if winter cover was provided as part of the overall management plan. An important advantage of minimizing the necessary distance of travel to winter cover would be to encourage higher rates of juvenile return to managed summer range, thereby ensuring greater carryover of management dividends from one breeding season to the next.

LICENSING OF TRADITIONAL WINTER COVER AS SHOOTING PRESERVES

Originally the Wisconsin Administrative Code prohibited the licensing of private shooting preserves in cover designated as "major wintering areas." This provision, however, proved to be ill-defined, difficult to administer, and in 1959 was rescinded along with other rule changes designed to stimulate expansion of the shooting preserve program. Since 1963, hunting of both sexes of pheasants has been permitted on shooting preserves between the mid-October opening of the statewide pheasant season and the end of February. As testimony to the effectiveness of these rule changes, preserve acreages in Wisconsin nearly doubled between 1957 and 1965 (Besadny 1967). Under present Department policy of encouraging the shooting preserve program, licensed acreages are certain to increase in the years ahead.

As shown by Besadny, some form of wetland cover forms the nucleus of virtually every shooting preserve. Wetland cover tends to restrict fall egress, an important consideration by preserve operators who are required by law to stock a certain minimum number of pheasants, and who depend to varying extents on these pen-reared birds for shooting. Applicants accordingly seek to license as much high quality wetland cover as feasible. Out of 70 preserves studied by Besadny, 25 percent of the licensed acreage was rated as good or excellent winter cover.

Because traditional winter cover will attract hens from considerable distances, the potential exists for serious reduction of off-preserve populations through hen-shooting in winter. On such grounds, we endorse Besadny's (1967) earlier recommendation, based in part on our findings, that regulations for preserves in Wisconsin's major pheasant counties be amended to prohibit shooting of hens in winter. From the timing of movements to winter cover observed at Waupun, any harvest of hens after November 30 runs the risk of substantially reducing next spring's breeding hen population in the entire area from which hens come to winter cover on the preserve. We also enclose Besadny's second proposal, however, which would exempt shooting preserves outside the major pheasant range of the state from such restrictions on winter hen shooting.

In our opinion, elimination of winter hen shooting would still allow preserve operators who stock hens ample time to harvest them before the main influx of wild-reared hens to winter cover. Under such a plan, shooting preserves could continue to fulfill the primary function for which they were intended—preservation of wetland habitat—meanwhile safeguarding breeding stock which has been attracted from outlying summer range.

LITERATURE CITED

ANDREWARTHA, H. G., and L. C. BIRCH
1954. The distribution and abundance of animals. Univ. Chicago Press, Chicago, Ill. 782 p.

BALL, K. E.
1950. Breeding behavior of the ring-necked pheasant on Pelee Island, Ontario. Canadian Field-Nat. 64(6):201-207.

BASKETT, T. S.
1947. Nesting and production of the ring-necked pheasant in north-central Iowa. Ecol. Monog. 17(1):1-30.

BESADNY, C. D.
1967. An evaluation of Wisconsin's licensed shooting preserve program. Wis. Conserv. Dep., Res. Rep. No. 24 (Game). Mimeo. 21 p.

BLANK, T. H., and J. S. ASH
1956. Marker for game birds. J. Wildl. Manage. 20(3):328-330.

BREITENBACH, R. P., C. L. Nagra, and R. K. MEYER
1963. Effect of limited food intake on cyclic annual changes in ring-necked pheasant hens. J. Wildl. Manage. 27(1):24-36.

BUE, I. G.
1949. Winter behavior and mortality of pheasants in relationship to various types of cover, food and predation. S. D. Dep. Game, Fish and Parks, Spec. Rep. for Projects 19-D-2 and 17-R-3. Mimeo, 38 p.

BURGER, G. V.
1966. Observations on aggressive behavior of male ring-necked pheasants in Wisconsin. J. Wildl. Manage. 30(1):57-64.

BUSS, I. O.
1946. Wisconsin pheasant populations. Wis. Conserv. Dep., Publ. 326, A-46. 184 p.

BUSS, I. O., R. K. MEYER, and C. KABAT
1951. Wisconsin pheasant reproduction studies based on ovulated follicle technique. J. Wildl. Manage. 15(1):32-46.

CHAMBERS, R. E., and W. M. SHARP
1958. Movement and dispersal within a population of ruffed grouse. J. Wildl. Manage. 22(3):231-239.

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

CONDER, D. J.
1949. Invididual distance. Ibis 91:649-655.

CURTIS, J. T.
1959. The vegetation of Wisconsin/An ordination of plant communities. Univ. Wis. Press, Madison. 657 p.

DAHLKE, P. D.
1943. Effect of winter weather on the feeding habits of pheasants in southern Michigan. J. Wildl. Manage. 7(3):343-344.

DAVIS, D. E., J. J. CHRISTIAN, and F. BRONSON
1964. Effect of exploitation on birth, mortality, and movement rates in a woodchuck population. J. Wildl. Manage. 28(1):1-9.

DUSTMAN, E. H.
1949. Nesting and production of the ring-necked pheasant in northwestern Ohio following a population decline. PhD. Thesis, Ohio State Univ., Columbus. 305 p.

EDWARDS, W. R., P. J. MIKOLAJ, and E. A. LEITE
1964. Implications from winter-spring weights of pheasants. J. Wildl. Manage. 28(2):270-279.

ERICKSON, A. B., D. B. VESALL, C. E. CARLSON, and C. T. ROLLINGS
1951. Minnesota's most important game bird the pheasant. Flicker 23(3):23-49.

ERRINGTON, P. L.
1937a. Emergency values of some winter pheasant foods. Trans. Wis. Acad. Sci., Arts, and Letters 30:57-68.

1939. Comparative ability of the bob-white and the ring-necked pheasant to withstand cold and hunger. Wilson Bull. 51(1):22-37.

FARNER, D. S.
1945. The return of robins to their birthplaces. Bird-Banding 16(3):81-99.

FRANK, E. J., and E. E. WOEHLER
1969. Production of nesting and winter cover for pheasants in Wisconsin. J. Wildl. Manage. 33(4):802-810.

GATES, J. M.
1966b. Crowing counts as indices to cock pheasant populations in Wisconsin. J. Wildl. Manage. 30(4):735-744.

1966c. Renesting behavior in the ring-necked pheasant. Wilson Bull. 78(3):309-315.

1970. Recommendations for a scattered wetlands program of pheasant habitat preservation in southeast Wisconsin. Wis. Dep. Natur. Resour., Res. Rep. No. 63. 24 p.

1971. The ecology of a Wisconsin pheasant population. PhD. Thesis, Univ. of Wis., Madison 912 p.

GERSTELL, R.
1942. The place of winter feeding in practical wildlife management. Pa. Game Comm., Res. Bull. No. 3. 121 p.

GIGSTEAD, G.
1937. Habits of Wisconsin pheasants. Wilson Bull. 49(1):26-34.

GREELEY, F., and R. K. MEYER
1953. Seasonal variation in testis-stimulating activity of male pheasant pituitary glands. Auk 70(3):350-358.

GREEN, W. E.
1938. The food and cover relationship in the winter survival of the ring-necked pheasant, *Phasianus colchicus torquatus* Gmelin, in northern Iowa. Iowa St. Coll. J. Sci. 12:285-314.

GRONDAHL, C. R.
1953. Winter behavior of the ring-necked pheasant, *Phasianus colchicus*, as related to winter cover in Winnebago County, Iowa. Iowa St. Coll. J. Sci. 27(4):447-465.

HALE, J. B., and R. S. DORNEY
1963. Seasonal movements of ruffed grouse in Wisconsin. J. Wildl. Manage. 27(4):648-656.

HAMERSTROM, F. N., JR., and FRANCES HAMERSTROM
1949. Daily and seasonal movements of Wisconsin prairie chickens. Auk 66:313-337.

HANSON, H. C.
1962. The dynamics of condition factors in Canada geese and their relation to seasonal stresses. Arctic Inst. No. Am., Tech. Paper No. 12. 68 p.

HANSON, W. R., and R. F. LABISKY
1964. Association of pheasants with vegetative types in east-central Illinois. Trans. N. Am. Wildl. and Natur. Resour. Conf. 29:295-306.

HAWKINS, A. S.
1937. Winter feeding at Faville Grove, 1935-1937. J. Wildl. Manage. 1(3-4):62-69.

HIATT, R. W., and H. I. FISHER
1947. The reproductive cycle of ring-necked pheasants in Montana. Auk 64(4):528-548.

HICKEY, J. J.
1943. A guide to bird watching. Oxford Univ. Press, New York. 262 p.

KABAT, C., R. K. MEYER, K. G. FLAKAS, and RUTH L. HINE
1956. Seasonal variation in stress resistance and survival in the hen pheasant. Wis. Conserv. Dep., Tech. Wildl. Bull. No. 13. 48 p.

KABAT, C., D. R. THOMPSON, and F. M. KOZLIK
1950. Pheasant weights and wing molt in relation to reproduction with survival implications. Wis. Conserv. Dep., Tech. Wildl. Bull. No. 2. 26 p.

KIMBALL, J. W.
1948. Pheasant population characteristics and trends in the Dakotas. Trans. N. Am. Wildl. Conf. 13:291-314.
1949. The crowing count pheasant census. J. Wildl. Manage. 13(1):101-120.

KIMBALL, J. W., E. L. KOZICKY, and B. A. NELSON
1956. Pheasants of the plains and prairies. *In* Allen, D. L., Ed., Pheasants in North America. The Stackpole Co., Harrisburg, Pa. and the Wildl. Manage. Inst., Washington, D. C. 490 p.

KIRKPATRICK, C. M.
1944b. Body weights and organ measurements in relation to age and season in ring-necked pheasants. Anat. Rec. 89(2):175-194.

KIRKPATRICK, C. M., and F. N. ANDREWS
1944. Development of the testis in the ring-necked pheasant. Anat. Rec. 89(3):317-324.

KIRSCH, L. M.
1951. Our winter storm losses. S. D. Conserv. Digest 18(4):2-3, 7, 12.

KOZLOWA, Mme. E. V.
1947. On the spring life and breeding habits of the pheasant *(Phasianus colchicus)* in Tadjikistan. Ibis 89:423-429.

LABISKY, R. F.
1959. Night-lighting: A technique for capturing birds and mammals. Ill. Natur. Hist. Surv., Biol. Notes No. 40. 11 p.
1968. Ecology of pheasant populations in Illinois. PhD. Thesis, Univ. of Wis., Madison. 511 p.

LABISKY, R. F., and S. H. MANN
1962. Backtag markers for pheasants. J. Wildl. Manage. 26(4):393-399.

LEEDY, D. L., and L. E. HICKS
1945. The pheasants in Ohio. *In* McAtee, W. L., Ed., The ring-necked pheasant and its management in North America. The Am. Wildl. Inst., Washington, D. C. 320 p.

LEFFINGWELL, D. J.
1928. The ring-necked pheasant—its history and habits. Occas. Papers No. 1, Charles R. Conner Museum, State Coll. of Washington, Pullman, Wash. 35 p.

LEHMANN, V. W.
1946. Mobility of bobwhite quail in southwestern Texas. J. Wildl. Manage. 10(2):124-136.

LEOPOLD, A., O. S. LEE, and H. G. ANDERSON
1938. Wisconsin pheasant movement study. J. Wildl. Manage. 2(1):3-12.

LYON, L. J.
1954. Pheasant winter roosting cover preference in north-central Colorado. J. Wildl. Manage. 18(2):179-184.
1959. An evaluation of woody cover plantings as pheasant winter cover. Trans. N. Am. Wildl. Conf. 24:277-289.

MALLETTE, R. D., and J. C. BECHTEL
1959. Movement of the ring-necked pheasant in the Sutter Basin of California. Calif. Fish and Game 45(3):189-202.

McCABE, R. A.
1949. A ten-year study of a refuge population of ring-necked pheasants. PhD. Thesis, Univ. Wis., Madison. 157 p.

McCLURE, H. E.
1948. Factors in winter starvation of pheasants. J. Wildl. Manage. 12(3):267-271.

MILLER, W. L.
1948. Pheasants killed by blizzard. N. D. Outdoors 10(9):4-6, 10.

MOHLER, L. L.
1959. Investigations of the Nebraska pheasant. Nebr. Game, Forestation and Parks Comm. 150 p.

MURPHY, D. A., and T. S. BASKETT
1952. Bobwhite mobility in central Missouri. J. Wildl. Manage. 16(4):498-510.

NELSON, B. A., and R. G. JANSON
1949. Starvation of pheasants in South Dakota. J. Wildl. Manage. 13(3):308-309.

NELSON, M. M.
1959. A study of late summer mortality in cock pheasants and the kill by hunters. Minn. Dep. Conserv., Quart. Prog. Rep. 19(3):54-65.

NICE, MARGARET M.
1937. Studies in the life history of the song sparrow. I: A population study of the song sparrow. Trans. Linn. Soc. New York. 247 p.

OLDENBURG, L. E.
1962. Pheasant movement studies, southeastern North Dakota, 1961-62. N. D. Game and Fish Dep., Pittman-Robertson Div. Proj. W-67-R-2. Mimeo, 17 p.

RANDALL, P. E.
1939a. Nesting habits and causes of nest mortality of the ring-necked pheasant. Pa. Game News 10(9):6-7, 30.
1940. causes of juvenile mortality of the ring-necked pheasant. Pa. Game News 11(3):10-11, 28.

ROBERTSON, W. B., JR.
1958. Investigation of ring-necked pheasants in Illinois. Ill. Dep. Conserv., Tech. Bull. No. 1. 137 p.

SCOTT, T. G., and T. S. BASKETT
1941. Some effects of the 1940 Armistice Day storm on Iowa's wildlife. Iowa Bird Life 11(2):23-29.

SEUBERT, J. L.
1956. Pheasant banding in South Dakota 1951-55. S. D. Dep. Game, Fish and Parks, Job Comp. Rep., Pittman-Robertson Proj. W-17-R-11. Mimeo, 17 p.

SHARP, W. M., and H. E. McCLURE
1945. The pheasant in the Sandhill region of Nebraska. *In* McAtee, W. L., Ed., The ring-necked pheasant and its management in North America. The Am. Wildl. Inst., Washington, D. C. 320 p.

SHICK, C.
1952. A study of pheasants on the 9,000-acre Prairie Farm, Saginaw County, Michigan. Mich Dep. Conserv., Lansing. 134 p.

SNEDECOR, G. W.
1956. Statistical methods applied to experiments in agriculture and biology. Iowa State Coll. Press, Ames. 534 p.

SOWLS, L. K.
1955. Prairie ducks. The Stackpole Co., Harrisburg, Pa. and Wildl. Manage. Inst., Washington, D. C., 193 p.

SPIEGEL, L. E., and R. E. REYNOLDS
1954. Responses in weight and reproduction of ring-necked pheasants fed fruits of gray dogwood and multiflora rose. Trans. N. Am. Wildl. Conf. 19:153-156.

STOKES, A. W.
1954. Population studies of the ring-necked pheasants on Pelee Island, Ontario. Ont. Dep. Lands and Forests, Tech. Bull. Wildl. Series No. 4. 154 p.

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

TESTER, J. R., and L. OLSON
1959. Experimental starvation of pheasants. J. Wildl. Manage. 23(3):304-309.

TINBERGEN, N.
1951. The study of instinct. Oxford Univ. Press, London. 228 p.

WAGNER, F. H.
1952. Pheasant-quail management research. Part III—Pheasant distribution and range survey. Wis. Wildl. Research 11(2):30-50.
1953. Pheasant population distribution survey and range analysis. Wis. Wildl. Research 12(3):21-47.

WAGNER, F. H., and C. D. BESADNY
1958. Factors in Wisconsin pheasant production. Wis. Conserv. Bull. 23(12):3-13.

WAGNER, F. H., C. D. BESADNY, and C. KABAT
1965. Population ecology and management of Wisconsin pheasants. Wis. Conserv. Dep., Tech. Wildl. Bull. No. 34. 168 p.

WESTON, H. G., JR.
1954. The winter-spring movements of the ring-necked pheasant in northern Iowa. Iowa State Coll. J. Sci. 29(1):39-60.

WHITE, K. L.
1965. Shrub-carrs of southeastern Wisconsin. Ecology 46(3):286-304.

WIGHT, HOWARD
1945. Breeding habits of the pheasant. *In* McAtee, W. L., Ed., The ring-necked pheasant and its management in North America. The Am. Wildl. Inst., Washington, D. C. 320 p.

TECHNICAL BULLETINS (1972-1974)*

No. 52 Mercury levels in Wisconsin fish and wildlife (1972) Stanton J. Kleinert and Paul E. Degurse

No. 53 Chemical analyses of selected public drinking water supplies (including trace metals). (1972) Robert Baumeister

No. 54 Aquatic insects of the Pine-Popple River, Wisconsin. (1972) William L. Hilsenhoff, Jerry L. Longridge, Richard P. Narf, Kenneth J. Tennessen and Craig P. Walton

No. 55 Recreation Areas and Their Use. (1972) Melville H. Cohee.

No. 56 A Ten-Year Study of Native Northern Pike in Bucks Lake, Wisconsin Including Evaluation of an 18.0-inch Size Limit. (1972) Howard E. Snow and Thomas D. Beard

No. 57 Biology and Control of Selected Aquatic Nuisances in Recreational Waters. (1972) Lloyd A. Lueschow

No. 58 Nitrate and Nitrite Variation in Ground Water. (1972) Koby T. Crabtree

No. 59 Small Area Population Projections for Wisconsin. (1972) Douglas B. King, David G. Nichols and Richard J. Timm

No. 60 A Profile of Wisconsin Hunters. (1972) Lowell L. Klessig and James B. Hale

No. 61 Overwinter Drawdown: Impact on the Aquatic Vegetation in Murphy Flowage, Wisconsin. (1973) Thomas D. Beard

No. 62 Eutrophication Control: Nutrient Inactivation by Chemical Precipitation at Horseshoe Lake, Wisconsin. (1973) James O. Peterson, J. Peter Wall, Thomas L. Wirth and Stephen M. Born

No. 63 Drain Oil Disposal in Wisconsin. (1973) Ronald O. Ostrander and Stanton J. Kleinert

No. 64 The Prairie Chicken in Wisconsin. (1973) Frederick and Frances Hamerstrom

No. 65 Production, food and harvest of trout in Nebish Lake, Wisconsin. (1973) Oscar M. Brynildson and James J. Kempinger

No. 66 Dilutional pumping at Snake Lake, Wisconsin—a potential renewal technique for small eutrophic lakes. (1973) Stephen M. Born, Thomas L. Wirth, James O. Peterson, J. Peter Wall and David A. Stephenson

No. 67 Lake sturgeon management on the Menominee River. (1973) Gordon R. Priegel

No. 68 Breeding duck populations and habitat in Wisconsin. (1973) James R. March, Gerald F. Martz and Richard A. Hunt

No. 69 An experimental introduction of coho salmon into a landlocked lake in northern Wisconsin. (1973) Eddie L. Avery

No. 70 Gray partridge ecology in southeast-central Wisconsin. (1973) John M. Gates

No. 71 Restoring the recreational potential of small impoundments: the Marion Millpond experience. (1973) Stephen M. Born, Thomas L. Wirth, Edmund O. Brick and James O. Peterson

No. 72 Mortality of radio-tagged pheasants on the Waterloo Wildlife Area. (1973) Robert T. Dumke and Charles M. Pils

No. 73 Electrofishing boats: Improved designs and operating guidelines to increase the effectiveness of boom shockers. (1973) Donald W. Novotny and Gordon R. Priegel

No. 74 Surveys of toxic metals in Wisconsin. (1974) John G. Konrad et al.

No. 75 Lake Sturgeon Harvest in Lake Winnebago, Wisconsin. (1974) Gordon R. Priegel and Thomas L. Wirth

No. 76 Mechanical and habitat manipulation techniques for aquatic plant management. (1974) Stanley A. Nichols

No. 77 Hydrogeologic evaluation of solid waste disposal in South Central Wisconsin. (1974) Alexander Zaporozec

No. 78 Estimate of abundance, harvest and exploitation of the fish population of Escanaba Lake, Wisconsin, 1946-1969. (1974) James J. Kempinger, Warren S. Churchill and Gordon R. Priegel

No. 79 Seasonal movement, winter habitat use, and population distribution of an east central Wisconsin pheasant population. (1974) John M. Gates and James B. Hale

***Complete list of all technical bulletins in the series available from the Department of Natural Resources.**

3500-3K40095-74

ACKNOWLEDGMENTS

Many persons participated in this investigation. Although space is too limited to properly acknowledge each individual, we do wish to mention a number that were especially significant.

The study was originally conceived by F. H. Wagner, Group Leader of Farm Game Research for the Wisconsin Department of Natural Resources between 1958 and 1961. C. D. Besadny, Group Leader during 1961-65, was also instrumental in the conduct of the project.

We were fortunate in having the Department of Wildlife Ecology, University of Wisconsin, act as cosponsor of the investigation. For generous loan of equipment and for advice during field work and data analysis, we are indebted to R. A. McCabe, J. J. Hickey, and L. B. Keith of that institution. Gates' academic training at the University of Wisconsin was supported in part by the Wisconsin Alumni Research Foundation, for which we are also grateful.

Much of the credit for the success of this study belongs to our seasonal and full-time field assistants, particularly D. M. Rubink (1959), R. D. Nass (1959-60), the late F. V. Holzer (1960), L. F. Wahl (1960-61), G. F. Martz (1961-65), A. E. Loomans (1963-64), and G. E. Ostrom (1964-65). But for the long and often tedious hours of field work carried out by these seven, the quantity and quality of data gathered would have been materially less. Throughout the study, E. E. Woehler, C. D. Besadny, and E. J. Frank, former colleagues on the Farm Game Research Group, contributed much-needed assistance whenever field work fell behind schedule. It is also a pleasure to acknowledge Sue, a Brittany spaniel and faithful field companion, whose enthusiasm in all phases of field work never faltered.

At least 150 residents of the study area permitted free access to their lands and cooperated in many other ways. Without the interest and support of these local people, such a study would not have been possible.

We were aided by many associates in analysis of data and in report preparation. R. T. Dumke, Susan (Hickey) Nehls, and R. Huempfner assisted in various phases of data tabulation. O. L. Loucks, J. H. Torrie, and J. C. Neess, of the University of Wisconsin, provided helpful assistance on statistical matters, as did D. R. Thompson of the Wisconsin Department of Natural Resources. For critical advice and editorial suggestions in writing we are indebted to C. D. Besadny, E. J. Frank, J. J. Hickey, C. Kabat, and C. Wilson.

We are especially grateful to the senior author's wife, Connie, for many hours of proofreading and for graciously enduring all the inconveniences and disruptions in family life necessitated by this long and arduous study.

This investigation was financed by the Wisconsin Department of Natural Resources through the Federal Aid to Wildlife Restoration Act under Pittman-Robertson Projects W-78-R and W-141-R.

John M. Gates was professor and chairman, Dept. of Wildlife and Fishery Science, S. D. State University, Brookings.

James B. Hale is chief of the Wildlife Research Section, Dept. of Natural Resources, Madison.

Edited by Ruth L. Hine