A Study of the Ecology and Behavior of Some Surface-feeding Ducks

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A thesis submitted in partial fulfillment of the requirements for the degree of Doctor of Philosophy at the University of Wisconsin.

Approved Joseph J. Hickey

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INTRODUCTION

Waterfowl management is dependent on basic information about the species. Complicated by increased hunting pressure following World War II, management needed new and improved techniques of breeding ground appraisal and it was in line with this need that the following ecological and behavior study was carried out.

In 1946 the U.S. Fish and Wildlife Service, the Dominion Wildlife Service and the Manitoba Game Branch began expanding the scope of their Canadian investigations. These government agencies were primarily concerned with extensive inventory work as a basis for game regulations.

Concurrently, the following intensive study was run at the Delta Waterfowl Research Station, Delta, Manitoba. Begun in 1946, it continued for five years and was terminated in October, 1950. The following report covers the findings of that study.

Objectives.--The objectives of the study were: (1) to determine the role of renesting in waterfowl production, (2) to determine the significance of migrational homing to management, (3) to study the land-water pattern and the cover requirements of the surface-feeding species, (4) to determine the effect of late seasons upon arrival and breeding, and (5) to evaluate the inventory method of counting breeding pairs.

History of the Study.--During 1946 and 1947 the study

occupied part of my time and about half of the nesting season was spent away from Delta. Owing to improved techniques, increased time on the project and the help of assistants, most of the data presented on the pages to follow was gathered during the years 1948, 1949 and 1950.

A summary of data along with other statistics concerning the scope of this investigation are given in Table 1.

The Study Area.--In 1946 a tract of approximately 3,115 acres was selected for a study area. This tract, shown in Figure 1, was about 2½ miles long, 2 miles wide, and ran in a north-south direction from the south shore of Lake Manitoba at the village of Delta to the prairie farmlands on the Portage Plains.[1] Through its entire length ran a public gravel highway along which was a narrow roadside ditch. A line of telephone poles ran along the highway, and these poles were numbered to serve as reference points.

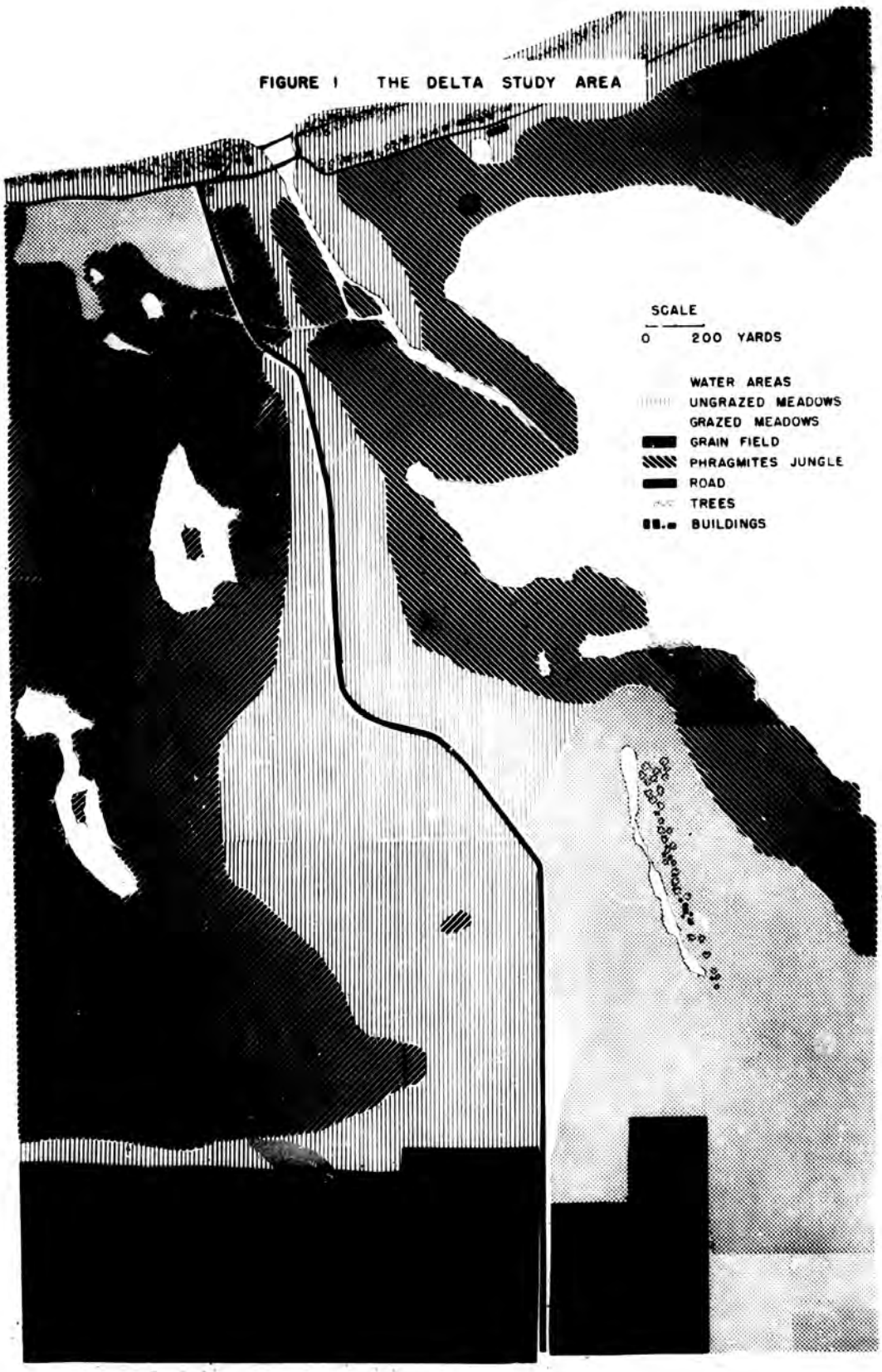
About 41 per cent or 1,277 acres consisted of tall yellow cane.[2] Another 19 per cent or 592 acres was water. It included part of a large bay, six potholes, a long narrow roadside ditch and a marsh channel. Ungrazed nesting meadows, grazed pastures and bordering submarginal grain-fields made up the remaining 40 per cent or 1,246

1. See Hochbaum (1944:3-12) for general description of the Delta marsh region.
2. See Appendix 1 for scientific names of animals and plants mentioned in the text.

TABLE 1. SUMMARY OF STUDY DATA

Year	Nests Found	Hens Marked	Drakes Marked	Ducks Reared and Released	Ducks Banded in August and September
1946	25	4	0	0	140
1947	41	10	0	0	0
1948	106	51	0	133	651
1949	231	91	4	352	520
1950	190	64	33	128	0
Total	593	220	37	613	1311

FIGURE 1 THE DELTA STUDY AREA



acres. It was in this area that most of the work described on the following pages was conducted.

The dominant vegetation on the ungrazed nesting meadows was whitetop, sow thistle, Canada thistle and pigweed. The grazed pasture was made up of bluegrass and cordgrass.

Study Techniques, Finding Nests by Systematic Search.--Most nesting studies in the past have used the technique of finding nests by systematic search. This method consists of having a man or line of men walk through nesting cover to flush hens from their nests. It is a sufficiently good method when only a sample of nests is wanted but for complete coverage it requires the support of other methods because: (1) systematic search fails to reveal nests when the hens are away, (2) some hens sit "tight" and allow a man to walk by them, and (3) nests may be begun and destroyed between searches.

In the Delta study additional methods were employed. These were: (1) the use of a dog to find nests by scent, (2) the dragging of a long rope between two men, (3) the dragging of a long rope between two cars, and (4) the use of a flushing bar along roadside ditch banks. The use of the above methods speeded up nest finding, cut down the amount of labor required and increased the percentage of nests found.

The dog I used at Delta was a Labrador retriever.

Nests were usually discovered as the hens flushed. The nests of laying hens, however, had enough scent to attract him, and in three cases nest forms without eggs were discovered.

The technique of rope-dragging between two men was advantageous on still days where vegetation was light. Where cover was heavy and on windy days when the rope made little more disturbance than the wind itself, the hens sometimes allowed the rope to pass over them.

Rope-dragging between two cars, when the ground was solid, was used to good advantage. The efficiency of such dragging was increased when tin cans, in series of twos, were fastened to the rope at 15-foot intervals. The cans made enough noise to flush hens which might have allowed a rope to pass over them. The above method could not be used when there were bushes, stumps, rocks or other objects which could hold up or break a rope. I found the technique valuable in cutting down the amount of time required to search large areas of grazed pasture where nesting density was low. An observer in the truck-box determined the locations of duck nests by watching the hens as they flushed.

On one occasion a baldpate, whose nest it was particularly important to find, was nesting someplace in a 200-acre pasture. After all other methods had failed, we dragged the pasture with a rope between two trucks and located the nest in two hours.

At Delta the roadside ditch bank was a favorite nesting

place for blue-winged teal. For this situation I found a flushing bar to be a valuable time saver. A 10-foot pole was attached to the rear of a truck by a swivel and was held in place at a 90-degree angle to the midline of the truck by means of ropes. The bar was free to swing down over the sloping ditch bank as the truck moved ahead. To the pole were fastened 6-foot lengths of baling wire at intervals of 2 feet and to each wire pairs of tin cans were attached. An observer watching from the truck-box could then see ducks leave their nests as they flushed in fromt of the bar. By this method both sides of a 2-mile roadside ditch bank could be covered in two hours, a stretch otherwise requiring eight to ten man-hours.

Finding Nests by Early-morning Watching.--In addition to systematic searching and the above additional methods, I used the technique of locating nests by watching and interpreting the early-morning activities of laying hens. This consisted of posting a watch at particular vantage points on the study area and noting the locations where hens dropped down into the grass following flights from water areas. These hens were invariably accompanied by drakes as they returned to their meadows to lay. After they had settled in the grass, their drakes returned to their waiting places. Important in the use of this technique was the time of day required for the watching.

At Delta I found that most laying hens went to their nests between sun-up and four hours thereafter. An observer with an 8-power binocular could cover an area of approximately a half-mile radius. It was important to have landmarks to aid in remembering and recording nest sites. On the study area I numbered the poles of an electric power line as well as the afore-mentioned roadside telephone poles. These two lines ran at right angles to each other and gave reliable reference points for mapping the locations of nest-sites.

After the approximate location of a nest had been mapped, the exact location was determined by the usual methods of search. This was usually accomplished by working the dog in an ever-increasing circle from the spot where the hen was seen to drop down into the grass. Hens varied in the time they required to go to their nests. Sometimes they lit near it. More often they dropped down fifty yards from it and approached by short flights, walking the last few feet. This delay in settling down made it necessary to hold up nest hunting until an hour after early-morning watching had ceased.

This technique was particularly useful when the nest of a marked individual or an uncommon species was sought.

Trapping Hens on their Nests.--In working with known individuals it was necessary to mark the birds for identification. This, of course, hinged upon the capture of the

nesting hen. Although several means for doing this had been devised, I found that two methods were satisfactory at Delta: (1) nest trapping and (2) hand netting. Using these two, 220 hens were nest-trapped during the five seasons of the study.

The nest trap has been described and figured in a previous paper (Sowls, 1949:262) and is shown here in Figure 2. It was patterned after a trap developed by the late Robert Harris who used the drop trap in catching hens (Hochbaum, 1944:158). Our trap consisted of a frame 2 feet square of 5/8-inch blacksmithing iron over which was attached 1/2-inch-mesh chicken wire. Lead weights were secured on the front of the trap to make it drop heavily. One side of the trap was propped up with a tripping stick while the other side was firmly held in place by two hinged rods pushed into the earth. To the tripping stick was attached a long twine which was laid out on the grass so that the trap could be pulled from a distance.

The trap was set over the nests of incubating hens at the time the nests were found. After waiting for two hours, a reasonable time for a hen to return and settle down, it was pulled. Trapping success was high in most species of ducks, but low for mallards which proved suspicious and wary. The main shortcoming of the trap was its failure to catch laying hens.

A laying hen seldom returned to a nest over which a

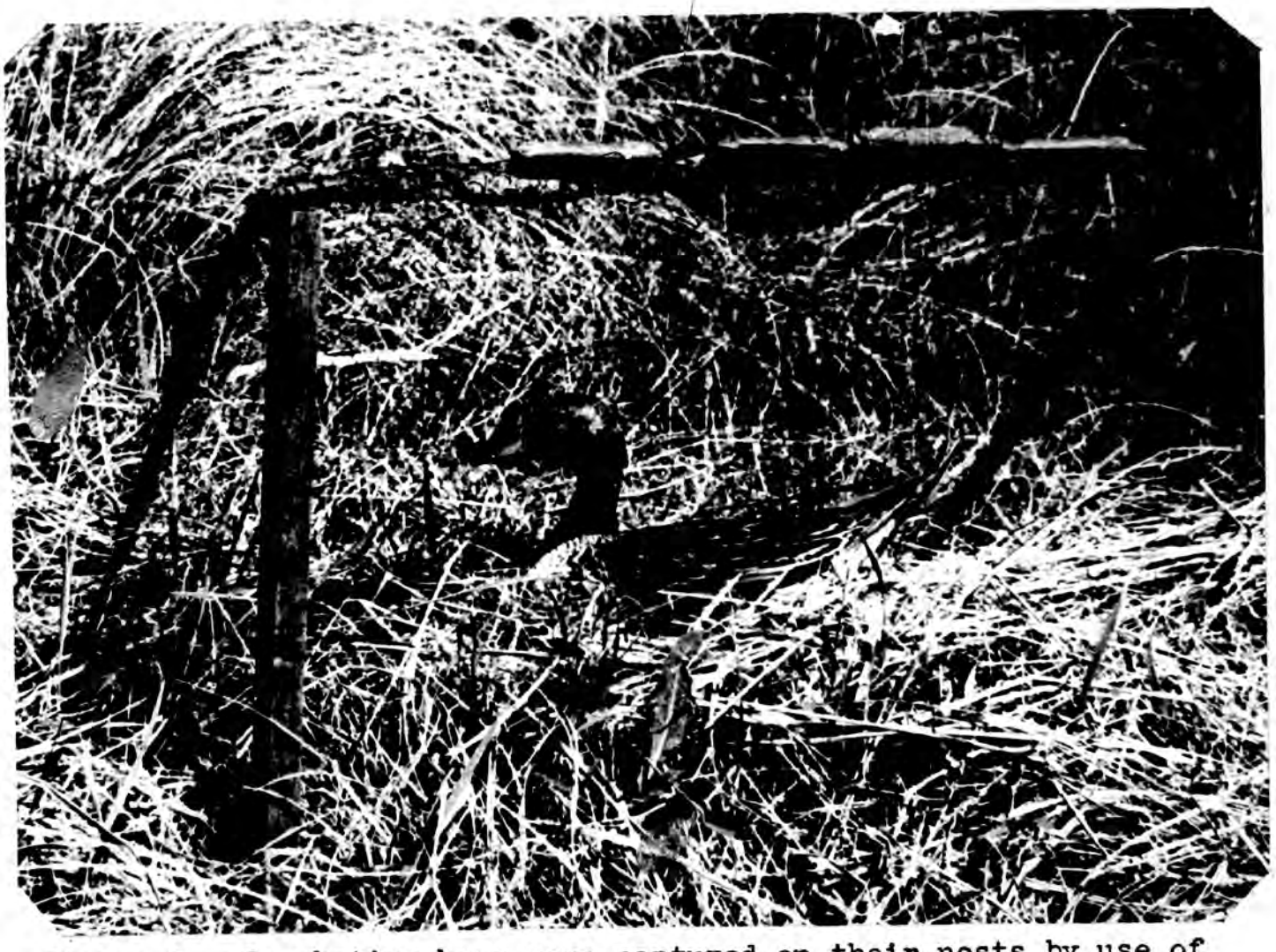


Figure 2 Incubating hens were captured on their nests by use of a drop trap set in place over the nest and tripped from a distance.

nest trap had been set. To capture hens in this period of the nesting cycle I used a large hand net with moderate success. It consisted of a 2-foot circle of 3/8-inch blacksmithing iron attached to a 5-foot pole and covered with netting. Its success depended upon the stealth of the operator in approaching the nest and placing the net squarely over the hen. The value of this kind of trap also varied with weather conditions and cover types. In windy damp weather when the noise of an approaching person was muffled, it worked fairly well. Nests located along the roadside ditch banks were easily approached. In open stretches of cover, where dead vegetation crackled loudly underfoot, a quiet approach was impossible and trapping was difficult. To accomplish precision in placing the net, the nest was marked when found. By placing two small sticks eighteen inches from the nest on the north and south sides, its exact position was indicated.

Airplane-dope Marking.--In my experiments at Delta I found that this paint (several brands of which were tried) was highly successful. The kind I liked best was made by the Testor Chemical Company, Rockford, Illinois.

This quick-drying paint has been used by many workers with small birds, and the technique has been handed from one to another. On its first use on birds Dr. Josselyn Van Tyne of the University of Michigan writes me (letter

dated February 3, 1950), "As far as I know the first person to use airplane dope to mark live birds was Arthur E. Staebler, then a graduate student here.... I think he first used it in the winter of 1941-42." Of its use Dr. Van Tyne says, "The method is an excellent one and I use it frequently. We now put the colors on the tail only (contour feathers mat badly and are unsatisfactory). We apply the color with a bit of cotton held in forceps. We sometimes renew the color from time to time but it may last two or three months or more without renewal."

In marking waterfowl I found that, in addition to painting the tail feathers, the proximal half of the primaries could be painted to increase the number of color combinations. Certain precautions in its use were necessary so that the feathers did not stick together or become too heavy. I applied the paint to the primaries with a dry coarse plant stem. By holding the wing in a stretched position, the plant stem could be run over the length of the primaries and the surface covered. The primaries were held in this position until the paint was dry (Figure 3). This required a few minutes' time. If the color did not show up well, another coat was applied, care being taken not to get an over-load of paint near the ends of the primaries. The technique worked better on the larger ducks, mallards, pintails, and gadwalls, than it did on the smaller blue-

Figure 3. Airplane-dope paint was spread on wings and tail to identify individuals.

winged teals and shovellers. Early in the study it was noticed that the smaller species could not carry the heavy weight of paint on their primaries with ease. For this reason the paint was put on the proximal end of the primaries and care was exercised to avoid putting it on too heavily.

I found that white, yellow and red proved satisfactory for marking waterfowl for field identification in renesting and behavior studies. When properly applied the birds in flight could be identified with an 8-power glass at a distance up to five hundred yards. The marking lasted for a period of about two months.

By using red, yellow and white paint on wings and tail, sixty-two color combinations could be obtained for each sex and species of waterfowl. Some of these were easier to see on a flying bird than others. In the renesting study hens were usually identified as they flew off the nest in front of us. Birds whose identifying colors were not clearly seen on flushing could often be observed at a later time when they were flushed again from the same spot.

Colored Bands.--The colored celluloid band was used as a more permanent marker of individuals. The shortcoming of this band when used on waterfowl is that it is sometimes lost. For example, of thirty pintails released near Delta, five had lost their bands within six weeks. Of ninety-one

Canada geese banded at Delta, twenty-four had lost their bands during the following two months. On the other hand, a wild shoveller hen banded by me in the spring of 1947 was still wearing her colored marker in 1950 after six migration flights.

Despite their shortcoming, the colored bands now available are indispensable aids in the identification of individual birds through one season and often from one season to the next.

The efficiency of colored band markers was increased when ideal loafing places were created. On the nesting study area I could observe banded birds only when they were standing on the edges of grazed potholes, sandbars or clear ditch banks. Where natural situations were lacking, I anchored floating logs on small water areas. In this way I was able to make frequent records of the color-banded birds.

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During the course of the study well over a hundred people helped in one way or another to carry on the field work, laboratory work and manuscript work. Some of them were visitors who joined in nest hunting, trapping and band-

ing or making observations. Many were farmers on the prairies who reported nests, brought in eggs or pulled us out of the April mud. The list of people who contributed to this study is too long to be completely presented here. Only those who contributed the most along with mention of their contributions are listed.

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CHAPTER I

MIGRATION AND SPRING ARRIVAL

Among the seasonal events on the northern prairie none is more prominent in the minds of men than the return of waterfowl. Wherever people gather one hears talk of the ducks. Of the prairie provinces of Canada these discussions are as characteristic as talk of crops and weather. They voice the hope of the winter-weary who look to the land, to seeding time, and to an abundant summer.

But the return of waterfowl does not mean the end of cold, ice, and snow. The lakes, sloughs and ponds still hold their frozen edges; and large snowdrifts remain in the prairie "bluffs", those narrow shelter-belts of timber that border meandering creek beds and lake edges. Winter is still championed by occasional snowy owls perched on hay-stubs and fence posts. Snow buntings flock over black fallow soil and temporary water sheets.

Here on the shallow ponds, before spring has laid true claim, the first ducks and geese will rest. Mallards, pintails and Canada geese come first; and, as their numbers increase and the temperature rises, new species swell the list of arrivals.

Arrival of Spring Migrants.--The dates of the first arrival of surface-feeding ducks at Delta over a twelve-year period are given in Table 2.

TABLE 2. SPRING ARRIVAL DATES OF FIVE SPECIES OF DUCKS AT DELTA, MANITOBA, 1939-1950 (Compiled by H. A. Hochbaum and the Writer)

Year	Mallard	Pintail	Gadwall	Shoveller	B-w Teal
1939	Mar.29	Apr. 3	Apr.22	Apr.23	Apr.26
1940	Apr. 7	17	23	21	22
1941	4	8	12	10	27
1942	Mar.23	3	25	12	21
1943	Apr. 3	5	17	13	21
1944	4	10	17	15	19
1945	Mar.20	Mar.20	24	27	27
1946	20	20	12	12	12
1947	Apr. 2	Apr. 2	26	9	28
1948	10	10	15	15	20
1949	2	7	21	9	20
1950	9	19	May 9	22	May 3
First	Mar.20	Mar.20	Apr.12	Apr. 9	Apr.12
Average	Apr. 2	Apr. 5	.21	15	23
Last	10	19	May 9	27	May 3
Standard Deviation in Days	7.0	8.0	7.0	6.0	5.0

During an extremely early spring the first mallards and pintails arrive at Delta by the last week in March. During a late spring, however, they will be seen about three weeks later. Sometime within this three-week span one may expect to see the first mallard and the first pintail within a day or two of each other. As the main flight occurs, the two species will be seen together.

The later arriving shovellers and blue-winged teals do not show so wide a span of variation in arrival dates. The Gadwall which does not occur in large numbers at Delta is also a late arriver but its arrival date is not easy to determine because of the comparatively few birds.

The tendency for early migrants to be less consistent in arrival date than later migrants is well known among other kinds of birds. In regard to this point Hickey (1943:24-25) says, "It is well known, for instance, that the first spring migrants vary widely in their arrival dates from year to year. From 1923 to 1927, I saw my first migrant robins around New York City on March 11, March 12, March 15, January 30 and February 26. As spring progresses, birds arrive with more and more regularity. Going through my notebook for an extreme example, I notice that on successive years my first redstarts were seen on May 1, May 1, May 2, May 10, and May 6."

Although we recorded the date of first individuals as

accurately as we could, it was apparent that the date of main flight had more significance in the picture of spring arrival. A lone bird was often cited several days before another individual was seen, the main flight occuring a week or more later.

The main flight of other species was comparatively inconspicuous and therefore more difficult to record. First arrivals coincided closely with the main flight of mallards and pintails.

A comparison of first arrival dates and dates of main migration of mallards and pintails for the years 1946 through 1950 is given in Table 3.

The First to Arrive.--Do the residents arrive on the breeding ground before the main flight of ducks pass through the area? In other words, are the first ducks to be seen each spring at Delta those which will nest in Manitoba, or are they the transients with the farthest to go? In the spring of 1950 I watched closely to see whether there was a mass movement of birds through the region before our resident birds arrived. The first lone pair of mallards was seen circling a nesting meadow within the study area on the evening of April 17. The hen was quacking noisily and exhibiting the behavior I had come to associate with the seeking of a nest site. Although the hen and her drake were not marked, further observation indicated that

TABLE 3 DATES OF FIRST ARRIVAL AND MAIN FLIGHT OF MALLARDS AND PINTAILS FOR THE YEARS 1946-1950 AT DELTA, MANITOBA

	Mallards		Pintails	
Year	First Arrival	Main Flight	First Arrival	Main Flight
1946	Mar.20	Apr.10-15	Mar.20	Apr.10-15
1947	Apr. 2	16-20	Apr. 2	16-20
1948	10	21-23	10	21-23
1949	2	10-15	7	10-15
1950	9	19-29	19	19-29

that the hen nested close to the area where the pair was seen that spring evening.

My observations of marked pintails resulted in further evidence that resident ducks preceed the transients to the Delta marshes.

The first pintail to be seen in the Delta region, which includes a wide section of the Portage Plains, was seen on a temporary pond in the study area on April 19. At 9:00 A.M. of that day one pair of pintails was recorded. Two days later two pairs of pintails were seen in the same spot. On the fourth day there were five pairs. On the fifth day there were nineteen pairs and on the sixth day there were twenty-five pairs. On the night of April 24 the edges of the temporary pond froze over. On April 25 the birds were standing together in the same spot on thin ice and their otherwise hidden legs were in full view through my 20-power spotting scope. Six banded pintail hens were among them, birds whose history was known for the previous nesting season. They had nested on the study area in 1949, and the next two months were to show that four of them would be found on nests again. The main flight of mallards and pintails did not pass through the Delta region until April 30 and no other large concentrations of birds were seen on the prairies in the meantime. Hence the resident adults were the first to arrive.

The locations of the nests of these birds in relation to their arrival point in 1950 are shown in Figure 4.

Migration and the Weather.--A comparison of spring arrival dates of five species for 1949 (an early spring) and 1950 (a late spring) is made in Figure 5. The weather data for this figure are based on information given by the Dominion Government Department of Transport, Meteorological Division of the Air Services at Winnipeg. Temperature readings were made at the Winnipeg station, seventy miles east of Delta. Arrival dates are for the Delta region including the Portage Plains immediately south of the Delta marsh. Although some difference in temperature may exist between Winnipeg and Delta, I believe it is too slight to have significance in these comparisons. The "normal" year is an average of temperatures for a period of seventy-six years. In no single year does such a steady rise in daily mean temperature probably exist. Instead, the newly arrived ducks are exposed to constantly changing temperatures. Where open water exists one day, it may be ice the next.

The year 1949 was ahead of normal in regard to the arrival of the first waterfowl and the above-normal temperatures that prevailed. The year 1950 was extremely late in both duck arrivals and temperature readings.

Lincoln (1939:31) describes the spring flight of the

FIGURE 4. RELATIONSHIP OF 1950 SPRING ARRIVAL POINT TO 1949 AND 1950 NEST SITES OF SIX BANDED PINTAIL HENS.

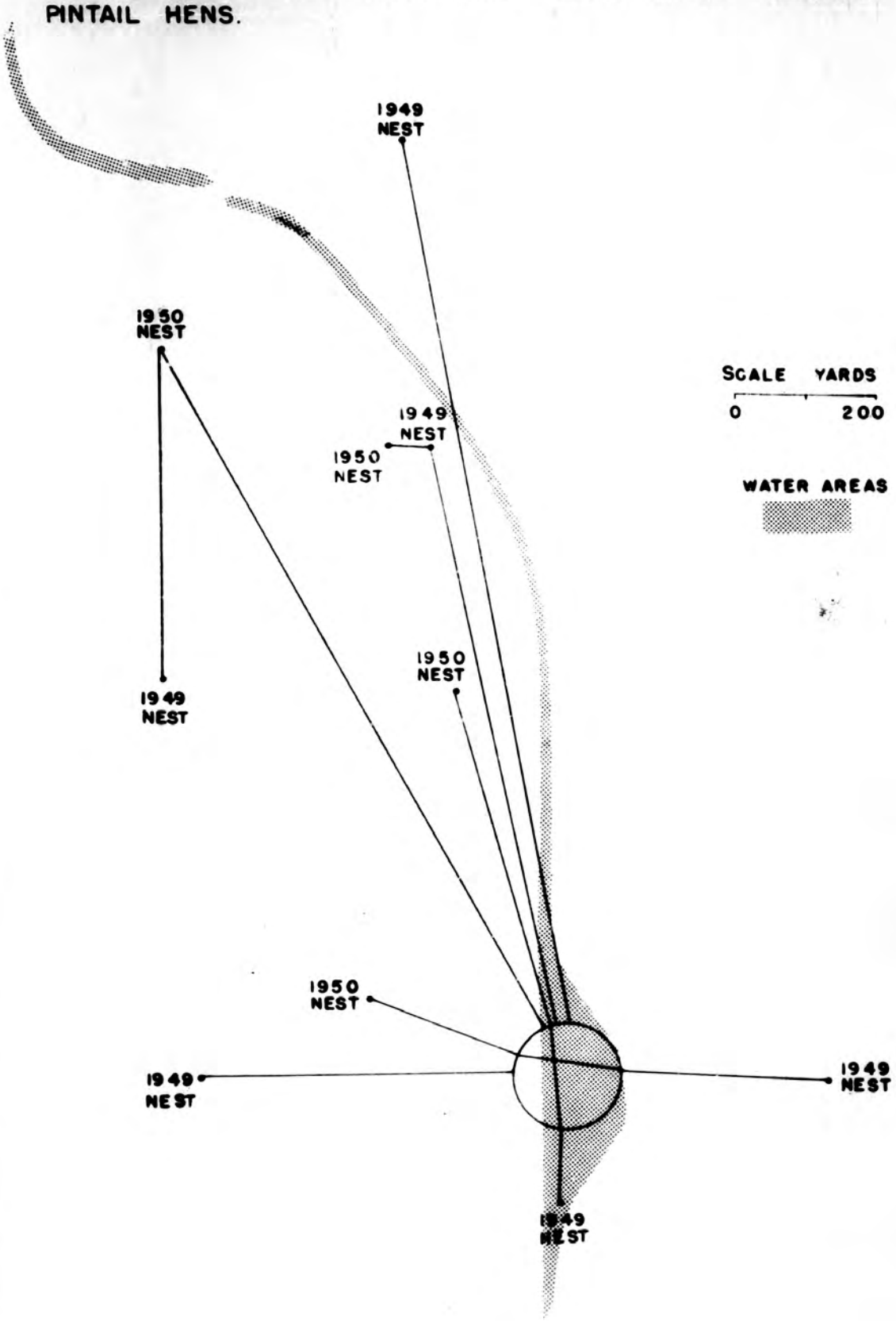
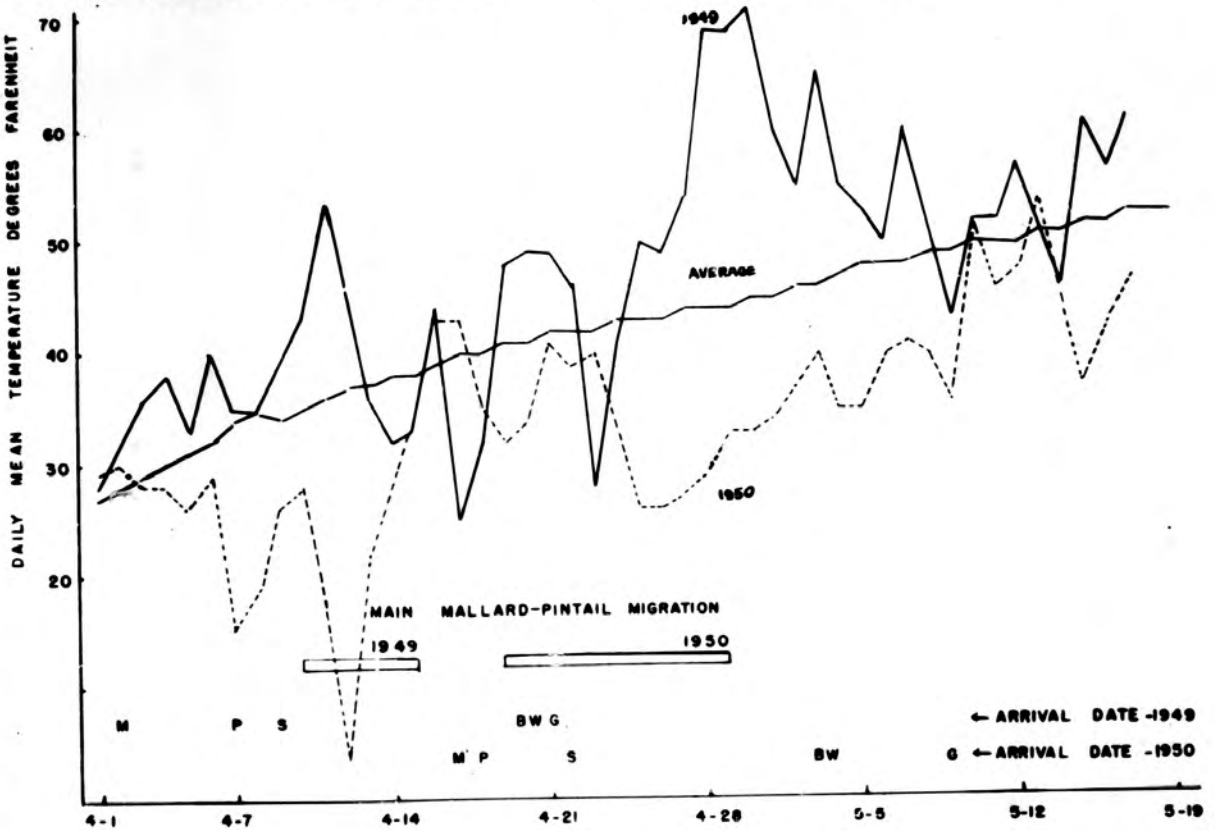


FIGURE 5 RELATIONSHIP OF TEMPERATURE TO SPRING ARRIVAL AND MIGRATION DATES DURING THE YEARS 1949 AND 1950 FOR MALLARD, PINTAIL, GADWALL, SHOVELLER AND BLUE-WINGED TEAL.



Canada goose and says that the northward migration keeps pace with the advance of the isotherm of 35 degrees Farenheit. The mallard and pintail apparently pass northward as fast as open water is available in the manner described by Lincoln, temperature being the dominant factor effecting their rate of migration.

Reverse Migrations.--In Figure 5 we see that temperatures fluctuate, in early spring, between thawing and freezing. Thus, loafing flocks of ducks are sometimes forced to retreat to favorable areas. Hochbaum (1944:14) says that ducks forced from the Delta marsh by cold weather retreat to open holes in the Assiniboine River twenty miles to the south. One such mass movement out of the marsh was seen in the spring of 1950. On April 17 the first mallards arrived, and on April 19 the first pintails were seen. From then on there was open water in the marsh, and mallards and pintails were scattered throughout the marsh in fairly large numbers. In some sections of the flooded prairies large flocks of transients were loafing and feeding. On the morning of April 26, seven pairs of mallards, fourteen pairs of pintails and one pair of baldpates were resting on a large flooded pond on the study area. That night the temperature dropped to twenty-five degrees and left only half of the pond open. The ducks remained there during the day. On the night of April 27

following the heavy freeze, about three thousand mallards and pintails were seen leaving the marsh and flying south over the prairie. This observation was made by Murry Werbiski, a reliable observer, twelve miles south of the Delta marsh. On April 28 the entire population was gone from the study area and very few ducks remained in the marsh. With the return of warm weather and open water on April 30, three days later, the birds were back and the same group of individual pintails, as determined by their leg bands, were again on the study area.

Abortive Migration Attempts.--As Hochbaum (1944:16) has pointed out, incoming arrivals move with a south wind. Only few exceptions to this conclusion occurred and these were explainable. When held up for long periods by poor weather, transient ducks get restless and make attempts to migrate. The attempt failing, they return to their resting place.

This behavior was most noticeable among diving ducks but was occasionally seen among puddle species. Lesser scaups that had come to the big bay near the Delta hatchery were seen starting off over the lake-ridge of trees to the north, were gone for a few minutes only, and were seen returning to the bay from which they had just come. On a May evening in 1950 an instance of a puddle duck migration which was apparently thwarted by a cold north wind was

observed by H. Albert Hochbaum, Peter Ward and myself. Four flocks of pintails and mallards ranging from ten to forty birds were seen coming over high from the south. After heading out over the lake in a northerly direction for about three minutes all flocks turned back toward the marsh, came in and settled down.

The effects of fog on the migration of birds can be observed easily where local fog banks roll across a body of water. On April 16, 1949, I saw a flock of thirty mallards migrating across the Delta marsh toward the lake. A fog bank was hanging over the shore and extended unbroken over the big lake. The mallard flock entered the fog and was thereupon suddenly dispersed. After flaring and wheeling back the flock reformed, returned to the marsh and settled down.

Regardless of wind and temperature I have never seen spring migrating flocks over the Delta marsh when a fog prevailed.

Resting and Feeding Places on Arrival.--Throughout the prairie provinces of Canada the first open water occurs on the fields. These ponds are temporary; most of them disappear by June. Here broad, shallow sheets of water cover old grain stubble; and waste grain along with weed seeds offer food for transient waterfowl. The bare edges make ideal loafing areas where ducks can rest.

When the previous summer has been dry the temporary ponds soon disappear into the earth and ducks will be forced to use small openings in the great marsh. But when the previous summer and fall have been wet the birds can use the temporary ponds through the nesting season.

During the springs of 1946, 1947, 1948 and 1949 nearly all of the large transient bands in the Delta area were found on the flooded parts of the Portage Plains. In the spring of 1950, however, large flocks of transients crowded into the first open water on the Delta marsh. This cannot be attributed entirely to an absence of flooded areas on the plains. The particular areas which held large numbers of transients in 1949 were still available in 1950 and appeared to be in the same condition as they had been in 1949. They did not, however, attract ducks in 1950, and I have no information to explain this apparent inconsistency.

Activity of Transients.--Activity of the transients during the spring passage is largely confined to feeding, loafing and courting. During this period mallards and pintails sometimes make daily or twice-daily trips to old grain stubble to feed. In the Delta region I have not seen other species make spring stubble flights.

The loafing of these birds is done largely on the dry banks of prairie ponds where great masses of them settle down together. On windy days they seek the shelter

of roadbanks and other similarly sheltered places.

Other than stubble flights, movement is confined to flights resulting from disturbance and to aerial pre-nuptial courtship.

Sexual Behavior.--By the time the puddle ducks reach Delta in April most of them are paired. One species, the baldpate, is an exception to the rule. On only two occasions have I seen pintail courtship display in the large flocks at rest on the Portage Plains. I suspect, therefore, that the last hens to obtain drakes do so before they reach their breeding marshes. I have never seen mallard displays in spring concentrations at Delta.

Of the time of pairing in the mallard and pintail, Hawkins observed that most of some ten thousand mallards in gatherings near Amarillo, Texas on January 24, 1943, were in pairs; and that, on the same day, a smaller percentage of pintails were paired (Hochbaum, 1944:21).

Thus, in a spring concentration of loafing pintails and mallards such as those found in Manitoba, few courting birds are seen. When a flock contains some baldpates, however, the air is full of courting parties. This species seems to be the last of the puddle ducks to pair. On one occasion in the spring of 1947, I saw twenty-three drakes pursuing one hen over the Delta marsh. In the spring of 1950 large groups of baldpates stopped on a

flooded pasture in the south end of the study area. Courting parties of four to ten drakes were common. These birds were transients as few baldpates nest in the Delta region.

The green-winged teal, an uncommon migrant through Delta and a rare nester in the area, was seen in courtship once. That occurred in the spring of 1949.

Distance Traveled and Time Involved.--In regard to the time of departure from the southern marshes Bent (1923:144) quote Beyer as saying of Louisiana, "...winter visitant individuals of the mallard, move northward very early, probably never later than the middle of January." Leopold (1925:9) gives late January as the time of the first mallard and pintail flights along the Rio Grande valley. Lewitt (1948:329) gives a January high for the pintails wintering along the Texas gulf coast and a large drop in February. He says, "...the pintails were the first to become restless, leaving in large numbers early in February." Of the northward flight of the pintail in Louisiana, Lynch (letter, January 16, 1948) writes me, "...the returning transients show up here in January (1947, first week in January, 1949, middle January)...and the migration lasts for about a month." Thus, by the time the ducks reach Delta, they have probably been enroute for about two and a half months.

Porsild (1943) says that pintails arrived May 9, 1934 in

the McKenzie River delta. Dixon (1943:53) gave May 29 as the arrival date for pintails on the arctic coast of Alaska in 1914. Dice (1920:177) gives the pintail's arrival in interior Alaska on May 13. Gabrielson (letter dated January 25, 1951) gives the early dates for spring arrival of pintails in Alaska as follows: "Selawik River, April 12; Adak Island, April 13; Forrester Island, April 20; Kuiu Island, April 25, Ketchikan, April 26; St. Michael, April 28; Nulato, about May 1; Bethel, May 1; Kantishna, May 7; Hooper Bay, May 8; Porcupine River at the 141st meridian, May 9; Base of the Kigulik Mountains, May 11; Kobuk River, May 14; and Fairbanks, May 17."

Thus, many of these ducks which stop at Delta have been on the way for two months since leaving their winter home far in the south. For those whose destination is the far north the entire migration flight will take about three months and the distance traveled may be in excess of four thousand miles.

Species Association during Migration.--The species found migrating together most commonly at Delta in spring are mallards and pintails. As has been shown in Table 2 these species arrive at nearly the same time. Also, the main passage of these ducks through the area occurs at the same time for both as shown in Table 5. Their course lines, time of day of migration, loafing areas and feeding areas

are generally the same. On almost every occasion during my study sex ratios and flock size observations for one of these species yielded information on the other.

On the flooded prairie fields and pastures it is not uncommon to find nearly all species of waterfowl together in spring. The baldpate, in particular, which moves through the Delta region in large numbers seems constantly to be associated with pintails and mallards in loafing concentrations. The blue-winged teal, green-winged teal, shoveller and gadwall prefer areas where at least some of their food can be taken as it floats on the surface of water. For this reason areas that dry up in summer and then come up to heavy growth of seed-bearing plants are especially attractive to these species. Such areas are numerous on the Portage Plains and, when flooded in spring, attract large numbers of migrating ducks from this group.

Flock Size During Migration,--Only for the mallard and pintail at Delta is it possible to get a large volume of figures on the size of migrating flocks. Sample counts of fifty-four such flocks of these species have averaged twelve birds per flock. The biggest flock in this sample numbered thirty-five. Occasionally a lone bird was seen migrating along the path taken by the others.

Sex Ratio of the Spring Flight.--Hochbaum (1944:15) has shown that a great preponderance of drakes exists among diving ducks as they arrive at Delta in spring. Of

the mallard and pintail he says that an almost exact 50:50 ratio exists as these species arrive. That only a slight excess of drakes exists in these two species is borne out by the sex ratio data collected by the entire staff of the Delta station since 1939. In a sample of 3,678 mallards counted between 1939 and 1950 the sex ratio was 51:49 in favor of males. During the same period a sample of 4,584 pintails showed a sex ratio of 53:47 in favor of males. There appeared to be little variation from one year to the next, even though yearly samples were small.

Although I have never seen spring groups at Delta in which males were greatly in predominance, there is some evidence that male flocks occasionally migrate as such.

A. Starker Leopold made the following observation at Lake Tecocomulco near Apam, Hidalgo, Mexico on February 4, 1945 (letter dated April 5, 1948): "Monday morning an enormous flight of pintails came over heading north. Great skeins strung one behind the other moved over without giving our lake a good look. Only a few flocks dropped down to swing the lake, and I actually didn't see any of these alight. Interesting enough of the 3,500 to 4,000 birds I estimated were in the flight, not over a few hundred were hens. Fully 90 per cent were drakes in their full spring dress, and some bunches of a hundred birds wouldn't have a hen in them. Even the pintails using the lake are 80 to 90 per cent

drakes. Either the hens winter elsewhere or they start north later." Similar evidence of drake pintail flocks is given by Bailey and Wright (1931:134) who say of Louisiana in winter, "Often several hundred males will be seen in a single flock." Petrides (1944:569) suggests that a differential sex migration occurs in the pintail and that a differential winter distribution of sexes also exists.

For Louisiana Lynch writes me (letter dated January 16, 1948): "Transient flocks in mid-October run heavily to adult males--sex ratio is pretty even toward the end of the winter but not among the transients which show up here in January; and there is a marked separation of sexes almost as conspicuous as during the southward flight the previous fall."

SUMMARY

1. Mallards and pintails are the first ducks to arrive on the northern prairies in spring. For these two species there may be a yearly variation of about three weeks in time of first arrival. Later arriving species such as the shoveller and gadwall show less variation in date of spring arrival.

2. The mallards and pintails often migrate together in spring; most migrating flocks of these birds have some of each species.

3. From evidence obtained through banding it seems likely

that resident ducks arrive in an area before the migrants bound for distant places pass through that area.

4. Temperature is the dominant factor effecting the northward movement of the mallard and pintail but has less effect upon the migration of the later migrating species.

5. Reverse migrations are occasionally seen following freezing weather after the first ducks have arrived on the northern marshes.

6. Abortive migration attempts follow long periods of undesirable weather which have held up the ducks in their northward journey. Ducks have been seen in an apparent attempt to migrate but are turned back by undesirable weather.

7. The favorite resting places for surface-feeding ducks upon arrival on the northern prairies are the shallow flooded grain fields. Their activity here is largely confined to feeding, loafing and courting.

8. Nearly all mallards and pintails are paired by the time they arrive in Manitoba. The baldpate is the latest species to pair and pairing courtship is common during spring passage in this species.

9. The northward movement of some species of waterfowl begins as early as January and is not terminated for those going the farthest until the middle of May. The distance traveled by some is in excess of four thousand miles between

winter headquarters and summer breeding marshes.

10. The sex ratio in mallards and pintails arriving at Delta in spring runs very nearly even. There is some evidence, however, that flocks of drake pintails may migrate as such.

CHAPTER II

MIGRATIONAL HOMING

On June 3, 1947, I captured and banded a shoveller hen on her nest near the center of the study area. One year later I caught the same hen on a nest eighty yards from her 1947 nest site. Again, in 1949, she returned and nested 250 yards from her 1948 location. In 1950 she returned again. Her 1950 site was located just 210 yards from her 1949 nest (Figure 6). Thus, during four consecutive years she was known to return to the same nesting meadow within an area of approximately seventy-five acres. Since no waterfowl winter in Manitoba, and Manitoba shovellers probably go to the Gulf Coast States of the United States or farther south to winter (Kortwright, 1943:221), the return of this hen involved two flights of at least two thousand miles each year. This remarkable feat is one illustration of the ability and habit of wild ducks to "home" to the same breeding area year after year.

This hen was one of forty-one hens that returned to their nesting meadows on my study area the year following first capture and banding.

The ability of adult birds of many species to do this has been known for many years. The number of species of birds in which homing has been found now includes representatives from nearly all families of birds. Since much of the work in the past has been of an experimental nature

Figure 6 Shoveller hen number 47-604004 returned to the same nesting meadow in 1947, 1948 and 1950.

not necessarily involving wild birds, it may be well to define "migrational homing." A good definition has been given by Hickey (1943:38-49) who differentiates between the homing of two birds and says, "Homing has been defined as the ability of animals to return great distances over a route, part of which is unknown or without landmarks", and speaks of (1) experimental homing and (2) migrational homing. The first of these involves the returning home of birds that have been experimentally moved. The later term refers to the natural movement of wild birds to the place where they were in previous years. It is the migrational homing of wild birds to their nesting grounds that is treated in this paper.

Homing of Adult Hens.--During the three-year nest trapping period 152 adult hens of the five species of meadow-nesters were trapped on their nests and banded with aluminum and colored bands. Of this number forty-one or 27 per cent were known to return and nest in the same meadow a following year. These data are summarized in Table 4.

In order to determine how strong the tendency to return is, we need to know what percentage of the survivors returned. Thus, in considering the statistical validity of our data, two things must be borne in mind: (1) the percentage of returning birds that were found, and (2) the

TABLE 4 NUMBER OF ADULT NEST-TRAPPED HENS KNOWN TO RETURN TO THE SAME NESTING MEADOWS A SECOND YEAR

Species	Banded	Returned	Percentage
Mallard	15	2	13
Pintail	44	17	38
Gadwall	16	6	37
Shoveller	19	8	42
Blue-winged Teal	58	8	14
Totals	152	41	27

expected mortality between one nesting season and the next. To appraise these data, each species is treated separately.

Although I know that some returning birds were not found, I believe that the number missed was small. The habitat of the study area was such that excellent opportunities for seeing birds existed. Bare, grazed edges of the roadside ditch and of several large potholes made excellent loafing areas where banded hens could be observed through a 20-power spotting scope. Anchored logs put in ditch and sloughs made even more loafing places. In early morning when the road was untraveled, hens were often seen standing on the gravel and many were identified there. In the spring of 1950 late cold weather froze the shallow ponds and mallards and pintails, with legs exposed, loafed as a flock on top of the ice. Furthermore, continuous nest trapping placed numerous hens in my hands giving me an opportunity to see their leg bands.

I had evidence that all females were not found when banded hens which I had not observed on the loafing bars were nest-trapped. Again, when three were caught wearing bands put on two or more years earlier and which had not been found during the intervening years, they had apparently been missed. One shoveller banded in 1947 was not found in 1948 nor in 1949 but was caught in 1950. Another shoveller hen banded in 1948 was not seen in 1949 but was seen in 1950.

No mallard, pintail or blue-winged teal hens were found returning to the study area a third year which had not been also seen in the year following first banding.

The question may arise as to whether some returning hens may have nested just outside the study area and were thus missed. As will be shown later in the discussion of nest locations, it is unlikely. Had any nests of returning hens been located outside the study area, their distances from the previous year's nest site would have had to be at least four times as great as the maximum known distance between the yearly nests of individual birds. This is because the study area was surrounded by non-useable nesting cover, made up of dense phragmites seldom used by meadow-nesting species.

Some clues to expected mortality can be obtained when we examine published data from banding studies. In the appraisal of my homing returns as compared with expected survival I have chosen to begin with the pintail, the species on which I have obtained the most data.

Adult Hen Pintails.--During the three years of banding from which a following year's observation was made, forty-four pintail hens were nest-trapped. Of this group seventeen or 38 per cent were known to return a second year to nest. No exhaustive work has been done in all of the North American flyways to show how long pintails survive and what percentage

can be expected to return a second or successive years to the same nesting meadows. Also, there is no way of knowing how old the pintail hens were when first banded on my area.

In British Columbia Munro (1944:61) banded 6,554 pintails between 1923 and 1943 and obtained a recovery of 1,154. Munro says, "Of this total 926 were taken in the first year after banding and the remainder as follows: second year, 140; third year, 36; fourth year, 19; fifth year, 14; sixth year, 6; seventh year 1; eighth year, 1; ninth year, 5; eleventh year, 2." Thus, 80.2 per cent of the recoveries were made the first year after banding.

Because this series of recoveries includes birds banded up to 1943, its summarization in 1944 inevitably leaves the older age classes unequally represented. One can, however, study the series as a minimum estimate of the average survival rate of adult pintails on the Pacific Coast during the years between 1924 and 1943. To do this, I have assumed for the purpose of this analysis that all Munro's recoveries referred to mortality reports (a small minority undoubtedly did not), and I have excluded reports of birds recovered within one year of their date of banding (since many of these unquestionably were banded while juveniles). The method of analysis otherwise follows that of Lack (1940:168) and is summarized in Table 5.

Since additional reports of these British Columbia birds in their eleventh year of life are possible as late

TABLE 5 CALCULATION OF APPROXIMATE SURVIVAL RATE IN PINTAILS FROM DATA GIVEN BY MUNRO (1944:61)

Years After Banding	No. Dying Each Year	No. Alive at start of Each Year	No. Alive at End of Each Year
1-2	140	228	88
2-3	36	88	52
3-4	19	52	33
4-5	14	33	19
5-6	6	19	13
6-7	5	13	8
7-8	1	8	7
8-9	5	7	2
9-10	0	2	2
10-11	2	2	0
Total	228	452	224

Average Minimum Survival Rate = $\frac{224}{452}$ = about 50 per cent per year.

as 1954, it is clear that the average survival rate of pintails probably exceeds 50 per cent per year. Average annual survival rates for mallards and black ducks banded in Illinois have already been calculated as slightly in excess of 50 per cent (Bellrose and Chase 1950:12). The figure here obtained is a plausible one.

Using 40 per cent as an approximation of the known return of banded pintails to Delta and assuming that another 10 per cent returned but were not found, the homing rate would be 50 per cent. If the survival is in the neighborhood of 50 per cent, this would mean that 100 per cent of the survivors returned. In any event it is at least clear that the majority of surviving pintail hens do return to the vicinity of their previous nesting sites.

Adult Hen Shovellers.--Of nineteen adult hen shovellers trapped and banded during 1947, 1948 and 1949, eight or 44 per cent were back on the same nesting meadow in years to follow. Very little published information exists on survival rates for this species. At the Bear River Refuge in Utah, Van Den Akker and Wilson (1950:371) say that of 1,087 shovellers banded eighty-nine recoveries were reported. Fifty-five or 61 per cent of these occurred during the first year, twenty-two or 24 per cent the second year and the remaining 17 per cent in the third and successive years.

There is no way to determine how these western data apply to Delta shovellers; or how much bias may occur due

to the small sample of shoveller hens banded at Delta. Assuming, however, that the Delta shovellers have a mortality rate similar to the Bear River shovellers, it seems likely that nearly our entire surviving population of banded shoveller hens returned to its nesting meadows a second year.

Adult Hen Gadwalls.--Sixteen adult gadwall hens were nest-trapped and banded during 1947, 1948, and 1949. Of this group six or 37 per cent returned to nest again in the same meadow. Just as in the instance of the shovellers and pintails, no accurate figure on mortality by years exists for the Mississippi flyway population. In the west where it is a more abundant species Van Den Akker and Wilson (1950:366) show that of 510 gadwalls banded, thirty-one returns were received. Of these nineteen or 61 per cent were killed the first year, six or 19 per cent the second year, and the remainder the third or successive years.

If the mortality found in this small sample of western birds is an indication of the kill farther east, it appears likely that almost our entire surviving population of adult gadwall hens returned to the nesting meadows of the previous year.

Adult Hen Blue-Winged Teal.--The blue-winged teal leads the list in number of adult nest-trapped hens banded during this study. But despite a comparatively large number of banded birds, the return of hens to the same nesting

meadows a second year was conspicuously small. During 1947, 1948, and 1949, fifty-eight adult blue-winged teal hens were nest-trapped and banded. In the three years of observation following, only eight or 14 per cent of these hens were known to return a following year. Considering the consistently higher returns from smaller samples of pintails, shovellers and gadwalls, I believe that this low return of teal has significance.

For this species better survival information exists. Bellrose and Chase (1950:14) examined the returns from 6,252 blue-winged teal banded in Illinois and found that the yearly mortality rate for the first five years following banding averaged 57 per cent. In other words the yearly survival rate would be 43 per cent. They conclude that although the blue-winged teal does not suffer the shooting losses that mallards do, its mortality is higher.

Of all ducks, the blue-winged teal has the lowest survival rate yet calculated. One would therefore expect a relatively lower rate of homing. This may not be the only reason for low homing return. Perhaps the blue-winged teal does not have so strong an instinct to return to the same nesting meadows as does the pintail. On the Delta study area, the nesting population of this species climbed rapidly during the period of study. The climb occurred despite the fact that in the course of the renesting study

few nests hatched on the area. Where the birds came from which made up the population increase was not known.

Adult Mallard Hens.--During the three years of banding, fifteen adult mallard hens were nest-trapped. Although this figure was about the same as that for gadwall and shoveller, only 10 per cent of the mallard hens or about one-fourth as many as gadwalls and shovellers, were known to return a second year to nest.

This low mallard return may have been partly caused by the difficulty of trapping mallard hens on the nest. Furthermore, the mallard is a relatively mobile species and the loafing places of the hens which nested on the study area may have been so far away that I missed seeing them as they stood.

Of all species here treated, the mallard would be expected to have a lower survival rate than any other except the blue-winged teal. In summing up the mortality and survival rates of these two species Bellrose and Chase (1950:25) say, "Although the blue-winged teal does not suffer the shooting losses that mallards do, its mortality is higher." These writers found through a study of banding returns that the yearly survival rate in mallards was 50 per cent and the yearly survival rate in blue-winged teals was only 43 per cent.

In terms of percentage of ducks in the hunters' bag

the mallard rates high throughout the Mississippi valley. At Delta during the years 1938-41 mallards made up 34 per cent of the entire bag (Hochbaum, 1944:133). During the years 1946-1950 it made up 56 per cent. In the Illinois valley Bellrose (1944:343-5) found that the mallard made up the bulk of the kill. During the years 1938 through 1942 the mallard and black duck made up between 57 and 75 per cent of the total bag there.

Summary of Adult Hen Data.--About 40 per cent of pintail, gadwall and shoveller adult nest-trapped hens of unknown age were known to return a second year to their same nesting meadows. Only 10 to 15 per cent of mallard and blue-winged teal hens were known to do so.

A summary of data pertinent to the homing of ducks to their breeding ground is seen in Table 6. A low kill of pintails at Delta coincides with a high return of pintails a second year and a high kill of mallards at Delta coincides with a low return of mallards a second year. The calculated survival rate for these two species, however, is nearly the same although the issue is clouded by the fact that the pintail survival figure was calculated for western birds instead of for Mississippi valley birds.

A low kill of blue-winged teal at Delta does not coincide with a high return. However, the low return of this species is reflected in the low survival figure. This is in agreement with the conclusion of Bellrose and Chase (ibid:25) who

TABLE 6 PERCENTAGE KILL, PERCENTAGE RETURN A SECOND YEAR AND CALCULATED SURVIVAL RATES FOR FIVE SPECIES OF DUCKS

Species	Delta '38-'41	Ill. Valley '38-'41	Return Delta Second Year*	Survival Rate
Pintail	5	10	38%(44)	50% (Munro)
Gadwall	5	2	37 (16)	?
Shoveller	4	2	44 (19)	?
B-w Teal	5	2	14 (58)	43% (Bellrose and Chase)
Mallard	34	63**	10 (15)	50 (Bellrose and Chase)

*Number in bracket represents number of birds banded.
** Black duck included with mallard. Illinois data from Bellrose (1944).

say that although the hunting loss in blue-winged teal is lower than the hunting loss in mallard, the mortality from other causes is apparently higher.

It is apparent that we need to know more about the survival rates of the pintail, shoveller and gadwall in the Mississippi valley.

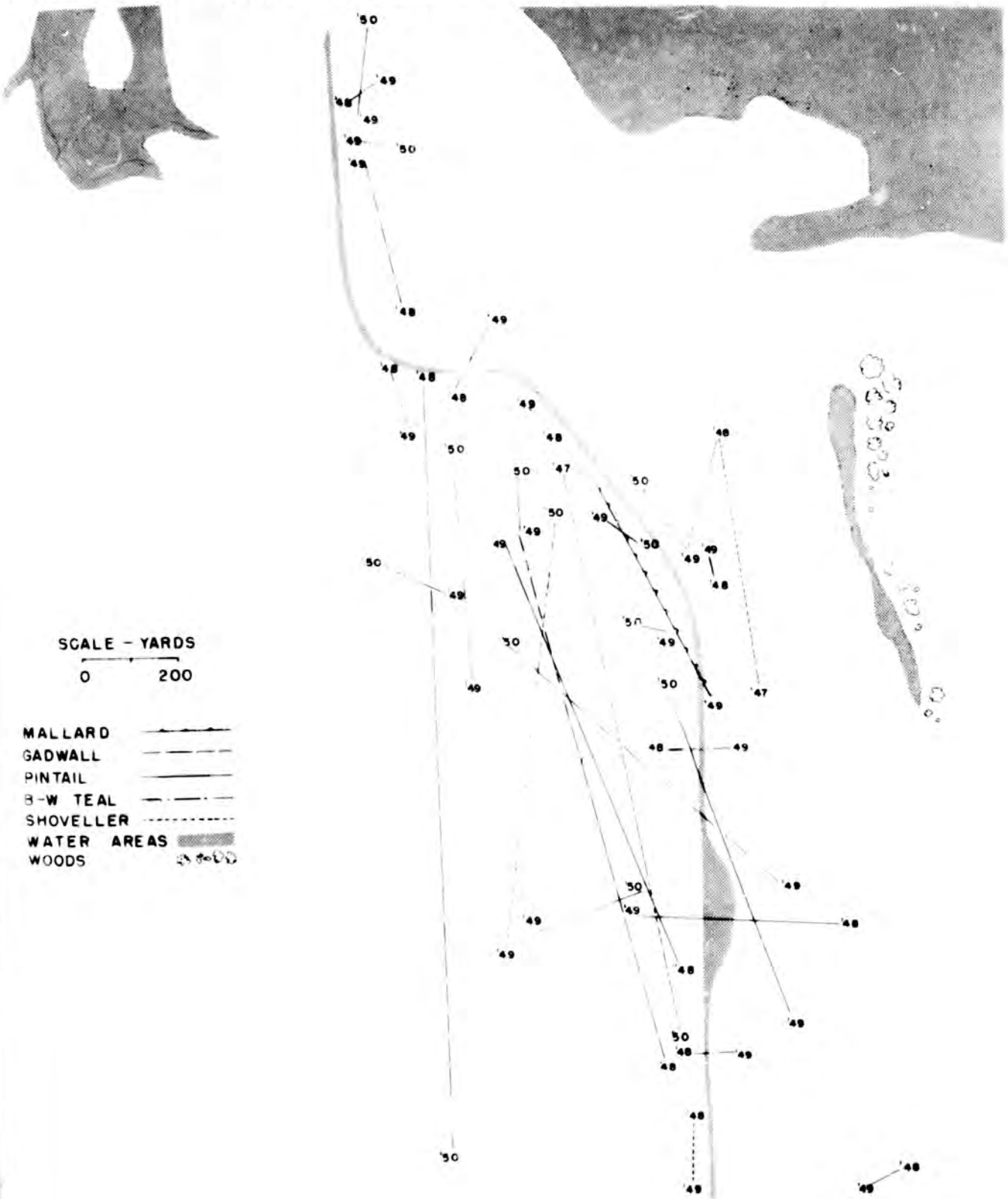
Locations of Second-year Nests.--Returning hens followed a consistent behavior in locating their second-year nests. On the long narrow study area all adult hens returned to the same general portion of the area where their former nest or nests had been located. In no case did a hen which nested in the south end one year nest in the north end the next and vice versa. The average, maximum and minimum distances between nests of different years are given in Table 7. The locations of the nests in relation to each other are given in Figure 7. It will be noticed that this map shows very nearly the same pattern as the renesting map in Chapter VII.

Adult Hens Returning Several Years.--Table 4 includes hens which returned to nest for two or more years, but it does not show the persistency with which some individuals returned. Of the fifteen pintail hens banded in 1948, six or 40 per cent returned in 1949 and three of them or 20 per cent returned also in 1950. Of the shovellers one hen was known to return for three consecutive years after first

TABLE 7 DISTANCES IN YARDS BETWEEN NESTS OF DIFFERENT YEARS OF INDIVIDUALS OF FIVE SPECIES

Species	Number of hens	Maximum Distance	Minimum Distance	Average Distance
Mallard	1	500	500	500
Gadwall	5	1600	120	830
Pintail	9	750	15	315
Shoveller	7	1160	30	306
Blue-winged Teal	5	750	40	256
Totals and Averages	27	952	141	441

FIGURE 7 NEST LOCATIONS OF RETURNING INDIVIDUAL HENS OF FIVE SPECIES DURING DIFFERENT YEARS.



banding; one other, banded in 1947, was not seen in 1948 or 1949 but was found nesting in the area in 1950. Of the nine shovellers banded in 1948, three were found on the area in 1949 and one of these was found there again in 1950. Of the eight gadwalls banded in 1948, three returned in 1949 and two returned to the area again in 1950. One of the fourteen blue-winged teal hens banded in 1948 was back on the area again in 1950, although only three of the 1948 birds had been seen there in 1949. No mallards were known to return for more than one year following their first nest-banding.

Again the record leads one to conclude that ducks normally return to the original nesting meadow a second and third and fourth year or so long as they survive and the area remains suitable.

The Return of Juveniles.--Until recently there has been considerable doubt that juveniles returned to their natal home. In 1939 Lincoln (p. 74) wrote: "Despite the great juvenile mortality, the weight of evidence from the banding data appears to indicate that 'homing instinct' does not operate until after the individual has nested and that the location of the first nest is largely a matter of chance in obtaining possession of unoccupied territory. Exceptions to this are of course birds that nest in colonies."

Hickey wrote (1943:39): "Some uncertainty still surrounds the question where birds nest for the first time. Do they return to breed in the locality of their birth? Or is the selection of their first nest site fortuitous--'anywhere', as one authority has postulated, 'within the natural range of the species'?" Hickey goes on to review numerous instances where banded fledglings of passerine species were known to nest near their birthplace and shows that of sixty-one robins banded as young and subsequently recovered during the breeding season, forty-five were found within ten miles of the point of banding. Farner (1945:97) made a similar analysis of a larger number of records and concluded: "There is a marked tendency among robins, Turdus migratorius migratorius, to return, as breeding birds, to their birthplace or its immediate vicinity.... There is no random dispersal among first year birds."

What of returning juveniles among ducks? McCabe (1947:107) has shown that captive-reared wood ducks returned to the place where they were reared.

In an attempt to measure the return of juvenile birds to their natal pond we began a program of releasing young birds at Delta in 1948. During 1948 and 1949, 352 captive-reared juveniles of five species were raised and released from the Delta hatchery. These birds were color-banded so that they could be easily identified if they returned to the

area the following year. They were released at the age of five to six weeks and they grew to flying age in the hatchery pond where they mingled and finally migrated with wild birds. The data from these releasee and the numbers known to return are given in Table 8.

In addition to the release of captive-reared birds, I trapped and banded wild birds in the fall on the study area. As these birds were sexed and aged at the time, numbers of juvenile hens among them give further data for this discussion. Since their place of hatching was unknown I refer to them as of unknown origin.

Returning Juvenile Hens.--The species order in which juvenile hens returned followed closely the order in which adult nest-trapped hens returned. These comparisons are summarized in Table 9 which shows the percentage of each species returning of both adult nest-trapped hens and released juveniles. Some bias from unequal sample size is probably present but it seems significant that the pintails have a high rate of return both as adults and juveniles and that mallards and blue-winged teals have a low return both as adults and juveniles.

Relation of Release Point (or Trapping Point) of Juvenile Hens to Nesting Place the Following Spring.--Of the eighteen juvenile hens which were known to return to the hatchery pond the year following release, nests of

TABLE 8 NUMBER OF CAPTIVE-REARED JUVENILES KNOWN TO RETURN TO AREA OF RELEASE THE FOLLOWING YEAR

Species	Males		Females	
	Released	Returned	Released	Returned
Mallard	13	0	20	1
Pintail	132	2	115	15
Gadwall	9	0	8	1
Shoveller	12	0	12	1
Blue-winged Teal	19	0	30	0
Totals	185	2	185	18

TABLE 9 COMPARISON OF RETURN OF ADULT AND JUVENILE HENS OF FIVE SPECIES

Species	Adults		Juveniles	
	Number Banded	Percentage Returned	Number Banded	Percentage Returned
Pintail	44	38%	115	12%
Gadwall	16	37	8	11
Shoveller	19	44	12	8
B-w Teal	58	14	30	0
Mallard	15	10	20	5

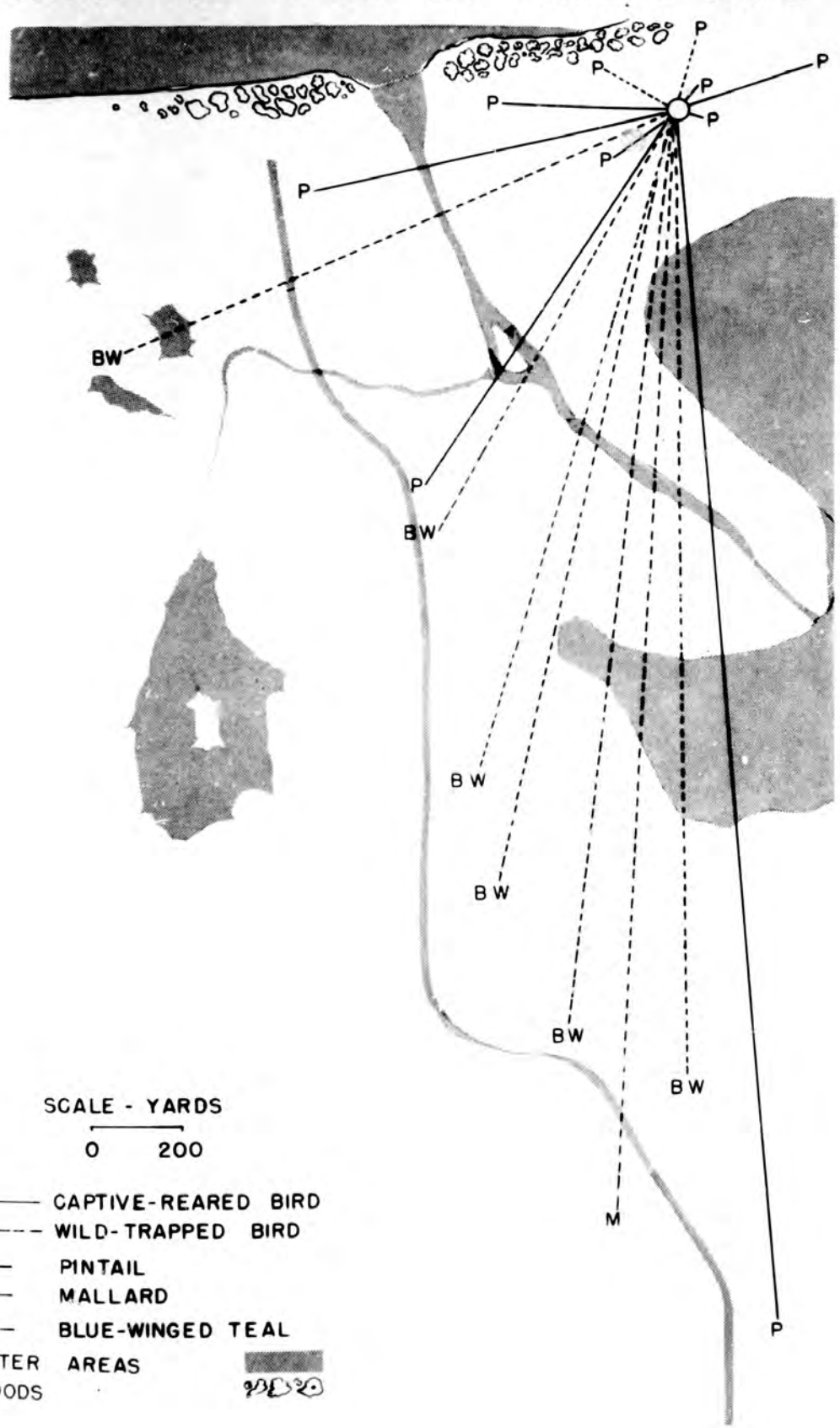
eight were found. The locations of these nests as well as the locations of nests of nine returning wild-trapped juveniles are shown in Figure 8.

The distances from the autumn release point to the spring nest sites of these eight hens (all pintails) were 40 yards, 40 yards, 190 yards, 300 yards, 400 yards, 800 yards, 1,000 yards and 2,600 yards.

Two wild juvenile pintail hens of unknown origin which were trapped and banded during the fall nested the following spring 180 yards and 110 yards from the point of capture. One juvenile mallard hen captured in the hatchery pond and released in September 1948 nested 2,500 yards from this pond the following spring. Six juvenile blue-winged teal hens of unknown origin captured and banded in the hatchery pond nested on the study area the spring following their capture. For these hens the distances between the fall capture point and their spring nest sites were 1,080 yards, 1,375 yards, 1,550 yards, 1,700 yards, 2,000 yards and 2,200 yards.

The dispersal of juvenile hens for their first nesting is a difficult thing to determine. How many juvenile hens survived and nested outside of the study area I do not know. I believe there is some significance in the fact, however, that during the years 1946 through 1949 I trapped 695 wild juvenile hens of unknown origin at the hatchery pond and

FIGURE 8. RELATIONSHIP OF SUMMER RELEASE POINT OF CAPTIVE-REARED JUVENILE HENS AND WILD-TRAPPED JUVENILE HENS TO NEST SITE FOLLOWING SPRING.



nine of these hens were known to nest within 2,500 yards of the point of capture and release the year following. During the same period Arthur S Hawkins captured, banded and released 1,947, almost three times as many as I, juvenile hens at two points, one mile and three miles southeast of my banding station but none of the birds banded by Hawkins were found nesting on my study area. No check was made to determine how many of the birds trapped by Hawkins returned to nest near the place where they were banded.

Return of Juvenile Drakes.--From Table 8 we have seen that of 185 juvenile females banded, eighteen returned to the same area the year following. Of the same number of males banded only two were known to return a second year. Both of those returning drakes were unaccompanied by hens when seen.

It is generally assumed that in waterfowl pairing takes place on the wintering ground and that the hen brings back to the nesting place a drake which probably has had no previous experience in the particular part of the breeding area where she returns. However, if males and females hatched and raised near each other migrated together and wintered together as members of a unit population, it would be reasonable to expect that a male might return to the vicinity of its natal marsh in the company of a hen also

raised in its vicinity.

In the spring of 1950 I collected a marked mallard drake at Delta. The bird was paired with a nesting hen. It had been banded by a coworker three miles southeast of my study area the previous fall. It seemed likely that this male had returned with a hen to nest in her natal marsh which was in the vicinity of either his natal marsh or a fall loafing area.

That males as well as females probably migrate through the same areas year after year has been indicated by Cartwright (1945:237) who obtained records of thirty-three birds (eight of them males) recovered in subsequent years at points within twenty-five miles of the station where first banded.

Although the figures I have given in Table 8 do not lend themselves to a statistical treatment, I believe that there is little doubt that it is the female that pin-points her flight to a definite area in spring and that the male, although capable of doing so, follows the hen to the place of her return and only occasionally by chance arrives at the same place he was the year before. This is in agreement with the conclusions made by Lincoln (1939:75) who says of ducks, "The evidence now available indicates that among these birds it is the influence of the female that is the determining factor in the movements of the male."

Significance of Homing to Management.--Management of waterfowl for maximum production on the existing marshes

must first insure adequate breeding stock. The duckless marshes that exist in both the United States and Canada are legion and now well known. The fact that these marshes do not have breeding waterfowl has not, in all cases, been due to changes in habitat but, in many cases, has been due to a definite shortage of breeding birds to occupy these marshes. This has been pointed out by Hochbaum (1947: 55). The fact that both juveniles and adults return to the marsh where they either nested before or to the marsh where they were raised the previous year makes breeding populations vulnerable to annihilation and marshes susceptible to what Hochbaum has termed "burning out". This term means the loss of the breeding population of an area due to early and heavy hunting. The reasons for this loss is (ibid.): (1) cropping too early and (2) harvesting too heavy. Where they occur the nesters and their progeny are killed off and the area becomes lacking in breeding birds. Conversely, when migrant birds are hunted, breeders from many sections of the breeding ground are mingled together and gunning pressure is therefore spread more thinly on many units of population rather than being centered on one.

In summing up the measures which might be taken to maintain breeding populations in an area Hochbaum says, "The new plan must protect the place and the bird at the same time. The two are inseparable, albeit the duck is

migratory. The unit area and the unit population must have equal protection."

In terms of management this means that early shooting seasons on the breeding grounds coming before the young birds and the adult hens have a chance to leave or mingle with migrants must be avoided.

Fortunately, at the present time, there is a trend toward later seasons in most of the areas where ducks are both raised and shot. And there is no doubt that these later seasons allow a dispersal of birds and a reduction in the percentage of birds shot in their breeding marsh.

Results from later seasons have not yet been thoroughly measured but in a few cases there are indications that later seasons may be bringing back populations. In the Delta marsh the hunting season in 1946 opened on September 16. In 1947 and subsequent years the season did not open until the seventh to the tenth of October. During the years between 1947 and 1950 substantial increases in breeding populations of two species was noted. The two species were the blue-winged teal and the redhead. In 1946 an estimated fifteen to twenty pairs of blue-winged teal were present on the study area; in 1947, twenty-five to thirty; in 1948, thirty to forty pairs; in 1949, forty-five to fifty pairs and in 1950, fifty to sixty pairs. Being an early-migrating species in autumn the blue-winged teal has escaped much

hunting pressure at Delta during the last four years when later openings were the rule. This can be seen in an analysis of the Delta kill. In 1946 the blue-winged teal made up 3 per cent of the number of ducks checked in hunters' bags. In 1947 it made up 1 per cent and in the years following 1947 less than 1 per cent of the total "take".

The increase in redheads at Delta was also conspicuous. On the study area alone, where no redheads were raised in 1946, nine broods were seen in 1950. There was also evidence that the redhead had made a remarkable recovery throughout the marsh.

The part that late openings at Delta and elsewhere have had in bringing about local increases in breeding populations is, of course, hard to determine. For that reason continued research on the role of homing as well as other factors in governing breeding population levels must be carried on. Certainly the strong tendency for adult hens to home to the marshes where they have nested must be an important factor in maintaining continuous breeding populations in any area. The success of adults in new areas when forced to move by fire, drought or drainage, is still an unanswered question. Another unanswered question is that of dispersal of the juveniles.

SUMMARY

1. The annual return of wild birds to the area in which they nested the year before or were raised has been called "migrational homing".

2. The existence of migrational homing in wild birds has been known for many years; the percentage of survivors returning and the differences in return between adults and juveniles are treated in this chapter.

3. During the years 1947-1949, 152 adult hens of five species of meadow-nesters were trapped on their nests and banded to determine the percentage of return in following years.

4. Of this number forty-one or 27 per cent were known to return and nest in the same meadow a following year. Mallard showed a 10 per cent return, pintail a 38 per cent return, gadwall a 27 per cent return, shoveller a 44 per cent return and blue-winged teal a 14 per cent return.

5. Comparing the above returns with expected survival it was determined that the majority and probably nearly all surviving pintails, gadwalls and shovellers do return to the same meadow a second year.

6. Blue-winged teals and mallards do not show so clear a picture of return. Although more adult blue-winged teal hens were banded than any other species their return was one of the lowest. This may be due to the fact that the

blue-winged teal has a lower calculated survival rate than that of any other species. The low mallard return may be due to the smaller sample size and the fact that mallards were difficult to work with and to observe.

7. Juveniles, too, showed a strong tendency to return, but the percentage of juveniles returning was far below the percentage of returning adults. Of 370 captive-reared juveniles released during 1948 and 1949, two drakes and eighteen hens were known to return the following year.

8. The fact that so few drakes returned to the same marsh the year following banding is probably due to the fact that pairing takes place on the wintering ground and that the hen determines the place in which the pair will breed the following year.

9. The fact that both adults and juveniles return each year to the same marsh to breed makes local breeding populations vulnerable to annihilation. The loss of a unit population results in a "burned out" marsh--an area devoid of breeders.

10. The prevention of this loss can be partly accomplished by later hunting seasons and lighter hunting on the areas where ducks are both raised and shot.

CHAPTER III

TERRITORIALITY AND HOME-RANGE

"Territory" in birds has received considerable attention during the past three decades. Nice (1941:441-487) discusses the history of the study and gives the following definition: "The theory of territory in bird life is briefly this: that pairs are spaced through the pugnacity of the males towards others of their own species and sex; that song and display of plumage and other signals are a warning to other males and an invitation to a female; that males fight primarily for territory and not over mates; that the owner of a territory is nearly invincible in his territory; and finally that birds which fail to obtain territory form a reserve supply from which replacements come in case of death of owners of territories."

Most territorial study to date has been concerned with passerine birds. In waterfowl, too, one is aware of this territorial behavior during the breeding season.

One of the earliest records of such behavior in waterfowl is cited by Nice (1941:442) from Ticehurst who quotes "Section 21 of 'The orders Lawes and Ancient Customes of Swanns', printed by order of John Witherings in 1632: "And yet neither the Master of the Game, nor any Gamster may take away any swanne which is in broode with any other mans, or which is coupled, and hath a walke, without the other's con-

sent, for breaking the brood."

According to Delacour and Mayr (1945:50) Geyr was the first writer to point out that pursuit flights in waterfowl were actually territorial defense flights. Hochbaum (1944: 56-78) has given us the most complete discussion of territory among ducks.

The main points of Hochbaum's discussion are as follows: (1) "At the time the pair is ready to nest it takes title to a small water area of the breeding marsh--a pothole, the corner of a slough, or a portion of bay edge. Day after day, as long as the drake and hen remain together as a pair, they may be found on this water area." (2) "The water area occupied by a pair of nesting ducks is defended by the drake; he establishes definite boundaries against the intrusion of other sexually active birds of his own species. (3) "A territory is a specialized piece of terrain in which four components must exist together: Water, loafing spot, nesting cover (adjacent or nearby) and food."

The foregoing concepts of territory in waterfowl have played an important part in the formation of breeding-ground-survey methods which have been developed and used in Canada and the northern states since 1946. Territorial behavior has been the basis for breeding pair counts in California. Earl (1950:336) says of the mallard there, "Observed territorial behavior following the pattern described by

Hochbaum (1944) reached a peak in the period of April 5 to 9,....Ditches bordered by roads were censused every day, and ditches not bordered by roads were censused every three days throughout the entire territorial period....The total number of territorial drakes determined from these counts... is used in calculating production."

Although I found that ducks do remain, more or less, within certain areas and that territorial behavior probably forms a sounder basis for transect counts than any other, there is a wider movement and more variation in behavior than the above definitions of territory suggest. In my opinion, therefore, certain aspects of the territory-in-waterfowl concept need clarification.

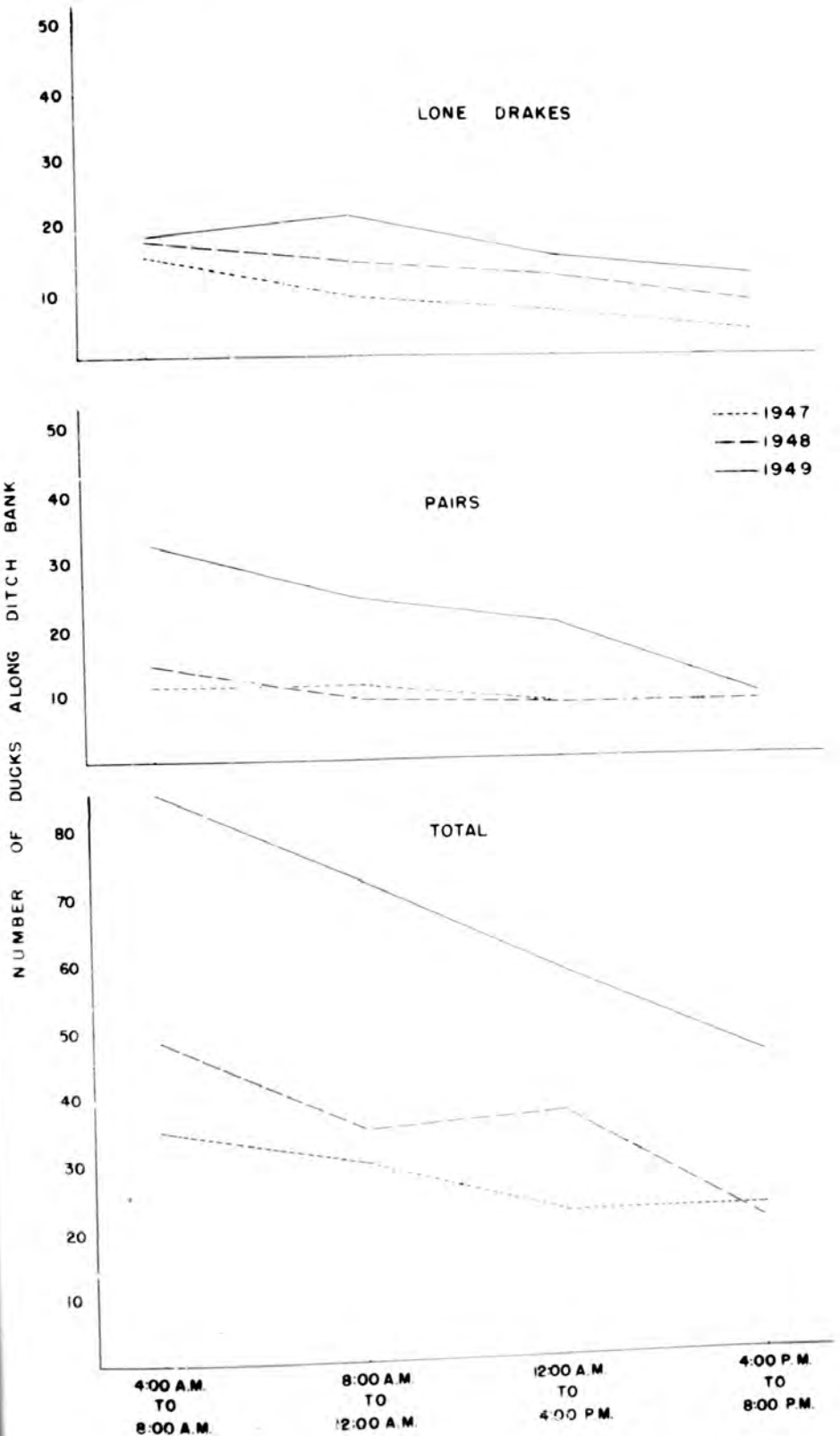
Movement of Pairs.--How faithfully do pairs remain in the same place? The question arises at once, what do we mean by the "same place" or by "a small water area of the breeding marsh"? On the study area at Delta, a long narrow roadside ditch runs through the nesting area; 500 yards northeast of it is a large bay with its own smaller, lesser bays; 450 yards east of it is a large slough, and 500 yards west, another slough. Applying the foregoing definitions of territory we would expect each of these water areas to support its own population of breeding pairs. Accordingly, we would expect little movement between bay and ditch or between ditch and slough.

In five years of study of the area, however, I found that movement between the areas not only existed but was great and that some marked pairs of birds used all of these during one breeding season. In many cases I could not identify as a territory or favored area any one or part of these water areas. I saw drakes of individual pairs of gadwalls and mallards "defend" from different areas at extreme ends of this block of land including all four water bodies which I have mentioned.

During the course of my study, counts of the individuals along the roadside ditch were made. The purpose of these counts was to obtain working information for locating nests, obtaining records of banded birds and predicting nesting season events.

These data from 118 counts of the entire ditch taken at various times of the day is plotted in Figure 9. Lone hens have been omitted from these figures except that they are included in the bottom figure of total birds. The number of lone hens recorded on these 118 counts totaled only twenty-three, most hens having been paired. It is apparent that the count of birds was always highest in the morning, dropping off later in the day. Birds which were counted early apparently went to the bay later, or to a neighboring slough. Thus, a drake that was counted as a breeding individual of the nesting area surrounding

FIGURE 9 CHANGE IN ROADSIDE DITCH POPULATION DURING THE DAY BASED ON 118 COUNTS MADE IN 1947, 1948 AND 1949



the ditchbank where he was seen might well be counted again in another place later in the day. The assignment of a certain population figure to any one of these water areas would be inaccurate unless counts for slough, bay, etc. were made simultaneously. Also, the time of day the count was made would certainly influence the figure obtained.

At the south end of the long Delta ditch, a small area made bare by cattle was particularly attractive to loafing pairs of ducks. Each year a pair of blue-winged teal could be seen frequently in about the same spot. Had the birds not been banded it would have been tempting to conclude that the pair (or the hen) was a constant occupant and that this spot was a favored area. Leg bands, however, indicated that this was not the same hen each year nor was it the same hen during the entire period of one nesting season. The spot was used by several distinct pairs over a period of a few weeks.

Another example of the use of a particular spot by several pairs was seen in gadwalls. In 1948 a gadwall pair (or waiting drake) was seen almost every morning at one spot along the roadside ditch near the center of the study area. Casual observation indicated that this was the territory of a pair. Early morning watching (as described under techniques), however, revealed that at least four pairs of gadwalls, rather than one, used this spot

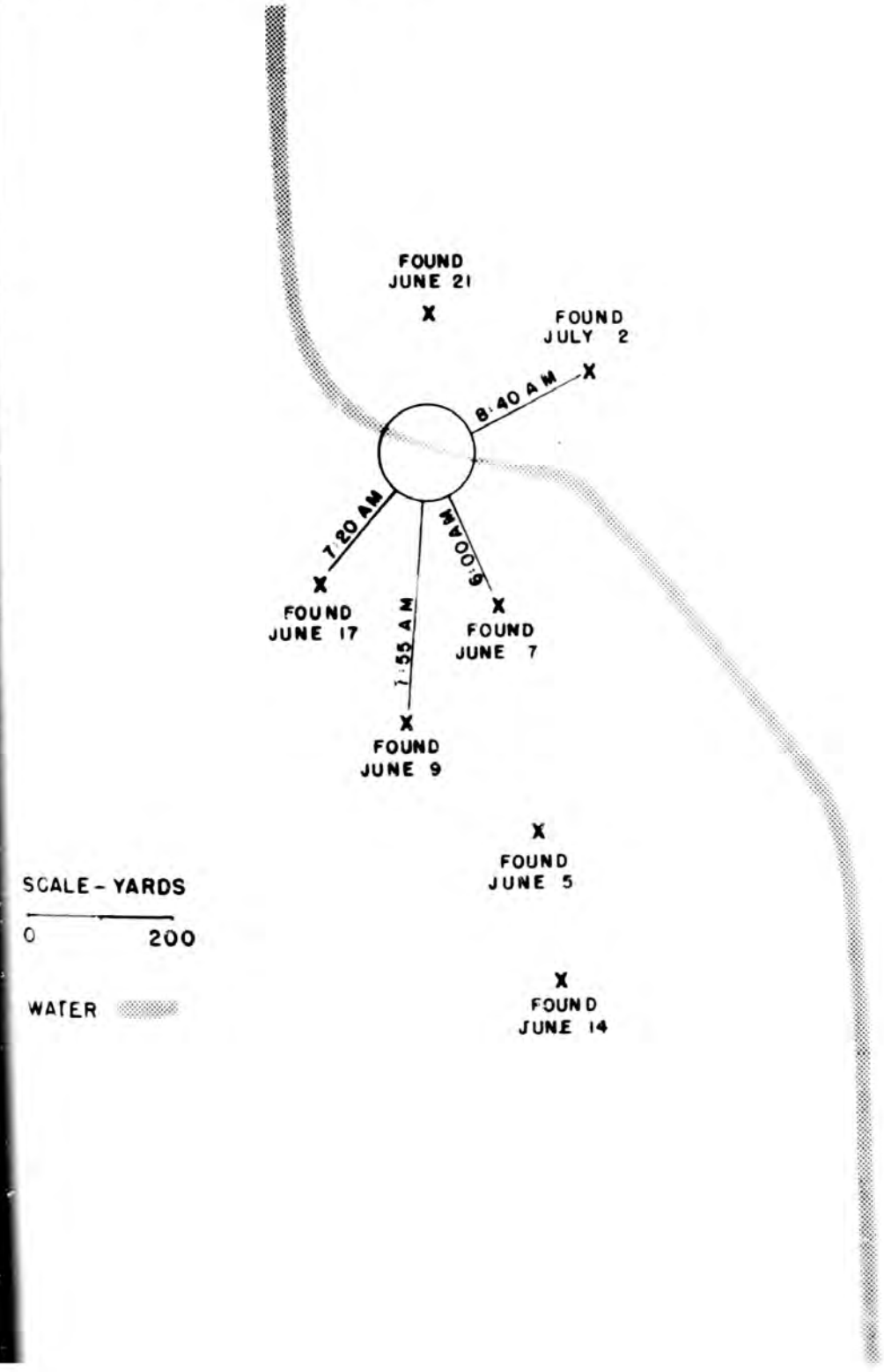
as a jumping off place to nests in the adjacent meadow. Defense flights were sometimes made from this favored area. Figure 10 shows the location of this jumping off place in relation to the nesting places of these birds and the hour and date the individual nests were found. Also shown in Figure 10 are the locations of three other gadwall nests found in the same general area during the period, but for which waiting or jumping off places were unknown.

The sharing of a favored area by teal was observed on June 7, 1949. At 11:00 A.M. a ditch count was made and a pair of blue-winged teal were noted sleeping on a loafing log at pole thirty along the roadside ditch. The hen was banded. At 11:45 A.M. another ditch count was made and although a pair of teal were still sitting on the log, the hen was not banded. Apparently another pair had moved in.

Thus we see that although the birds do consistently use favored spots, they may favor more than one spot; and that two or more individuals or pairs may share a favored spot at different times.

Territorial Boundaries.--Some students of territory among small birds recognize specific boundaries of the defended areas of a breeding pair. Two well known references are Nice (1937:71), who [illegible]s the territorial boundaries of breeding song sparrows, and Lack (1946:133) who shows similar boundaries for the English robin.

FIGURE 10 SHARED JUMPING-OFF PLACE AND NEST LOCATIONS OF FOUR GADWALL HENS DURING THE SPRING OF 1948 AND NEST LOCATIONS OF THREE OTHER GADWALL HENS



If pairs of ducks remained within small, limited areas during the breeding season, we could probably assume that they, too, respected fairly limited boundaries. But as I have pointed out, movement, even during the laying period, is so great that one cannot always recognize specific boundaries.

I have tried to assign a pair or a lone drake to an area with definite boundaries but have seldom been able to do so. Nor have I been able to observe an invariable defense behavior. I have seen pairs of mallards and pintails and gadwalls move freely about over areas up to 300 acres in size. These birds were using several water areas. Defended boundaries were seldom identified as such, although defensive behavior was occasionally seen. At the same time that such movements were apparent, the number of pairs using the area was as high as twenty-five or more of mallards and a comparable number of pintails. These pairs were all simultaneously using the study area of only two square miles.

It is important to remember that there is also the simultaneous existence of many behavior patterns owing to the many phases of the reproductive cycle that occur in individual birds at one time. Thus, while some hens are laying, some are incubating, others are going through a period of idleness prior to renesting, others have been thwarted in their attempts and have given up or failed.

Some drakes have abandoned their hens but are being teased by renesting hens and some are no longer in breeding condition.

Seasonal Home Range.--Although it is not new to ornithology, the concept of "home range" has been slighted by workers in the field of waterfowl. Yet it is here that its application may clarify a complex behavior which is only clouded by superimposing the territory concept as defined for passerines.

Burt (1946:20) defines home range in mammals by saying: "The area around the home region that the animal traverses in its normal activities of food gathering, mating and care for young is its home range." Burt gives three different types of home range for mammals: (1) permanent home range, (2) semipermanent home range, and (3) seasonal home range. The first two of these refer to sedentary mammals and the last to migratory mammals.

Kendeigh (1947:72) makes reference to home range in warblers by saying, "In the earlier study of territorial behavior in warblers (Kendeigh 1945a), males of several species were found wandering considerable distances outside of their defended territories. The same tendency toward a wide home range was noted in the present study, although due to the large number and concentration of birds which were present, the movements of individuals over great distances

could not be so readily followed."

The use of the term "home range" for ducks was suggested to me be J. J. Hickey when we watched the morning movements of ducks on the Delta study area one June morning in 1948.

Applying Burt's third classification, seasonal home range, I would define the term as follows: Home range in ducks is the area within which a bird spends its period of isolation between the break-up of spring gregariousness followin spring arrival and the re-formation of fall gregariousness. (It should be remembered that short periods or reversion to gregarious behavior may interrupt this period in cases of thwarted hens joining a band of loafing waterfowl between nesting attempts.) Home range in ducks is the area within which a bird remains from the time it settles down to breed until the time breeding is over. It is the area with which the bird is most familiar. It is the area to which the hen, so long as she is alive and so long as it is acceptable, will return year after year to breed.

An Example of Home Range.--Shoveller hen #47-604004 which was known to return to the Delta study area for four consecutive years (at which time the present study was completed) was known to nes[illegible]ch year within an area of approximately seventy-five acres (producing four first nests,

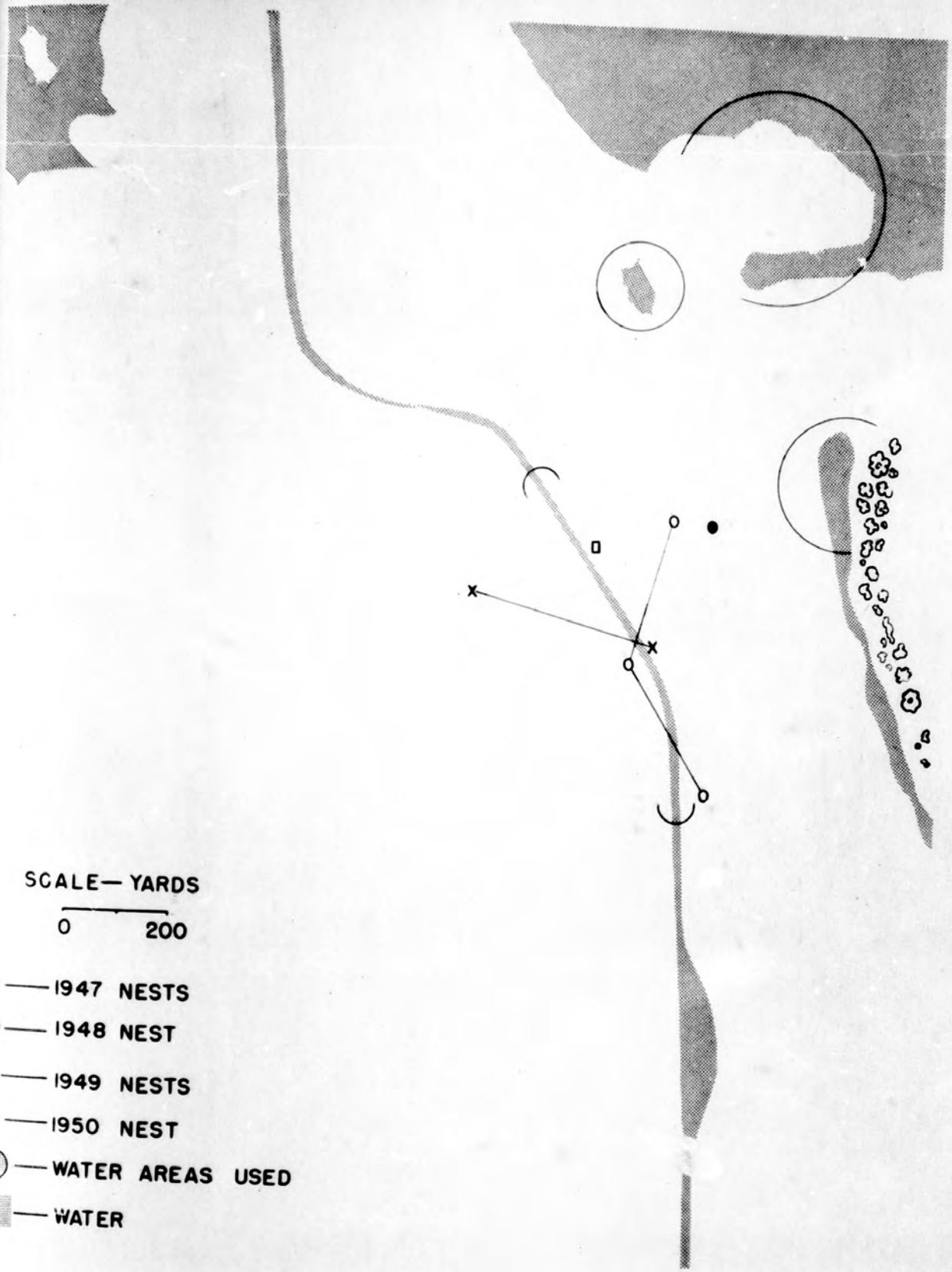
three renests). The home range of this bird is shown in Figure 11. It included a segment of roadside ditch bank, known to have been used by her, 800 yards long. A large slough, 450 yards to the east, and two small bays were also known to have been used by her. Also included in it were the nesting meadows between and around these water areas. The whole map of this particular bird's home range would include about two hundred acres of land. It was, of course, used simultaneously by many other birds, including shovellers.

In the summer of 1947, the first year that this bird was known to be on the study area, she apparently remained somewhere within this block of land for ninety-three days. I could not always find her, even during her laying period, but often when I failed to find her on the ditch bank I could find her at the bay edge or in the slough.

The aggressive behavior of her drake was most intense when the pair was loafing on the ditch bank, but it was also frequently observed when the pair loafed on one of the nearby potholes. Defensive behavior of her drake did not appear to be the defense of a particular piece of ground but rather an attitude that accompanied the pair wherever it moved within its home range.

Duration of the Home Ra Attachment, Variation between **Sexes.**--There is variation between sexes in their attachment to their home range, and attachment to home

FIGURE 11 HOME RANGE OF SHOVELLER HEN 47-604004 DURING 1947, 1948, 1949 AND 1950



range presumably varies likewise with the physiological status of the individual. The hen remains attached to her home range longer than her drake does. When first efforts to nest are begun, the pair is together; but a nest failure may find the original drake already advanced to the gregariousness of the postnesting period. For him the attachment to his home range has weakened, and he has joined a growing band of bachelor drakes. Meanwhile his hen retains her attachment to her home range and may have brought in another drake before making her first renesting attempt. As we will see in Chapter VII, she will renest near her first nest failure; and her attachment to her home range will hold until she is either successful in raising a brood or until she ceases to try--a period of sometimes up to five months or longer.

SUMMARY

1. Territoriality in passerine birds has received considerable attention during the past three decades.

2. Although there is scattered early mention of territoriality in waterfowl, the first treatment of length and significance was Hochbaum's, published in 1944.

3. The main points of his discussion are: (1) that a pair at the beginning of the nesting season takes title to a small water area and can always be found there so long as the drake and hen remain together; (2) the drake defends

definite boundaries of this water area, and (3) all requirements except the nesting site, are contained within these definite boundaries.

4. These concepts of territorial behavior have formed the basis for spring breeding ground appraisals of waterfowl.

5. During the five years of this study the movement of marked waterfowl on the study area has indicated that the above concepts of territory are too rigid and limiting.

6. There is evidence that several favored areas may be used and that drakes "defend" from more than one. Definite boundaries of favored areas do not always exist.

7. All of the requirements of a breeding pair are not within the favored area but are within a less definite and larger home range.

8. The home range of breeding waterfowl is defined as the area in which a bird spends its period of isolation between the break-up of spring gregariousness following spring arrival and the re-formation of fall gregariousness.

9. The attachment to the breeding home range is longer for hens than for drakes.

CHAPTER IV

NESTING TERRAIN

Brown dead grasses cover the prairie meadows. Here and there large patches of old weeds, thistle and pigweed, are black in the late April sun. Last year's growth forms the nesting cover for spring's earliest nesting ducks. Many ducklings will be hatched before a single blade of new green grass shows through the dry cover.

Nesting terrain has two main components: (1) the nesting meadows and (2) the loafing and feeding waters which are near.

Nesting Cover Types.--In the ever-changing complex of plants that form the nesting meadows, certain key species are important. These vary with locality, soil and climate. In the region of the Delta marsh, of which my special study area was but a part, the nesting cover plants for 685* mallard, pintail, gadwall, shoveller, and blue-winged teal nests are given in Table 10.

Certain plant preferences on the part of these species are evident in these data. For example, 278 or 42 per cent of all nests found were located in whitetop or in cover containing some of this plant. Cordgrass ranked second and contained 118 or 17 per cent of all nests found. Bluegrass ranked third with 86 or 12 per cent. Of the remainder of

* Includes 90 nests observed by me in a 1939-1940 study at Delta.

TABLE 10 COVER PLANT SPECIES FOR 683 DUCK NESTS OF FIVE SPECIES (t--trace or less than 1 per cent)

Cover Species	Percentage of nests in each type				
	Mallard	Pintail	Gadwall	Shoveller	B-w Teal
Size of Sample	143	222	58	65	215
Whitetop	58	51	58	27	24
Cordgrass	12	8	18	26	27
Bluegrass	5	10	8	18	19
Quackgrass	0	2	0	20	17
Annual weeds	5	6	15	3	2
Phragmites	11	3	0	0	1
Skunk grass	t	4	0	1	4
Grain stubble	t	6	0	0	0
Brome grass	0	0	0	0	5
Sedges	0	4	0	4	0
Goldenrod-Aster	3	2	0	0	1
Bulrush	4	1	t	0	0
Snowberry	0	1	0	0	0
Willow	0	1	0	0	0
On muskrat house	0	t	0	0	0

the cover types, quackgrass contained less than 5 per cent of the nests. The above cover plants will predominate or be absent according to land use, water levels and other influences. Principal land use types of the nesting grounds in the Delta marsh region are as follows:

Grain Stubble and Fallow.--The Portage Plains south of the Delta marsh, are typical of many regions of the Prairie Provinces. It is "grain country"; wheat, barley, flax and oats are the dominant crops. Many mallards and pintails begin nesting in spring before the crop is sown; and the occurrence of a good number of nests of these species in old stubble is frequent. The amount of cover on the stubble fields is often slight (Figure 12). It is not uncommon for pintails to nest in areas so bare that the bird can be seen sitting on her nest up to forty yards away. Pintail nests in such light cover are often placed in depressions (Figure 13). Many of the early nests are plowed under at seeding time.

Because of the serious and heavy infestation of fields by sow thistle, wild mustard and Canada thistle, it is a common practice to leave some fields fallow about one year in three. These fields are plowed and disced throughout the summer to kill the weeds but no crop is sown. There is almost no vegetation to conceal the birds on these bare stretches. Nevertheless, such fallow fields are

Figure 12 The amount of nesting cover on old stubble fields was often slight.

Figure 13 In such situations pintails often placed their nests in depressions.

occasionally used by nesting mallards and pintails. These fields are rarely plowed early in spring but are worked when the farmers have seeded their other acres. Hence, late spring tilling of the land occurs after nesting birds are established and brings with it nest losses.

On the study area at Delta where stubble and fallow fields made up 7 per cent of the area, fourteen or 6 per cent of pintail nests and one of 109 mallard nests were found there over a five-year period.

Grazed Pastures.--Very little grassland in southern Manitoba is left ungrazed. It seems to be the general rule to graze pastures heavily, and to carry a number of cattle which is probably beyond the ideal. On the study area 14 per cent of the land area consisted of heavily grazed pasture. Here the grazing was so heavy during the first four years of the study that bluegrass seldom reached a height of one inch before it was eaten off.

Ungrazed Meadows.--Ungrazed marsh meadows formed the most important and most productive cover at Delta. It made up 14 per cent of the study area and contained 517 or 89 per cent of the 595 nests found on the study area. The most important cover plant in these meadows was whitetop. Second in importance was cordgrass. Other plants were annual weeds, goldenrod-aster, quackgrass.

Some of the ungrazed meadows on the area are cut for

hay in July and August, but they are grown up enough by fall so that good nesting cover is available again the following spring.

Roadsides.--The narrow strips of roadside that border marsh roads are built up above marsh level and are therefore comparatively dry. As a result a group of plants grow there that are not to be found in the marsh. At Delta these plants are bluegrass, quackgrass and brome grass. Of the 683 nests found, sixty-five or 10 per cent were located along roadsides.

Phragmites Jungles.--Heavy stands of tall yellow cane cover large areas in the Delta marsh. On the study area 78 per cent of the land was covered by this heavy vegetation. In this type seventeen or 10 per cent of all mallard nests were found, seven or 3 per cent of pintail nests, and two or less than 1 per cent of all blue-winged teal nests. It contained none of the gadwall or shoveller nests. In all cases these nests were either in an isolated clump of phragmites within three yards of some other cover type or were just at the edge of a large stand of phragmites. I doubt that any of the surface-feeding ducks nest deep within phragmites jungles. The plants are sometimes over eight feet high and almost impenetrable by birds or man (Figure 14). The vegetation is so dense that it makes entirely unsatisfactory nesting cover.

Brush and Trees.--Along the edges of most Canadian

Figure 14 Phragmites formed dense jungles seldom used by nesting ducks.

marshes there are some low shrubs and trees. At Delta the trees are willow, bur oak, boxelder, cottonwood, dogwood and red-berried elder. I have found these areas to be seldom used by the puddle ducks for nesting. Of the 683 nests, only three (all pintails) were found in this cover type.

Influences upon Nesting Cover, Water Levels.--The most important factor effecting nesting cover is the water level. In 1946 when this study was begun, levels were low in the Delta marsh. In 1947 they continued low but in 1948 they responded to a sudden rise in Lake Manitoba. Both marsh and surrounding meadows were effected. Water continued to rise in 1949 and reached its highest level in 1950. The effects upon nesting-cover plants was apparent throughout this period.

Plants making up the nesting cover at Delta reacted in different ways to rising water. The reactions of some of the most important of these plants to changing water conditions is summarized in Table 11. The line of separation between moisture conditions is, of course, not a sharp one and the degree of drought or flooding that plant species will tolerate may vary. For the purposes of this table three moisture conditions are used: (1) "dry years" when the ground is no longer mo- and heavy vehicles can be driven over it without sinking in, (2) "wet years"

TABLE 11 REACTIONS OF IMPORTANT MARSH PLANTS TO VARIOUS WATER CONDITIONS IN THE DELTA MARSH, MANITOBA

Plant	Moisture Conditions and Plant Reactions		
	Dry Years	Wet Years	Under Flooding
Phragmites	Survives	Thrives and spreads	Dies out
Cattail	Dies out	Thrives, invades new areas	Dies out
Hard-stem Bulrush	Dies out	Thrives	Survives
Whitetop	Survives but does not bloom	Thrives, blooms profusely if ground covered with shallow water in spring	Dies out in some places where water is deepest
Quackgrass	Thrives	Dies out	Dies out
Wild barley	Thrives	Thrives and spreads	Dies out
Cordgrass	Survives but does not bloom	Blooms profusely	Dies out
Willow	Invades marshes	Survives	Dies out
Cottonwood	Invades marshes	Survives	Dies out

when the ground is muddy, vehicles sink into the earth and a shallow sheet of water covers the ground in spring, and (3) "under flooding", when a foot to several feet of water covers the ground during the spring months.

In 1946 and 1947 no blooming whitetop grass was evident. Quackgrass patches thrived and bloomed on the meadows. Cordgrass did not bloom.

Following the rise in water levels in 1948, large blocks of whitetop bloomed profusely for the first time during the study and continued to flourish in 1949 and 1950. At the same time that the whitetop flourished, quackgrass began to die out. During the wettest year of the study, 1950, cordgrass bloomed profusely for the first time.

Continued high water encouraged hard-stem bulrush, soft-stem bulrush and cattail to take over in some areas where water was deep. Thus, in five years, a change from dry non-blooming whitetop and flourishing quackgrass to bulrush and cattail occurred.

Temporary waters function in the same way as plowing or extremely heavy grazing in that they revert plant succession to its first stage. Areas that were temporarily submerged in spring produced wild barley following the June dry-up.

Influence of Grazing.--Heavy grazing of a nesting meadow effects the cover in so far as the cover species

are palatable to the cattle. During the years 1946 through 1949 bluegrass in the grazed parts of the Delta study area remained short. Only pintails used such light cover for nesting (Figure 15). A pasture of bluegrass becomes almost useless to ducks when heavily grazed. In the other portion of the grazed pasture, however, despite the heavy grazing, plant species unpalatable to cattle thrived and were as good for nesting cover as they were in ungrazed meadows. Cordgrass (Figure 16), wild barley and Canada thistle made good nesting cover in heavily grazed pastures where the palatable bluegrass was eaten to the ground.

Influence of Wild Mammals.--Two species of ground squirrels inhabit the nesting meadows and their borders at Delta: the Franklin ground squirrel and the Richardson ground squirrel. The first of these inhabits the brushy marsh borders and plays an important part as a predator upon duck nests (Sowls, 1948:150) but exerts practically no influence upon nesting cover. The Richardson ground squirrel inhabits heavily grazed pastures but, so far as is known, seldom disturbs nesting ducks. Its effect upon nesting cover, although of little significance, is great enough to be noticed. Occasionally areas are made bare of vegetation where this mammal is abundant.

The abundance of the Richardson ground squirrel in-

Figure 15 Only pintails tolerated extremely grazed bluegrass but situated their nests beside a stalk of some unpalatable plant left by the cattle.

Figure 16 Even under heavy grazing unpalatable cordgrass furnished excellent nesting cover.

creases with grazing, and this relationship has been conspicuous on the Delta study area. No Richardson ground squirrels were seen in ungrazed meadows. The only existing population in the entire marsh, with the exception of the southern marsh border, was in an isolated five-acre pasture in the village of Delta. The population, completely cut off from any other, maintained itself and flourished where cattle kept the grasses short.

Other Mammals.--Besides ground squirrels other abundant rodents in the nesting meadows were the pocket gopher, meadow mouse, and woodchuck. With the exception of large mounds of earth which were made by the pocket gopher, no real effect on nesting cover was produced by these rodents. Gopher mounds were known to bury nesting vegetation over small areas.

Throughout the course of the study the meadows were used by white-tailed deer, mink, long-tailed weasels and skunks with no appreciable effect on the nesting cover.

Water-area Types.--When the ducks arrive in spring, residents and transients alike settle down on the shallow temporary ponds that are scattered over the broad Manitoba prairies. As migration ceases, the density of loafing birds decreases until only the residents are left. These continue to rest on the dry edges and to feed on the abundance of weed seeds and waste grain well into the

nesting season.

Along old creek beds and channels, long narrow sloughs are numerous. These are permanent water areas, and they serve as loafing and feeding areas for waterfowl during the nesting season after the temporary ponds have disappeared. Here the vegetation consists of a larger and more permanent variety of plants: cattail, bulrush, pondweeds, water milfoil, bladderwort, duck weed, and a variety of other aquatics. The edges of the sloughs may be either good or poor for loafing birds, depending largely upon the extent to which the area is grazed. Ungrazed edges are dense with vegetation and therefore unattractive to ducks. On the study area at Delta three such sloughs existed. Only one of these was used extensively by breeding birds. The one used had a heavily grazed edge (Figure 17) as contrasted with the other two which had shorelines heavily grown over with bulrush and cattail (Figure 18).

Gravel roads across marsh areas in southern Manitoba are made by piling earth and gravel along section lines. The earth is removed from the sides of the road as the construction crew advances. When the road is finished, one or two roadside ditches, often full of water, run along beside the road, sometimes for miles in a stretch. The ditches, when occurring on the prairie, often dry up in summer but in marsh areas remain full throughout the season.

Figure 17 Heavily grazed sloughs offered attractive edges for loafing ducks.

Figure 18 Ungrazed sloughs with dense edges were not attractive to loafing puddle ducks.

The ditches are important to nesting ducks as loafing and feeding places. The roadside ditch on the Delta study area was two miles long and was heavily used by ducks during the nesting season. Obviously, not all roadside ditches were of equal importance. Travel disturbance, bare clay bottoms or dryness often made them useless to the birds.

As surface-feeding ducks are primarily birds of the open country during the nesting season, they use the large bays and marshes less in spring than during fall-gathering time. In contrast to this, ditches, potholes and sloughs have fewer ducks in late summer and autumn than they do during the breeding season. The movement of ducks from small water areas to larger water areas follows the end of the breeding season.

The Land-water Pattern.--At the beginning of this chapter nesting meadows and loafing and feeding waters were given as the components of nesting terrain. The usefulness of a breeding area depends upon the amount and distribution of these components, upon the proportions and pattern. Both good and poor land-water patterns were apparent at Delta when the special study area was compared with other parts of the Delta marsh.

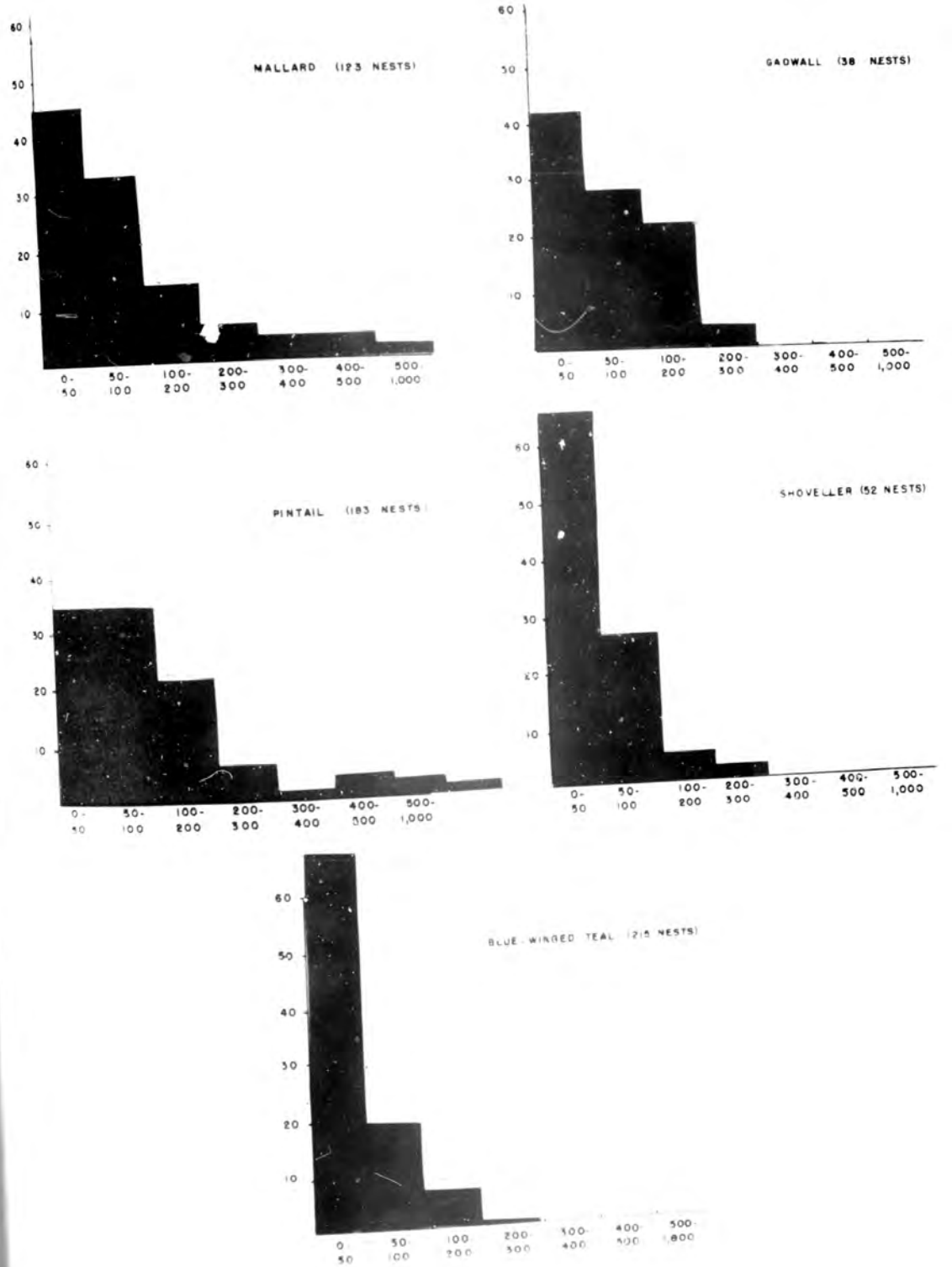
Egg-hunting for hatchery purposes has been carried out in most parts of the 30,000-acre Delta marsh. Simultaneously, during the past five years, intensive nest hunting has been

done on the study area. It has been apparent from these studies that the special area, selected mainly because of convenience, proved to be consistently better as a nesting unit than any other similar-sized area in the marsh. This was true for the species named: mallard, pintail, gadwall, shoveller and blue-winged teal.

One of the reasons for the area s being better than all others of comparable size was its interspersion of good nesting cover and water. The concept of interspersion of cover types for breeding waterfowl follows that for other game. Leopold (1933:451) defines interspersion as: "The degree to which environmental types are intermingled or interspersed on a game range." In the Delta marsh other large nesting meadows outside the study tract appeared to fulfill all requirements but lacked nearby water. A clue to the water-nesting area relationship can be found when we consider the distances from water that the nests of various species are located. Distances from water of 611 puddle duck nests are given in Figure 19 which shows the percentage of nests of each species found at various distances from water.

Difference in Quality of Areas.--On the Delta study area where the long roadside ditch is flanked on both sides by nesting cover and beyond that by sloughs and bays, certain sections of the area were consistently better

FIGURE 19 PERCENTAGE DISTRIBUTION OF DISTANCES FROM WATER OF 611 NESTS OF FIVE SPECIES OF PUDDLE DUCKS



waterfowl producers than other sections of equal size. To demonstrate this difference I arbitrarily selected a section of the roadside ditch at the southern end which I henceforth will call area "A" and a section of the same length at the northern end, area "B". Whereas A was characterized by good loafing areas, large adjacent nesting meadows and grazed edges (Figure 20); B had heavy cover, phragmites, and grown-over ditch banks (Figure 21).

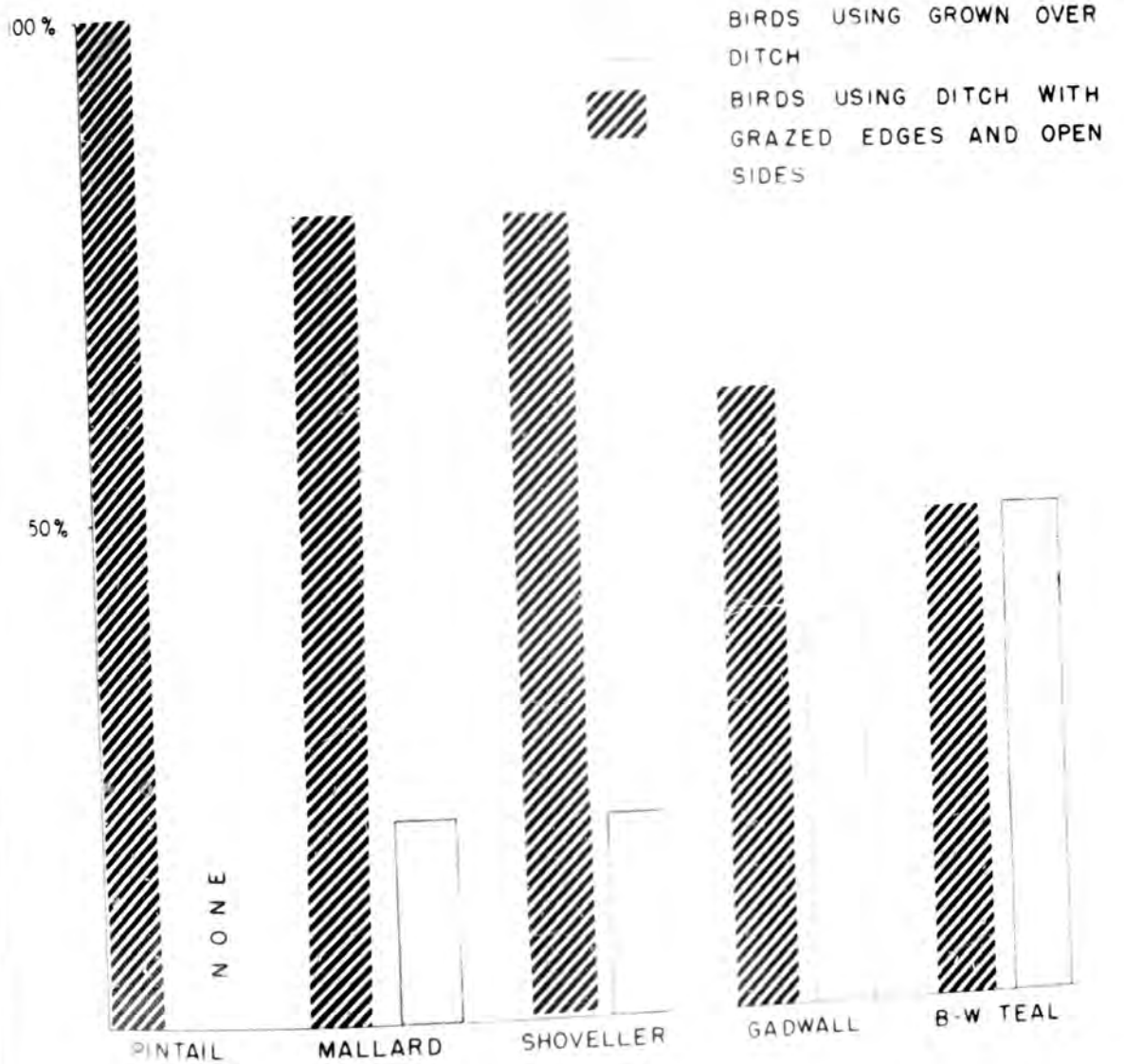
Figure 22 is made up of comparative indices and includes a base figure of the total number of ducks of each species counted from March 25 to July 20, 1947 on these two areas. The dry year of 1947 was selected for this comparison to avoid the complicating influence of occasional flooding which occured in area A when ditch banks overflowed. Only counts made of the entire ditch without intervening delays were used.

In comparing populations of resident birds it was clear that pintails preferred area A and during 1947 did not use area B at all. Being almost exclusively a bird of the open, the pintail will not tolerate heavy phragmites and grown-over ditch banks. Mallards, shovellers, and gadwalls preferred area A too but tolerated the heavy cover and lack of good loafing areas of B to some extent. Only the blue-winged teal showed no preference between the two sections of ditch. The very short distance between nest and water

Figure 20 Ditches with grazed edges were better for loafing ducks...

Figure 21 ...than were ditches [illegible] grown over edges.

FIGURE 22 COMPARATIVE POPULATIONS OF FIVE SPECIES OF PUDDLE DUCKS ON TWO EQUAL LENGTHS OF DITCH DURING 1947 BASED ON 22 COUNTS



area of this species makes it unnecessary that large nesting meadows exist, smaller areas of nesting cover such as a roadside being adequate.

Management of Nesting Terrain.--From these data it is apparent that the mallard, pintail and gadwall nest over a wide area and farther away from water than do the shoveller and blue-winged teal. Thus, nesting cover over a hundred yards from water accommodated only 10 per cent of the blue-winged teal nests and 4 per cent of the shoveller nests. However, this over accommodated 24 per cent of the mallard nests, 31 per cent of the pintail nests and 29 per cent of the gadwall nests.

In the management of a marsh for maximum waterfowl production it may be desirable to build ponds and ditches where large meadows exist without water. The distance between these ditches and ponds depends upon which species we are trying to encourage and upon the cost of ditching. If we desire to encourage the more mobile mallard, gadwall and pintail the ditches could likely be up to two hundred yards apart, but if we desire to also encourage the shoveller and blue-winged teal, the ditches should probably not be over a hundred yards apart. In regard to the expense of ditching, it should be remembered that muskrat cropping might help support the project and that diving ducks might also be encouraged by the above treatment.

We need also to bear in mind that muskrats and diving ducks require an abundance of emergent vegetation and where such plant species as bulrush and cattail become dominant, the crowding of ditches may make them useless as loafing places for surface-feeding ducks. Moderate grazing might be helpful in maintaining loafing edges. The practicability of ditching will vary too with the soil. If the soil is too poor to support aquatic plants and the animal life that accompanies it, it will not support a breeding population of ducks.

SUMMARY

1. The components of a nesting terrain include (1) the nesting meadows and (2) the loafing and feeding waters nearby.

2. Data on cover types for 685 nests of mallard, pintail, gadwall, shoveller and blue-winged teal showed that, at Delta, whitetop was the most important nesting cover plant.

3. Mallards and pintails often nest on the bare grain stubble fields and sometimes on bare fallow ground. Many of these nests are plowed under by farmers during early spring plowing.

4. Most pastures in Manitoba are so heavily grazed that little if any nesting cover is left for ducks except where plants unpalatable to cattle occur (such as wild barley and cordgrass).

5. Heavy phragmites forms dense jungles which are seldom

used by nesting ducks.

6. Water level is the most important factor influencing the vegetation of nesting meadows. In dry years cattail and bulrush die out, trees invade the nesting meadows, phragmites, quackgrass and wild barley thrive, and whitetop survives but does not bloom.

7. In wet years short of flooding, cattail and bulrush thrive, trees survive, phragmites thrives and spreads, quackgrass dies out, wild barley thrives and spreads; and whitetop and cordgrass thrive and bloom profusely.

8. When meadows remain flooded quackgrass, cordgrass, trees and phragmites die out. Cattail and whitetop may survive in places and only hard-stemmed bulrush survives.

9. Wild mammals have little effect upon the nesting cover of waterfowl at Delta.

10. Water areas used by ducks during the breeding season include potholes, sloughs, ditches and large bays. Large bays are used less by surface-feeding ducks during the breeding season than they are later in the summer and autumn.

11. The value of a marsh for breeding waterfowl depends upon the amount, quality, and distribution of the required nesting, loafing and feeding areas.

12. Information obtained on the distances of 611 nests of five species from water showed that the mallard, pintail, and gadwall nest over a wider area and farther from water

than the shoveller and blue-winged teal.

13. Nesting cover 100 yards or more from water accommodated only 10 per cent of the blue-winged teal nests and 4 per cent of the shoveller nests but had 24 per cent of the mallard nests, 31 per cent of the pintail nests and 29 per cent of the gadwall nests.

14. Ditching of a marsh to increase the nesting population would depend upon the species it is desireable to encourage and upon ditching costs. Muskrat management of man-made water areas may aid in paying for ditching.

15. Ungrazed ditches that had heavy vegetation on their banks and a shortage of dry nesting meadows adjacent to them were less used by ducks than those with bare, grazed edges. Pintails showed the greatest preference for open, bare banks; mallards were second, shovellers third, gadwalls fourth. Blue-winged teal used the areas with grown over ditch banks as frequently as they used those with grazed edges and adjacent to an abundance of nesting cover.

16. In the case of blue-winged teal, the narrow strip of roadside grass was adequate as a nesting place.

CHAPTER V

THE NESTING SEASON

Winter has scarcely gone from the prairie when the first ducks begin to nest. Over frozen ground and against a background of snow-banked prairie bluffs and ice-packed bays, the first mallards and pintails begin nesting. The shoveller, gadwall and blue-winged teal, later to arrive, begin to nest after the snow has disappeared but before the meadows have los their dead-brown color.

The calendar of activities which make up a nesting season is a rapidly moving one. Although it is definite in pattern, there is sometimes an overlapping of events. The chronology of happenings for several years varies with the conditions of each year; and the time of occurrence of activities is not the same for all species.

The over-all span of the nesting period at Delta has been discussed by Hochbaum (1944:94) who illustrated graphically the laying dates of the species that nest there.

In the present study an attempt was made to determine the length of the nesting season to show up the differences between years as well as the variation between species; and to determine the effects of weather upon the time of beginning and length of the nesting season.

There is more than one way to obtain such information. For example, masses of brood data might be gathered and the

ages of broods plotted to show the results of nesting activity. From this we could get some idea of when nesting peaks occurred. But obviously this method takes no account of predation on early nests. If 90 per cent of all first nests were destroyed, the peak comes too late in the season to represent the actual nesting activity that preceeded it.

Another method, and the one I used at Delta, was to find nests, determine their beginning dates, then plot these nest-startings by weeks and species.

In order to determine the starting date of each nest it was necessary to save the embryos, then back-date to the day the first egg was laid. Since a hen normally laid one egg each day, the formula was: number of eggs in nest plus number of days of incubation equals the number of days since the first egg was laid. For example, a nest of ten eggs was found on May 20. It was determined to be in the tenth day of incubation. Hence, ten (number of eggs) plus ten (number of days incubated) equals twenty (number of days since first egg was laid). Thus we know that this nest was started on (or about) May first.

By this method mistakes of a few days may have occurred but, despite these, it was a far better method than any other for determining the starting dates of nests. Errors may have occurred because: (1) hens may have dropped eggs outside the nest when disturbed at laying time. When this happened our

calculations would have been thrown off one day for each egg dropped. (2) It was not always possible to know whether a laying hen had deposited her egg for the day when her nest was found. Hence, a one-day error could have occurred in this manner. (3) The aging of embryos for field work is not accurate to within less than a day. The aging of embryos involved the breaking of one egg from each nest and comparing it with a collection of known-age embryos that I had prepared in the hatchery. This technique was used in 1949 and 1950.

The errors involved in the above discussion are of small importance in comparing the nesting chronologies for several years. Nor are the important in comparing the nesting chronology between species for any particular year.

Figure 23 shows the nesting chronology of the mallard, pintail and blue-winged teal for the years 1949 and 1950 as determined by the percentage of nests started by weeks of the season.

Figure 24 shows the chronology of the shoveller and gadwall seasons based on number of nests started during the different weeks of the season.

Description of Data.--For the years 1949 and 1950 starting dates for 63 mallard, 15 gadwall, 110 pintail, 29 shoveller and 115 blue-winged teal nests were determined. The volume of data for the mallard, pintail and blue-winged

FIGURE 23 NESTING CHRONOLOGY OF MALLARD, PINTAIL, AND BLUE-WINGED TEAL FOR THE YEARS 1949 AND 1950 DETERMINED BY THE PERCENTAGE OF NESTS STARTED BY WEEKS OF THE SEASON.

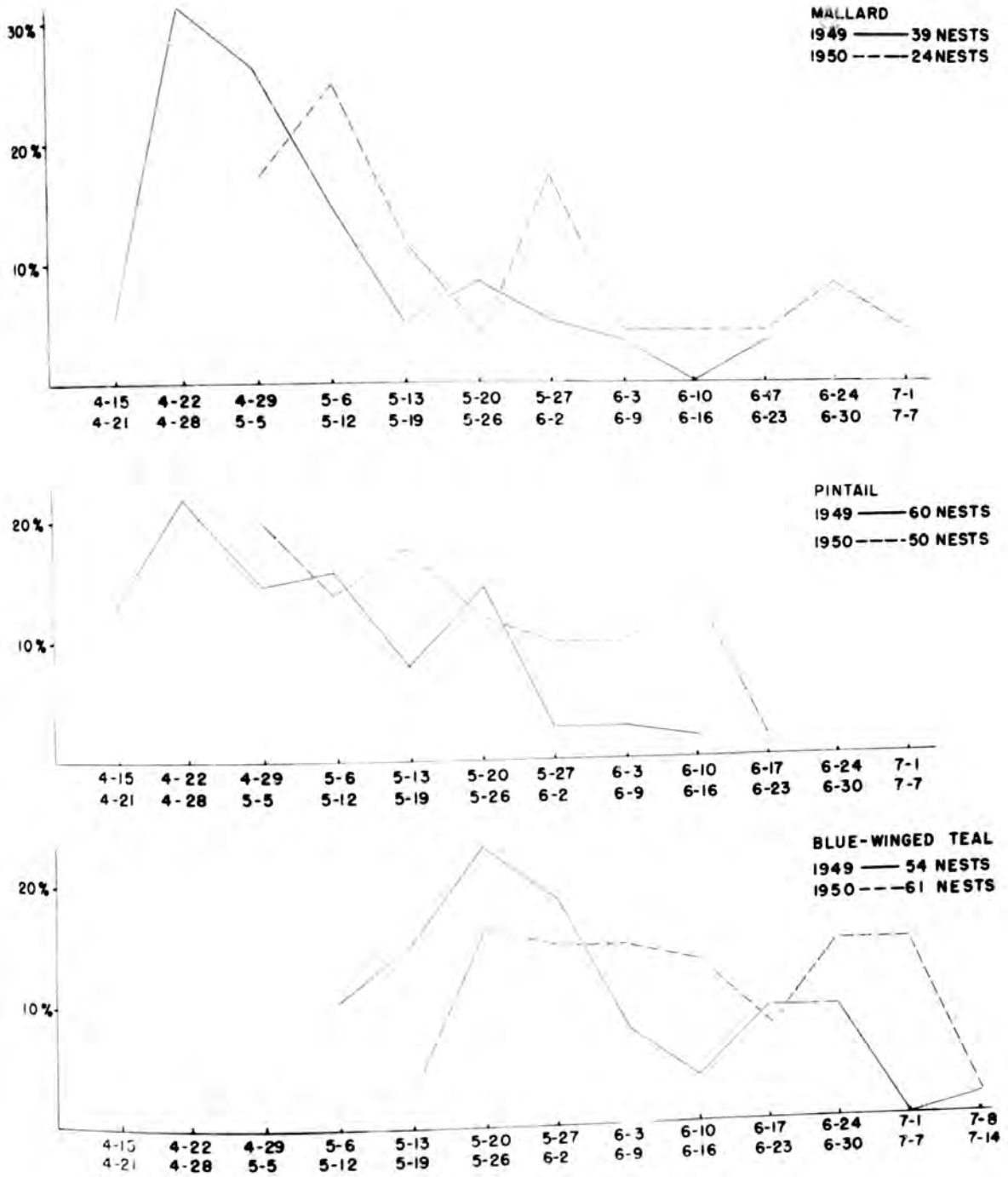
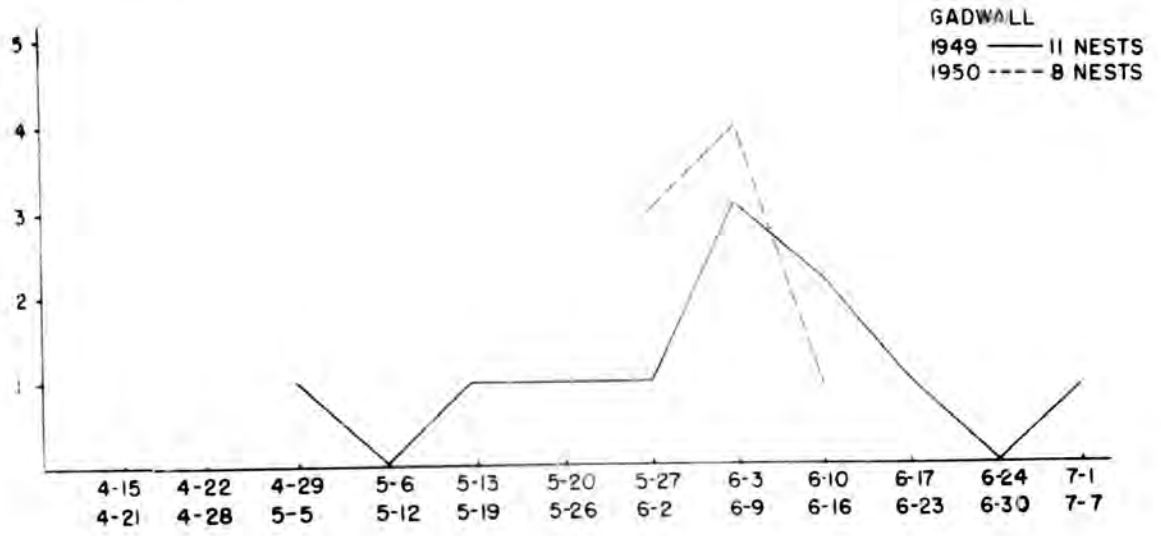
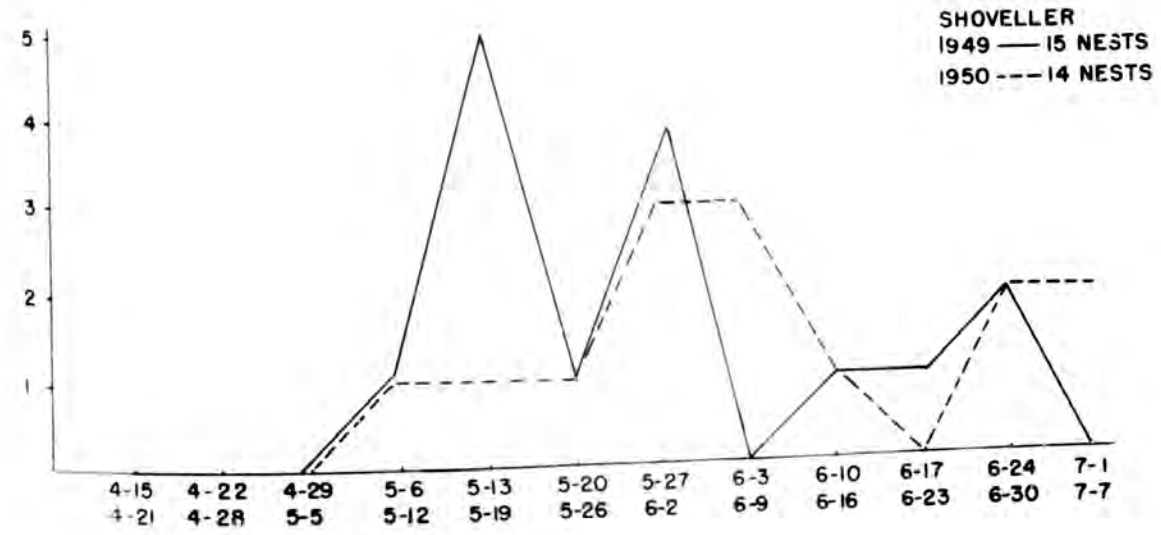


FIGURE 24 NESTING CHRONOLOGY OF GADWALL AND SHOVELLER FOR THE YEARS 1949 AND 1950 DETERMINED BY NUMBER OF NESTS STARTED BY WEEKS OF THE SEASON





teal is sufficiently great to give a good curve of the nesting chronology for these years. The small quantity of data for the shoveller and gadwall allows a limited interpretation.

A Comparison of the Nesting Dates of Five Species.--From these figures we see that the mallard and pintail nesting peak is reached before the last three species begin nesting. This is the usual situation in southern Manitoba. The mallard and pintail are the early-nesting species and the gadwall, shoveller and blue-winged teal are always later. Just as the pintail and mallard are first to begin nests (one or two weeks before the others), they also end their nesting earlier.

The gadwall and shoveller curves show two important points: (1) the difference in the time that these species began nesting as compared with the earlier species; and (2) the difference in chronology that existed between the two years.

A Comparison of the 1949 and 1950 Nesting Seasons.--In the opening chapter I discussed the arrival dates of the various species and pointed out that they vary considerably between years. The variation in arrival of the mallard and pintail was two weeks; of the gadwall, shoveller and blue-winged teal, one week. Just as the arrival dates vary with years, so do the beginnings of nestings vary. The spring of

1949 was near normal for southern Manitoba but the spring of 1950 was one of the latest on record. The difference in nesting chronology between these two years was a conspicuous one. To illustrate the difference I have plotted nesting data by species.

From Figures 23 and 24 it is apparent that the mallard and pintail began nesting two weeks later in 1950 than they did in 1949 and extended their nesting season by about the same length at the end. The blue-winged teal began nesting one week later in 1950 than in 1949 but ended its nesting season at about the same time both years. The shoveller began nesting during the same week in 1949 as it did in 1950. The peak of the nesting season, however, was reached two weeks later in 1950 than in 1949. There was no perceptible difference in the close of the season.

Hence we see that of all species studied, the shoveller was the only one which started some nests during the same week each year. Consistent with this evidence is the four-year record of an individual shoveller hen given in Table 12. She began nesting in late-spring 1950 even earlier than in early-spring, 1949.

Small numbers of gadwall nests were found during the last week in April in 1949 and the majority were found that year the first week in June. This seems to indicate that the nesting of this species was delayed by the cold weather and

TABLE 12 FOUR-YEAR NESTING RECORD FOR SHOVELLER HEN NUMBER 47-604004

Year	Date 1st nest started	Number eggs 1st clutch	Number eggs 1st renest	Number eggs 2nd renest
1947	May 20	12	8	8
1948	May 21	12	?	?
1949	May 18	1	*12	?
1950	May 16	12	?	?

* A continuous laying record

that most of the hens began nesting at about the same time.

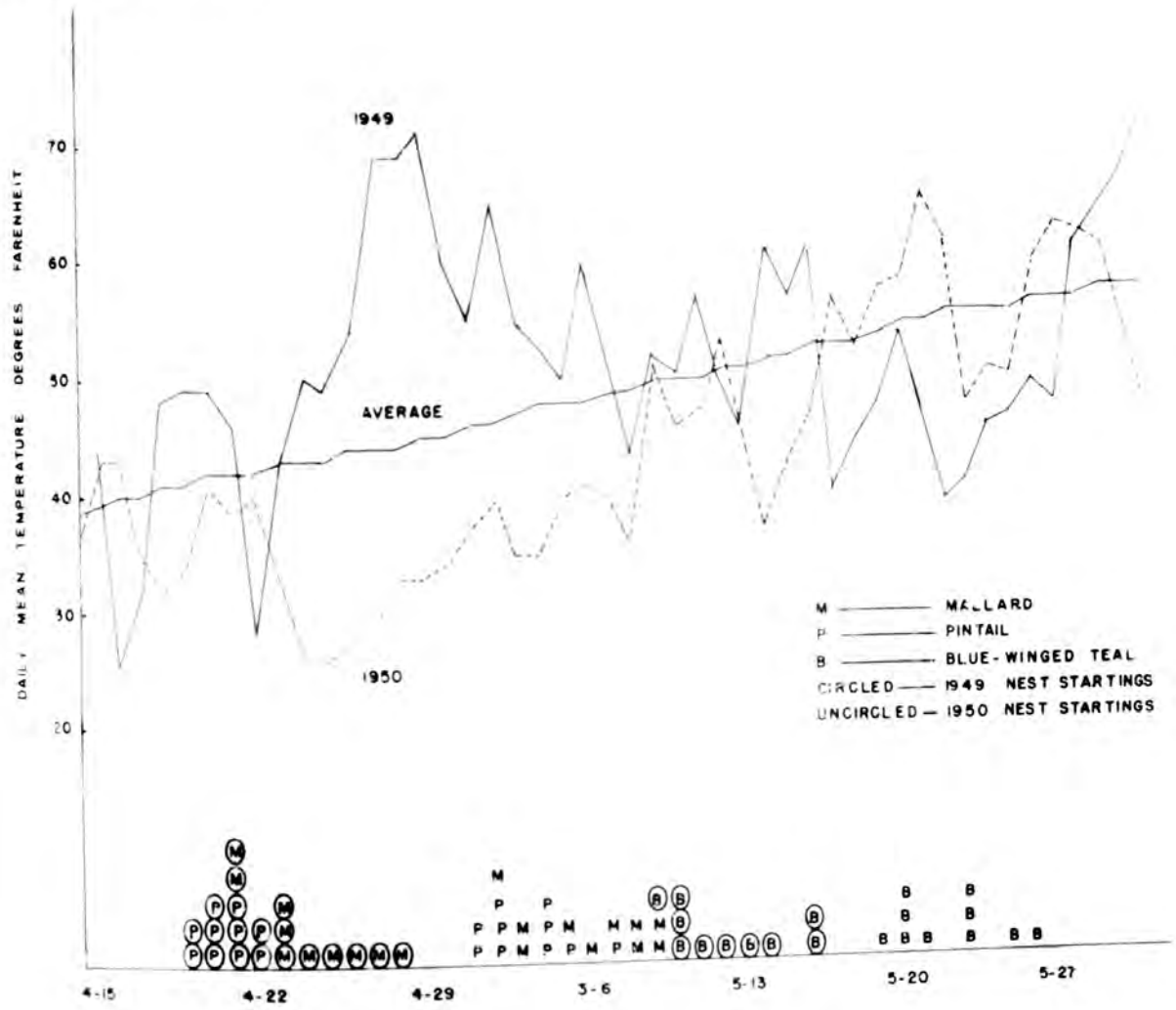
In interpreting these data it is more difficult to understand the end of the nesting season than the beginning. For all species, including the gadwall and shoveller, for which there are only meager data, I know that the beginning date demonstrates, for each year, the date when nesting actually began. For the end of the season, however, the picture is less clear. Only for the mallard, pintail and blue-winged teal are there enough data to warrant a conclusion. For these species it seems likely that an extension of the nesting season e isted in 1950 comparable to the delay which occurred at its start.

The Effects of Temperature on the Nesting Season.--Just as it has been shown (p. 26) that temperature is an important factor in determining the arrival dates of waterfowl, it can also be shown that temperature is important in determining the beginning of nesting. It is clear that nesting began in 1949 much earlier than in 1950. A look at the weather record for the period shows us that the 1950 delay in nesting coincided with continued low temperatures.

A comparison of mean daily temperatures for these two years for the period April 15 to May 30 and the beginning nesting dates of five species of ducks for these two years is shown in Figure 25.

The mean daily temperature of a "normal" year for this

FIGURE 25 RELATIONSHIP OF TEMPERATURE TO START OF EGG-LAYING DURING THE YEARS 1949 AND 1950 FOR MALLARD, PINTAIL, AND BLUE-WINGED TEAL



period is forty-seven degrees Farenheit. In 1949 the mean daily average was fifty degrees Farenheit and in 1950 it was only forty-three degrees Farenheit. Furthermore, 1949 had no prolonged below-normal periods, whereas 1950 had well-below-normal temperatures most of the time.

The period April 15 to May 30 is an arbitrary one selected because most first nestings probably begin in this period.

The effects of temperature on the beginning of nesting are seen when we com are the beginning dates for the two years by species.

The effect of temperature on all activity during the spring was easily observed both in the wild and in the captive birds on the station pond. On warm evenings following the first arrival of the birds one saw mallard and pintail pairs cruising over the marsh, apparently selecting nesting locations. But on cold evenings this activity ceased. In the hatchery pond where we maintained a flock of hens there was constant courtship activity on the part of wild drakes which came into the pond. This activity reached its peak on warm evenings, but was greatly retarded or ceased when the temperature dropped to about freezing. Apparently there is a temperature threshold just above freezing where activity stops. At exac what temperature the threshold exists is difficult to determine.

Although we have not been able to measure this precisely we have been able to predict changes in activity due to temperature changes. A mild evening following a cold period brought on the resumption or beginning of this activity. Temperature fluctuation from one day to the next and during one day coincided with considerable activity or the complete absence of it.

The question arises, what happens to hens and their nests when a severe cold spell follows a warm spell. I heard rumors that ducks were dropping eggs on the edges of prairie ponds indiscriminately during cold weather without building nests. These rumors were run down to their sources but were unfounded. Dropped eggs are a fairly normal thing during the nesting season, but I have found no evidence of excessive egg-dropping due to cold weather.

It is conceivable that the temperature might drop to a point where even the eggs themselves when unguarded (as they are during the laying period) might be damaged by cold.

The temperature limits which effect the hatchability of wild duck eggs have not been determined. Considerable work on the effects of temperature on hatchability of domestic chicken eggs has been done. Recent experiments show that chicken eggs can stand considerable cold without being harmed. Of this Jull, McCartney and El-Ibiary (1948:140) say, "Chicken and turkey hatching eggs can be subjected to considerably lower

temperatures for longer periods than has usually been considered possible without seriously affecting hatchability.

"Holding chicken eggs for one day at 20°F. reduced hatchability considerably and hatchability decreased materially each succeeding day to the fourth day with zero hatchability. Subjecting chicken hatching eggs to −1°F. for as long as 10 hours, the internal egg temperature being approximately 30.2°F., did not seriously impair hatchability. The longer that chicken eggs are held at −1°F. the greater the decrease in hatchability. Subjecting chicken eggs to −10° to −13°F. for 9 to 10 hours gave relatively as good hatchability as their respective controls. In one series at −10° to −13°F. the temperature dropped to −20°F. on one occasion, resulting in a relatively high percentage of cracked eggs but as high as 25 percent hatchability was secured from the fertile eggs incubated. Chicken eggs in which the internal temperature was approximately 5.2°F. produced some chicks."

At Delta during a cold spring it was not uncommon to hear tales of great losses of duck eggs from freezing. I have found no evidence, during the study, of frost causing a loss of eggs. It should be determined, however, at what temperatures duck eggs will be killed and to what extent ground cover and nest lining protects eggs from frost damage.

The most significant effect of low temperatures seems

to be the delay in the beginning of the nesting season.

Determining the End of the Nesting Season.--Nest hunts during both years of this study were begun as soon as the first ducks arrived in spring and continued until after repeated searches yielded no nests at all. In addition to nest data there are other means of determining the end of the nesting season, and it is also possible to get information about the percentage of hens which were unsuccessful nesters. In 1950 the end of the nesting season, as indicated in Figure 23, was followed closely by an influx of pintails into the Delta marsh. This population did not consist entirely of males as would have been the case had all hens been still renesting. For one small water area within the study area counts of pintails were begun as soon as the influx became apparent and were continued until the drakes were so far into eclipse plumage that they could no longer be identified from females. These counts over a period of ten days are given in Table 13.

SUMMARY

1. The beginning dates for nesting can be most accurately determined by taking an egg from each nest found and by aging the embryo, counting the number of eggs in the nest and back dateing to the time the nest was begun.

TABLE 13 SAMPLE COUNTS OF SEX-RATIO OF PINTAILS IN POST-BREEDING SEASON GATHERINGS AT DELTA, 1950

Date	Drakes	Hens	Percentage of Hens
June 13	52	24	32
14	68	19	22
15	60	18	23
16	73	26	26
19	70	20	22
20	93	26	22
23	104	34	25
Total	520	167	Av. 24

2. During 1949 and 1950 beginning dates of 63 mallard nests, 110 pintail nests, 15 gadwall nests, 29 shoveller nests and 115 blue-winged teal nests were obtained.

3. These data showed that in 1949 the mallard and pintail began nesting during the week of April 15-21 but in the cold late spring of 1950 they did not begin until about two weeks later.

4. There is some indication that in these two species the season was extended at the end by approximately the amount it was delayed at the beginning.

5. In the case of the blue-winged teal, a later-nesting species, the delay was only one week. The nesting season of this bird was apparently extended the amount it was delayed.

6. The shoveller showed no appreciable difference in nesting dates between the two years during which data was collected.

7. Gadwalls apparently were delayed by at least two weeks in 1950 as compared with 1949. There was no perceptible difference in the close of the season for this species during the two years.

8. The lateness of the season in 1950 did not appear to seriously reduce nesting opportunity. For the early and comparatively rapid-developing species the season was not so late that large numbers of young would unable to fly at

freeze-up time.

9. The most significant effect of low spring temperatures seems to be the delay in the beginning of the nesting season. No evidence was obtained in this study to indicate that large losses of eggs are caused by freezing.

10. Large numbers of pintail hens were seen in mixed gatherings just as the nesting season came to a close. Sample counts on one area showed that from seven counts, 24 percent of the birds were hens. These hens were apparently unsuccessful nesters who were no longer trying to renest, as all successful hens should be with broods or on nests.

CHAPTER VI

NESTING BEHAVIOR

Again let us return to mid-April. It is then that the interesting and important behavior patterns of our puddle ducks are first manifested. Still only small patches of open water are available, and few mallards and pintails are on the breeding grounds. The main flight has not yet arrived. On a warm evening loud quacking comes from potholes along the lake ridge. Follow the sound and you see a pair of mallards standing on the ice edge. The pair takes to the air, hen leading; and with continuous loud quacking she leads him in great circles over the marsh. As they fly over another pair the second drake makes a short flight after them but they continue to circle, hen calling, until long after the sun has set.

Far out in the marsh at the prairie's edge pintail pairs are circling too, but theirs is a noisless flight.

The behavior of the puddle ducks in spring is a subject which is both fascinating and valuable as a key to predicting nesting season events and understanding the reproductive status of individuals and flocks. One phase of it, territoriality, I have already discussed.

In this section other phases of behavior will be considered: the selection of the nest site, lding of the nest, addition of nesting material, building of the nest canopy,

rate and time of egg laying, the behavior of the drake during the laying and incubating periods, hen's inability to identify her eggs or to discriminate between addled and fertile eggs, desertion of the nest by the hen, courtship behavior of the incubating hen which leads to re-pairing and renesting, and activity of the laying and incubating hen around her nest.

Behavior of the Laying Hen, Selecting the Nest Site.-- The evening flights of paired mallards and pintails occur several days to a week before the first egg is found at Delta. They appear to be search flights for suitable nesting places, feeding grounds, loafing spots and the other requirements which exist within the home range of the birds. To many of the old hens the terrain is familiar because of the experience of former years. To some of the young hens, although less familiar, it is not new.

The question arose as to the interval of time between the evening flights and the first nesting. I collected six mallard hens from isolated pairs during late April, 1950. These hens were exhibiting the evening flight behavior described above.

In five of the females the largest follicles were the size of a pea or about 8 millimeters in diameter. In one there were four follicles larger than a pea running up to 22 millimeters in diameter. In order determine the period of time still needed by these hens before they could lay, I

assumed that the development of their follicles would proceed at the same rate as they do in a normal laying hen when one egg is deposited each day. One normal laying mallard hen was collected during the spring of 1949 to serve as a comparison. A photograph of this hen's reproductive system is shown in Figure 26. There was one egg in the oviduct fully developed except for its shell. The next follicles in order by millimeters in diameter were 38, 29, 22, 19, and 6. At this rate of development the five hens collected on their early evening flights in April would probably have been ready to lay in four or five days and the one hen whose largest follicle measured 22 milli eters would probably not have been ready to lay for another three days. This is further substantiated by the fact that these hens were collected on April 21, 22, and 25 and that no eggs were found before May 3.

As soon as egg-laying was in full progress, evening flights ceased. Why such flights do not occur later on, following re-pairing and prior to renesting, I do not know. Perhaps by then the hens are fully familiar with their area and the same loafing and feeding places will be used again. As we shall see later, the second nest will be located in the same general area as the first nest.

The fact that cold weather delays brings temporary cessation to the evening flights of pairs as well as a delay

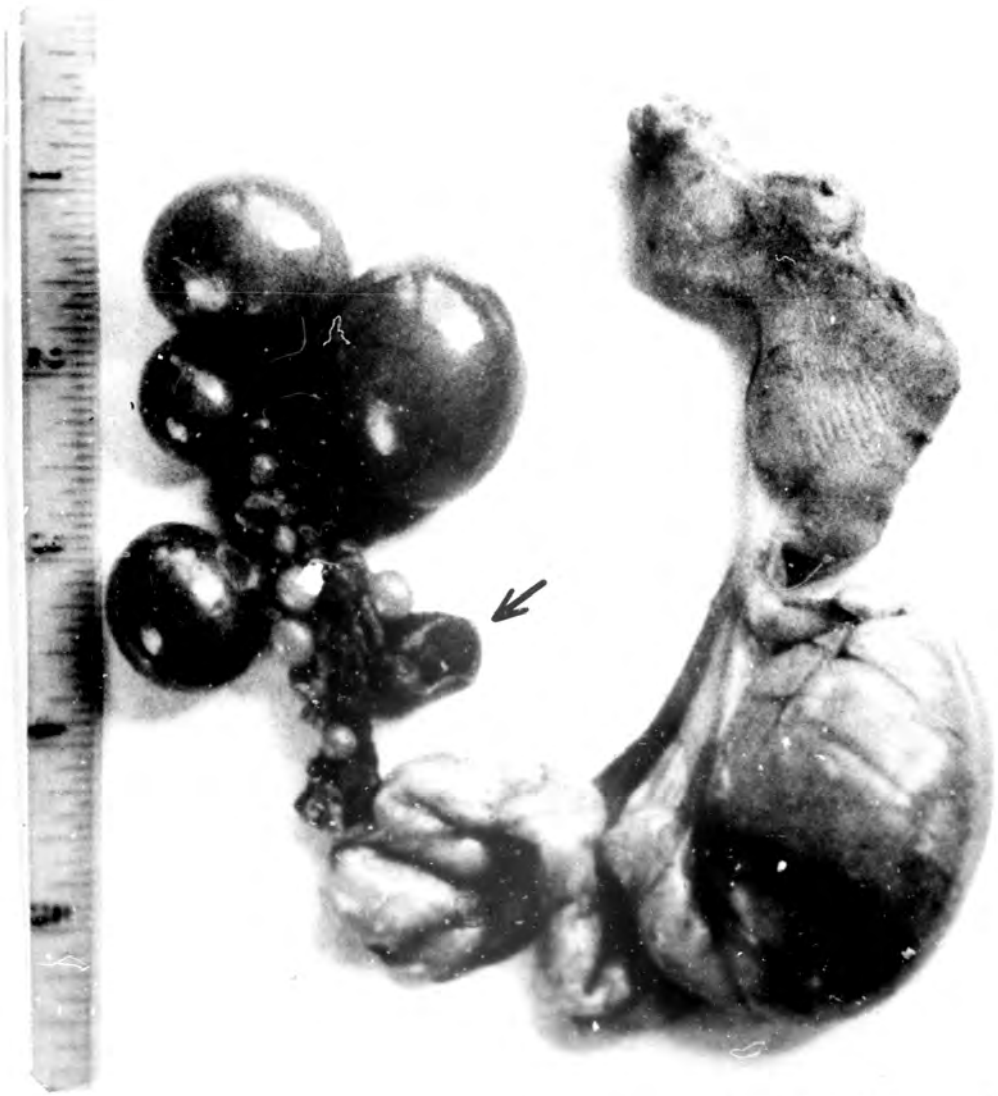


Figure 26. Reproductive tract of a laying mallard hen. The arrow indicates an ovulated follicle from which the large egg in the oviduct probably came.

in nesting indicates a close tie between the bird's physiological status and the weather. The details of this relationship are little known but worthy of further research.

Building the Nest.--Unlike most other kinds of birds, the construction of the nest of surface-feeding ducks does not preceed, but rather accompanies egg-laying and incubation. In this detail the surface-feeders differ even from the diving duck species. Hochbaum (1944:47) says of the canvasback that the hen often begins building and often abandons several nests before laying and that nest construction begins two or three days before the first egg is laid. A similar account of the time of laying in relation to nest construction by the redhead is given by Low (1945:50) who says, "Construction of nests was often begun two or three days to a week before egg-laying started." Evidence among puddle ducks seems to indicate that the only preliminary preparation to the laying of the first egg is the construction of the nest bowl or scrape. For all of these species it is essentially the same except for size. Here, size corresponds to the size of the duck. It is a simple, shallow, hollowed-out depression in the ground from which vegetation has been partly removed. The task of making this depression appears to be accomplished by scratching (as evidenced by claw marks in the earth). Over the deep scratches the base of the scrape is worn smooth from the movements of the hen's breast and belly against the moist fresh earth. It is in this bare nest bowl with only a small amount of nesting

material added that the first egg is deposited. Even after the clutch has been completed, the first egg laid often retains a coat of mud picked up as it rolled about in the nest bowl under the duck's body.

The time during which the nest bowl is dug is unknown. It may preceed the laying of the first egg by several days. Of this Merrill C. Hammond of the U.S. Fish and Wildlife Service writes me (letter dated December 20, 1949): "Data gathered in 1949 at the Lower Souris Refuge in North Dakota suggests that mallards were digging six days before first egg-laying and pintails four days before:...on May 13...I suspect that some gadwalls were digging nest bowls. This date was four days prior to first egg-laying for gadwalls."

Addition of Nesting Material.--The nests of puddle ducks are constructed entirely of material that lies within reach of the hen as she sits on the nest. There is no evidence that the surface-feeding ducks ever carry nesting material from points outside their reach as they sit. I have, on several occasions, deliberately taken nesting material from nests, forced the hen to reach more material and found that as more and more material was used up the density of the surrounding vegetation became thinner. I have watched the extraction of nest material as I sat in a blind; and have seen hens reach far out with open bill grasp leaves and stems, pull these toward the nest (Figure 27)

and tuck them around the nest perimeter (Figure 28).

Building the Canopy.--When located in heavy grass nests of puddle ducks invariably have a well-constructed canopy. The bending of grasses to form this hiding structure is apparently accomplished by the hen as she sits. Its fuction could be both to hide the hen and offer shelter from wind, sun, and rain. On July 7, 1949, I planted a clump of grass near a shoveller's nest beside which I had placed a blind. Soon after the hen returned and settled on her nest she began pulling the grass tops over her (Figure 29). After each pull, the grass was held firm for about five seconds.

Rate of Laying.--Laying ducks normally deposit one egg per day. This fact has been generally accepted and was borne out by the data collected in these studies. Of eighteen nests representing nine blue-winged teals, six pintails, two mallards and one shoveller, I found that the number of eggs in the final clutch equaled the number of days taken to complete the clutch. There were no exceptions to this rule in any case where a complete history of egg-laying was obtained.

Time of Day for Egg-Laying.--The majority of the mallards, pintails and gadwalls go to their nests to lay between sunrise and four hours after sunrise; most records having occurred during the first half of this period. For

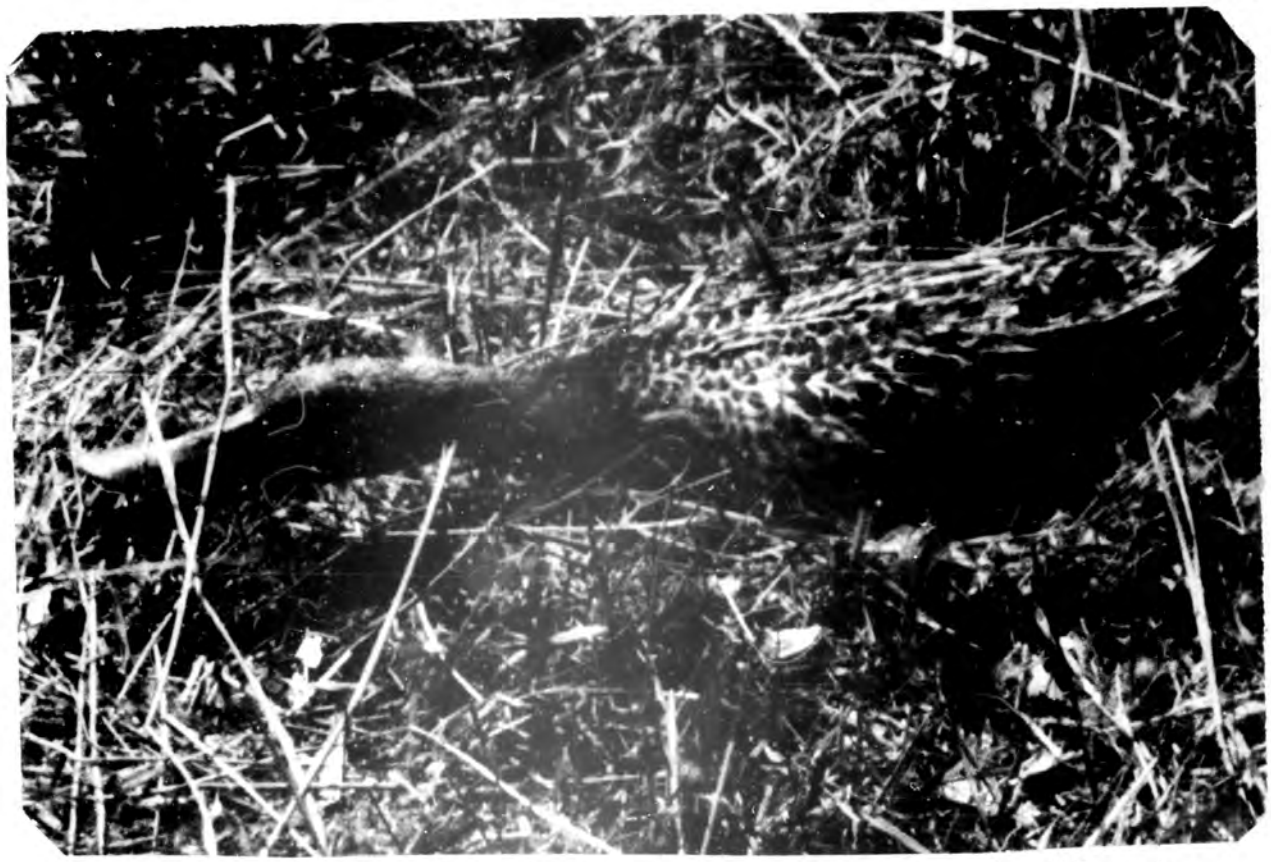


Figure 27. A hoveller hen reaches for grass to line her nest...

Figure 28. ...and tucks the grass into the nest perimeter.

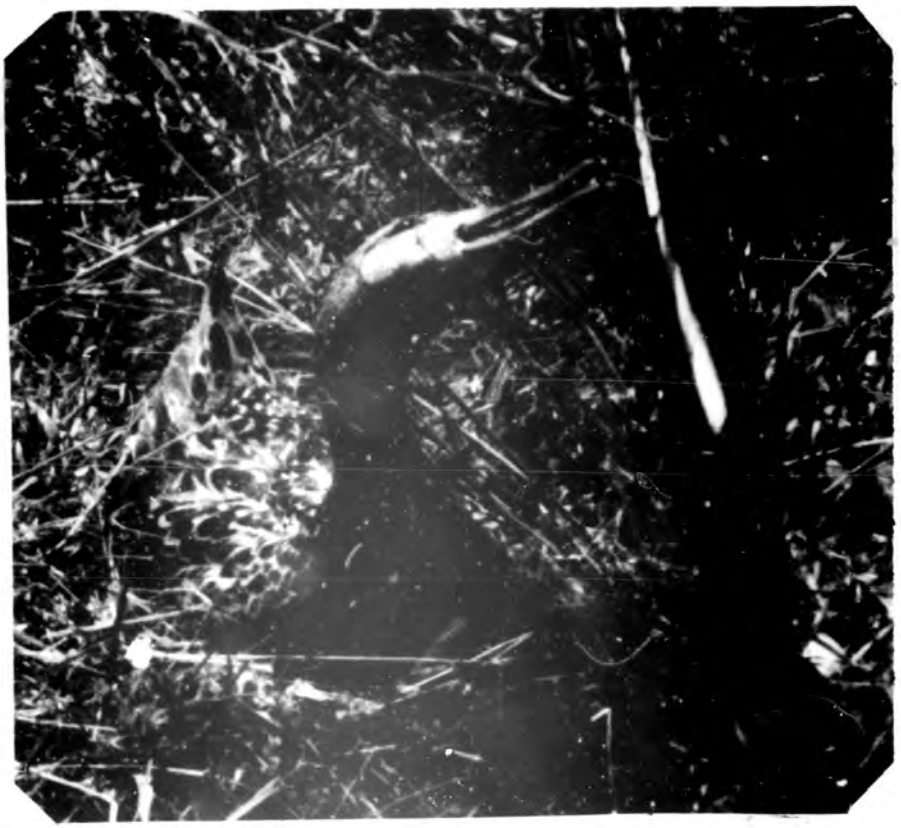


Figure 29 ... A shoveller hen reaches for a live blade of grass...

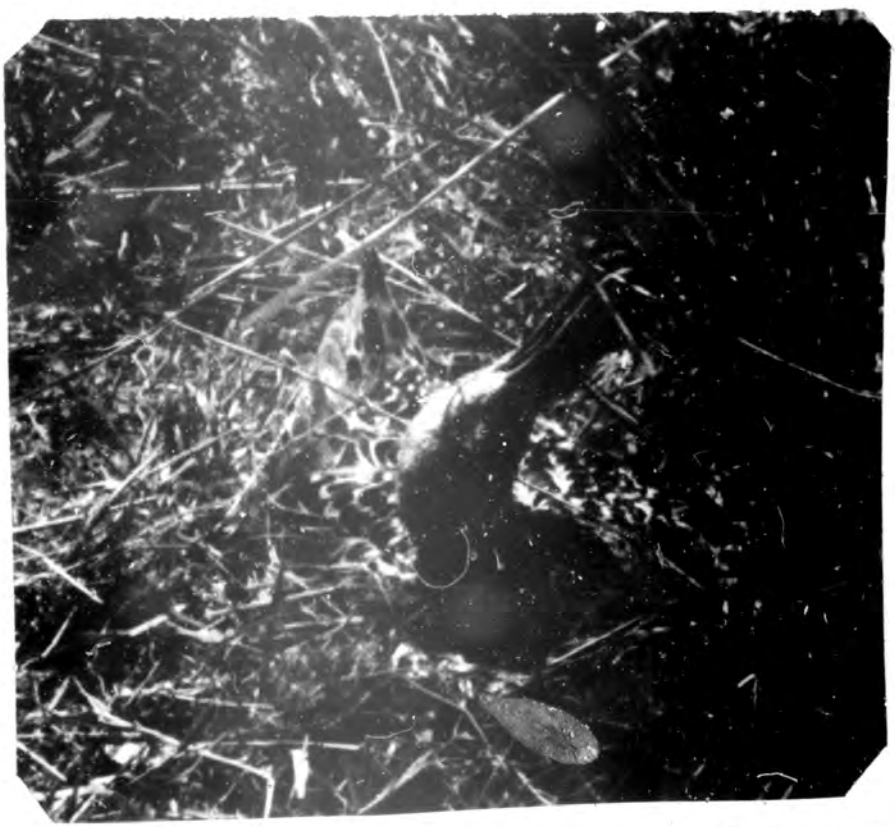


Figure 30 ...pulls it over her back and holds it there for several seconds.

these three species the actual observation of the hen's arrival in the meadow was the best indication of laying time. These were the relatively mobile species which came from distant water and loafing areas to lay and for which pair counts and lone-drake counts were difficult to obtain. Among the less mobile blue-winged teals and shovellers, however, pair counts and counts of lone drakes during the early days of the laying period indicated that the hens of these species normally went to their nests during the latter half of the forenoon. This conclusion was borne out by the fact that "early-morning watching" to locate nests (as described in the introduction under techniques) yielded comperatively few nest locations for these species.

Behavior of the Drake, Accompanying the Hen.--The hen was accompanied by her drake when she was searching for a nest-site and when she was making her daily trip to her nest to deposit an egg. Invariably she led and he followed. At all times during the laying period the drake accompanied his hen when she was not on the nest. Even when she was sitting on her nest, he waited near-by and sometimes flew over the meadow in an apparent search for her.

During this period I often saw lone mallard and pintail drakes circling a particular spot in a nesting meadow and occasionally calling. Following such flight, the drake usually returned to a near-by loafing bar to sleep or wait.

By watching these drakes and later searching the spot over which they were calling, I have found nesting hens. Thus, the drakes were found to be circling and flying over the spot where each knew his hen to be. Although the calls of the drakes were insistent, the females were never known to answer. The mallard drake's call was the usual low quack, less audible than that of the hen's as I heard them on their evening flights preparatory to nesting. The pintail drake's call was the low double whistle which has been described by C. Oldham as a "quuck quuck" (Witherby, Jourdain, Ticehurst and Tucker 1939:271).

Dissolution of Pair Status.--That mallard, pintail and gadwall drakes leave their hens a few days after the clutch is completed was apparent from observations of paired birds, of lone drakes waiting for hens and of bachelor bands of drakes. The shoveller and blue-winged teal drakes, on the other hand, generally remained paired far into the incubation period, although they usually left their hens before the eggs hatched.

Behavior of the Incubating Hen, Sitting on Dead Eggs.--When eggs are infertile or when the embryos are killed (as occasionally happens when fire sweeps a prairie marsh), hens often sit for long periods beyond the normal hatching date. This is true of many kinds of wild birds, other than wildfowl. Numerous accounts of such behavior can be found in the

literature. East (1930:6) tells of a barn owl which sat on infertile eggs for twelve weeks, ten weeks beyond the normal incubation period. Laskey (1940:188) says that where eggs were sterile or embryos dead, the eastern bluebird which has a normal incubation period of from thirteen to fifteen days, sat for twenty-one days. For the same species, Thomas (1946: 156) gives an account of a female sitting for thirty-three d days. An even longer period has been described by Swanson (1926:339) who tells of a female bluebird sitting on addled eggs for thirty-six days. Odum (1942:430) tells of the Carolina chickadee, a bird having an incubation period of eleven days, sitting for twenty-four days. In the western crow, a species having a normal incubation period of sixteen to eighteen days, Emlen (1942:150) says that birds sat on sterile eggs up to thirty-two days before abandoning. Of game birds, Leopold (1933:367) quotes Stoddard as saying that the bobwhite quail has been known to incubate dead eggs up to fifty-six days or thirty-three days beyond a normal incubation period. Leopold (1933:367) quotes Sprake as saying that the Hungarian partridge has been known to sit on dead eggs up to seven days beyond a normal incubation period. Bird (1930:418) says, "One pintail hen whose eggs were scorched on May 2, continued to sit on them until the first week in August."

My longest record was of a pintail which sat on two dummy nest eggs made of wood from April 28 to June 28, 1949,

a total of sixty-two days or forty-one days beyond the normal incubation period of twenty-one days. Another pintail hen sat on dead eggs, which had been substituted for her own eggs, from May 17 to July 15, 1950, a total of sixty days or thirty-nine days over the normal period. On the sixtieth day the rotten eggs exploded from heat when the hen had been kept off her nest by disturbance. Desertion followed.

A similar behavior has been found to exist in the mallard, gadwall, shoveller, and blue-winged teal where hens were kept incubating for shorter periods of time beyond their normal incubation periods.

From the standpoint of production, this waste of effort on the part of hens would be important only if it occurred on a great scale. Abnormally cold weather and heavy rains during the laying season might addle large numbers of eggs and, if the eggs were not cracked, hens might continue to sit for long periods. The only case of several hens sitting for long periods was given me by M. C. Hammond (letter dated December 20, 1949) who says that following a heavy frost on June 8, 1937, he found six sets of dead eggs with hens sitting on them past the normal incubation period. One pintail sat for thirty days, one forty-eight days, a mallard forty-nine days, a shoveller forty-five days and another shoveller, forty-two days. A baldpate sat forty-six days.

How often hens return to burned over nests is hard to

determine. Leedy (1950:264) gives an account of a mallard and a black duck returning to burned nests where at least part of the eggs had been severely scorched and the embryos probably killed. It was not known how long the hens remained on these nests because they were later destroyed by predators.

Since we do not know how frequently hens sit on addled eggs, it is difficult to evaluate the effect of this behavior on the production of young, but I conclude that it could be an important factor in areas where weather or fire are particularly destructive of eggs.

The persistence of incubating hens to sit on eggs for long periods and their inability to recognize artificial eggs made it possible for me to photograph them from a blind and to obtain shots of the following activities: egg-shell carrying, grass tucking, nest lining, the building of the canopy, egg rolling and the approach to the nest.

Nest Desertion.--Desertion as the result of disturbance is most likely to occur during the early part of the laying period. It is most frequent with the mallard and least frequent with the blue-winged teal. Thus, all but one of eighteen mallard nests having four eggs or less were deserted by the hen as a result of our disturbance. Only one of twelve nests were deserted when the hen had already laid between five and eight eggs. No desertion from flushing occurred after the eighth egg was laid or during incubation.

The pintail showed a lesser tendency to desert even at the early stages. Ten of twenty pintail nests found prior to the laying of the fifth egg were deserted after the hen was flushed once. Only three of twenty-seven pintail hens deserted after being flushed once between the laying of the fourth egg and ninth egg. No pintails deserted after being flushed from nests during incubation. The blue-winged teal showed only a slight tendency to desert after one flushing. Only one of seventeen hens deserted before the fifth egg was laid and only one of twenty-one between the fourth and ninth egg. None deserted after the eighth egg or during incubation.

Since these figures represent only the hens which failed to return to their nests after being flushed once, it does not represent the whole story or indicate how much disturbance hens will tolerate. It has been suggested by Leopold (1953:366) that a desertion limit may exist, a certain time during the laying period or the incubation period at which the hen would no longer desert after disturbance. It must be remembered, however, that desertion varies with the degree of disturbance and with the individual bird.

Courtship.--Two periods of courtship have been described by Hochbaum (1944:22) for the species of ducks breeding in the Delta region: "...the competitive prenuptial courtship preceding pairing, and the possessive nuptial courtship of the mated pair."

Only occasional prenuptial courtship of surface feeding ducks was seen at Delta because most of the birds were paired when they arrived and were already in their nuptial period. An exception to this was the baldpate in which prenuptial courtship was common at Delta in late April and May each year. The prenuptial courtship activities of the puddle ducks consisted of various displa ys, postures, and pursuit flights as described by Millais (1902), Wormo d (1910), Lorenz (1941) and Delacour and Mayr (1945). As the last two authors have pointed out, courtsh p pursuit flights are often confused with pursuit flights associated with territorial behavior. At Delta the two flights were clearly distinguishable.

For the first few weeks of the breeding season each year, flights of mallards, pintails and gadwalls were largely limited to flights associated with territorial behavior. These occurred in mallards and pintails at the time baldpates were making aerial courtship flights.

As the season advanced a new type of flight was seen. This was the renesting courtship. It was evident that the hen initiated the flight by a series of teasing calls. In the pintail a lone hen uttered a teasing "yank-yank-yank" and threw her head back along her side. This was apparently the incitement call that Heinroth (Witherby et al, 1943) termed the incitement note in the European pintai nd described as "rarrerrer." The actions of the hen followed closely those

described by Lorenz (1941) in his discussion of the sexual incitement notes and actions of both mallards and pintails. I have watched pintail hens teasing drakes in the meadow for a half hour or more at a time. On each occasion short flights of from ten to fifty yards, hovering, teasing calls and head throwing kept several drakes alert and drew them to the hen. Following a series of calls the hen made a towering flight, continuing her calling intermittently. As she did so she hunched her body, drew her wings in and dropped momentarily in mid-air as her head went back. I have seen pintail hens climb to what appeared to be over a thousand feet above the prairie on such flights. As the flight began a number of drakes pursued, the number decreasing as many of them dropped out until at last one alone remained with her.

Each year at Delta we observed these late-season aerial courtships of mallards and pintails, although they were absent during the first three weeks of the nesting season. Hochbaum (1944:16) attributed this to the late arrival of unpaired birds and says: "The single drake is a rarity in April as sex tallies of hundreds of birds show an almost perfect 50:50 sex ratio. In early May, however, unmated mallards and pintails reach Delta, such late transients showing a preponderance of males. Hereafter drakes outnumber hens, and one sees courting parties of four or five to a dozen or more drakes in pursuit of a single hen."

Evidence from my observations of marked individual hens whose nests I have robbed indicates that much of this late courtship is associated with re-pairing of hens which have lost their nests after their drakes have left them; it does not necessarily involve late arrivals. In 1948, three marked pintail hens whose nests I robbed were later seen "teasing" drakes, and later still found to be renesting on the study area. In these three cases the original drakes had abandoned their hens by the time I robbed the nests. In no case have I seen courtship flights follow nest destruction where the hen and drake were still paired.

In addition to behavior observations of marked individuals, I have collected hens which were seen teasing drakes and examined their ovaries for the presence of ovulated follicles (Kabat, Buss and Meyer, 1948:399-400) to see whether or not they had previously laid the same season. Four such hens of known behavior were collected in 1948 (three pintails, one mallard). Three of these showed signs that they had done so. I was unable to tell whether or not the fourth hen had laid that year.

It was further noticed that the incitement call of the teasing behavior could sometimes be induced. On approaching the nest of an incubating bird whose drake was no longer with her I came to expect the incitement call as she flew off in alarm and found that this behavior (uttering the incitement call) was, in fact, stimulated or released by my disturbance.

There were no drakes near and, since the bird was, in each instance, surprised by me, the behavior must have been caused or set off by my approach.

No part of the teasing behavior was ever seen in laying hens which were still paired with their drakes or in incubating birds which left their nests normally and without disturbance.

The existence in incubating hens (no longer paired) of a latent teasing ability which will attract drakes and lead to re-pairing greatly expedites renesting following nest destruction.

While these late-season or renesting courtship flights of mallards, gadwalls and pintails are common, one seldom sees them in the shovellers and blue-winged teals. I suspect that the difference is due to the length of time the drakes stay with their hens after the clutches are laid. Blue-winged teal and shoveller drakes do not abandon their hens until incubation is well advanced, while mallard, pintail and gadwall drakes abandon their hens shortly after the clutch is completed. This means that few unmated hens result from early nest destruction among shovellers and blue-winged teals, while unpaired hens of the other species are common.

Retrieving of Displaced Eggs.--Eggs occasionally roll out of a nest when the hen leaves quickly. When she returns and is on her nest again, the hen retrieves these using the

under part of her bill. Retrieving behavior has been described for several species of birds and this literature is reviewed by Noble and Lehrman (1940:36).

Lorenz and Tinbergen (1937:10-11) describe and illustrate the retrieving of eggs by the grey-lag goose (Anser anser). The retrieving behavior of the grey-lag as they describe it is similar to the retrieving behavior as I have seen it among ducks.

In July, 1949, I experimented with a shoveller hen to see how and whether she would retrieve eggs when they were placed outside her nest. Figures 31 and 32 show the method by which this incubating shoveller hen recovered the displaced eggs. All retrieving was done by the hen from her position on the nest. No attempt was made to retreive eggs by means other than the underside of the bill or from distances greater than she could reach as she sat on the nest. I found that eggs which could not be retrieved by the means shown or from a distance the hen could easily reach, were abandoned. One example of this was an observation made on July 16. I had left three eggs in the nest and had put two more eggs ten inches from the nest. On her return the hen quickly pulled two eggs into the nest but the third egg rolled away each time when it struck a grass clump. After thirteen attempts to bring it in the hen ceased trying and left the egg where it was. No variations in proceedure were attemoted.

Figure 51 A shoveller hen reaches far out to retrieve an egg that has been placed outside her nest...

Figure 52 ...and brings it under her by using the under side of her bill.

Lorenz and Tinbergen (op. cit.) have found that the grey-lag goose retrieved only objects with an unbroken surface. I found that the shoveller hen retreived only unbroken eggs and that eggshells were carried away. One pintail hen, however, carried away some of the broken eggshells and retrieved others using the same method as that described for the shoveller, apparently not always differentiating between whole eggs and shells.

Rest and Feeding Periods.--The time spent away from the nest has been measured by Low (1945:48) who used a recording instrument to indicate frequency and length. He concluded that, "No definite rhythm of incubation was detected in redheads as rest periods away from the nest came at irregular intervals during the day and night."

Of the canvasback, Hochbaum (1944:50) says, "I observed no fixed hours of departure from the nest during incubation. Short rest periods during the morning and evening twilight appear to be regular, but the hen also leaves the nest at irregular intervals during the day. Departures become less frequent, and of shorter duration, as incubation advances."

Girard (1941:258) writes of the mallard, "Nesting observations indicated that the incubating hens permitted themselves two feeding periods per day

Bennett (1938:49) says of the blue-winged teal, "The female left the nest for exercise, rest and feeding purposes

once or twice each day. Usually the rest periods were about 7 A.M. and 7 P.M. The females were observed to stay away from the nest 20 minutes to 2 hours. Occasionally females were seen to leave the nest during the middle of the day."

Of fifty observations recorded at Delta it was found that hens leave their nests between seven and eight in the morning (twenty observations). Of thirty afternoon observations, none occurred after dark. My observations of the five species of ducks here treated indicated that hens probably leave their nests to feed, stretch, bathe, and preen once or twice each day. The time of day and number of times per day seems to vary with individuals.

The activity of the hen during this off-nest period appeared to be unhurried. I have watched incubating hens feeding along the ditchbank and pothole edges and have had the impression that food was a secondary consideration. Most of the off-nest period seemed to be spent in preening, bathing, stretching and sitting. Contrasted with the eagerness with which ducks consume food at other seasons, it appeared that food consumption at this period was at a minimum. Perhaps food requirements of an incubating hen are greatly reduced because of reduced activity.

Egg Recognition.--Eggs taken from hens for use in the hatchery were often replaced with the eggs of another species. It was found that pintails accepted blue-winged teal eggs,

mallard eggs, redhead eggs and shoveller eggs. One mallard hen readily accepted teal eggs despite their much smaller size. One blue-winged teal accepted mallard eggs but in smaller number than her own clutch. One pintail hen continued to sit on a mixed clutch containing teal eggs, canvasback eggs and pintail eggs.

Of five mallards given wooden nest eggs in April, 1949, all deserted. Of fourteen pintails given wooden nest eggs during the same week, all but two deserted. How much of this desertion would have occurred if the wooden eggs had not been substituted, however, is not determined. All of the mallards and five of the pintails were still laying. One incubating shoveller hen in 1949 was given two wooden nest eggs along with three of her own eggs. This hen buried the two wooden eggs underneath the nest lining deep in her nest and continued to sit on her own three live eggs. The size of the nest eggs may have influenced her as they were considerably longer than her own eggs.

Farley (1939:57) gives an example of a pintail sitting on stones. In my experiments at Delta, ducks have shown no ability to differentiate their eggs from those of other species and, in many cases, from wooden eggs. The acceptance of dummy eggs, however, did not meet with uniform success and they were sometimes recognized as not acceptable.

Eggshell Carrying.--An early description of a mallard hen carrying an eggshell has been given by Oates (1905:33)

who believed that the egg had been cracked and that the hen was removing it in an attempt to clean out her nest.

Hochbaum (1944:92) comments on egg-carrying by wild mallard hens as seen by local guides at Delta. He also describes seeing a shoveller hen carrying an egg but concludes: "I have no evidence which might explain such behavior." Lindsey (1946:491) observed the New Mexican duck carrying what, from his description, apparently were whole eggs and believed it to be associated with nervousness and desertion.

I have observed wild hens carrying an eggshell on four occasions and have been able to induce eggshell carrying by adding shells to nests of wild birds in order to learn the details of this rarely seen behavior.

My first observation of eggshell carrying was made on June 8, 1946 in the evening. A shoveller hen was seen at a distance of about forty yards carrying parts of (or an entire) egg.

My second observation of eggshell carrying occurred when Albert Hochbaum and I watched a pintail hen on the evening of June 17, 1946. She was first seen preening along a ditch bank. From all appearances she was an incubating bird away from her nest for the evening feeding and preening time. She appeared to be almost ready to return to her nest.

After a few minutes she walked slowly up the ditch bank, craned her neck for a slow examination of her surroundings

and then flew directly west and alighted in the grass a hundred yards away. About two minutes later she flew back over the ditch with an eggshell in her bill, dropped it over the water and returned to her place in the meadow from where she had just come. We immediately walked over to the spot. As we approached, the hen fluttered away low over the grass and dropped down about sixty yards away. There in the whitetop was a partly destroyed nest. Three whole eggs remained, still warm. Three more eggs had just been destroyed. A tiny wing of the almost-ready-to-hatch embryo lay at the edge of the nest along with matted down and fresh blood. On examining the undamaged eggs we found them to be within a few days of hatching. It seemed likely that the predator, apparently a Franklin ground squirrel, had been at the nest when the hen was away and had been frightened by her return.

The third observation was made on June 3, 1947 at 9:05 A.M. when a pintail hen came over the roadside ditch, dropped an eggshell into the water and then joined her drake on the ditch bank. She remained there for thirty minutes after which the pair made a flight over the adjacent cover and returned to the ditch bank for another eight minutes. Then the pair made a second flight. This time the hen dropped down into the cover and the drake returned to his ditch bank alone. I then walked into the whitetop until, on approaching the nest, I saw the hen fly off with another eggshell. She circled over the ditch, dropped the shell over the water and, when

joined by her drake, flew off to the bay a thousand yards away. The nest had no down. One eggshell remained with fresh unincubated contents. The eggs were cold but had been freshly broken by what appeared to be a Franklin ground squirrel. This was a new nest. The hen, on her morning visit to deposit an egg, had found her nest destroyed or being destroyed.

A fourth observation was made on June 21, 1947 at 7:00 A.M. when Nina Elder William Carrick and I saw a pair of shovellers make several trips over whitetop cover across the road from the Delta ditch. The hen lit in the grass as her drake returned to the ditch bank. One minute later the hen flew out of the grass with an eggshell. The hen then made three flights back to the nest and each time came out carrying an eggshell. Each time the shell was dropped into the water of the roadside ditch. After almost two hours of watching we walked into the meadow to examine the nest from which the shoveller had taken the shells. Five whole eggs and one broken egg remained. A Franklin ground squirrel was at the edge of the nest when we approached and ran into the dense grass as we came nearer. The nest was at the very moment being destroyed by the squirrel. The remaining five eggs were fresh and unincubated, showing that the hen was apparently still laying and had been returning to deposit another egg at the time the squirrel was eating the eggs. Since the hen took shells from the nest at the time when the

squirrel was destroying the nest, her arrival must have driven off the squirrel temporarily.

Induced Eggshell Carrying.--The rarity of the above observations becomes apparent when we consider that the approximate number of my full days afield on the breeding grounds each year was over a hundred and also that the phenonenon was watched for by others. Furthermore, the years 1948 and 1949 passed without yielding a single glimpse of this behavior, albeit more than the usual time was spent afield. During 1947 and 1948 several attempts were made by William Carrick and me to erect a blind near a going nest in the hope of being able to plant shells and of seeing the resultant behavior. These attempts failed due to complete predation.

In July, 1949, a year later, a wild shoveller hen nested within the confines of the large hatchery predator-proof pen at the Delta station. This pen covers about one acre and is surrounded by a high fence. Within the fence is a man-made pond covering about one-tenth acre. Thirty yards from the pond, where the nest was discovered, a blind was placed, and on July 5 our first shell-carrying experiment was begun.

Our hen was well into the incubation of her eggs as we had determined their hatching date to be the ninth of July, but four days off. Consistent with the closeness of incubation, she was firmly attached to her nest and as tolerant as we could expect any hen to be.

First of all, six fresh shoveller eggs were substituted for her own clutch, the latter being placed in an incubator for hatching. The purpose here, of course, was to induce her to stay on her nest for a longer period than would otherwise be natural. Then, five hatched shoveller eggshells were added to her nest, being placed on top of her whole eggs.

Within thirty minutes of this interruption our hen returned to her nest. She alighted twenty feet from the nest, walked toward it until she was within twelve feet, then, in a "sneaking" posture, proceeded to walk the last six feet. She settled herself on her eggs and eggshells and crushing them beneath her by a rock-the-boat motion attempted to settle down. One shell refused to be settled and grasping this with her bill, she flew away to the pond (Figure 33) and quickly submerged the shell after alighting on the water.

Following this preliminary experiment, thirteen more trials were made. In each trial shells were added to the nest and the bird's behavior watched and studied. Our hen made eighty-one trips from nest to pond, each time carrying away a shell.

Further experiments were carried out in 1949 and 1950 to see whether other species of ducks also removed broken eggshells from their nests. On July 12, 1949, Eugene F. Bossenmaier put ten broken eggshells in a wild blue-winged teal's nest which was about half-way through incubation. No

Figure 53 A shoveller hen flys away from her nest with an eggshell

Figure 54 A pintail hen hesitates with an eggshell before flying away with it.

blind had been constructed by the nest so the hen's activities were watched from a distance by use of binoculars. After fifteen minutes had elapsed, the hen returned to her nest and after about one minute flew off in the direction of the roadside ditch. Seven trips were made by the hen between nest and ditch during a period of one hour. From our distance we were unable to tell whether or not the hen had an eggshell in her bill. Examination of the nest after one hour, however, showed that no eggshells had been removed by the hen.

On the same day eggshells were put into a lesser scaup nest which was also well into incubation. This hen returned to her nest but left quickly and never returned.

In 1950 I erected blinds beside two pintail nests and added eggshells to the nests in the same manner as described above. One of these hens returned to the nest each time within fifteen minutes and, after considerable hesitation and delay, seized an eggshell, paused beside the nest (Figure 54), and flew away with it in the same manner as the shoveller had done. Her flight line took her out of my view so I was unable to tell exactly where she went. On each occasion, however, she headed for the roadside ditch. Each time that shells were added to the nest this hen carried away one or two and then sat on the remaining shells along with her eggs.

The other pintail hen was extremely wary and returned

to the nest cautiously after one hour away from the nest. She carried out one eggshell and then failed to return. Assuming that she had permanently deserted her nest, I left the blind. Although I discovered her on her nest again the following day, I carried on no further experiments with this bird.

In 1950 I erected a blind beside a wild baldpate nest in the Delta hatchery pen. When I gave this hen eggshells, she deserted her nest. One lesser scaup which was given eggshells in 1949 also deserted at the time the shells were added.

The tendency for ducks to carry eggshells to water probably accounts for the shells which are often found in the bottoms of dried up sloughs in summer.

Toleration of Nest-moving.--A common story of the farmers to every interviewer interested in waterfowl is the story of nest-moving. In it a farmer cultivating his land comes upon a nest, moves it unto newly plowed earth, and the hen later returns to the nest in its new location. It is most frequently told of mallards and pintails, the early nesters in Manitoba.

One such incident occurred in the spring of 1947. Mr. Murry Werbiski, a farmer on the Portage Plains, nine miles south of the Delta marsh, reported a pintail nest which he had moved and requested that we take the eggs for the duck hatchery so that they would not be destroyed. This

nest had been moved four times. The first time it was moved about seven feet, the width of the cultivator. The second and third times it was moved about the same distance and the fourth time it was moved about twenty feet. When first found the hen was nesting in an old shallow stub which remained of a straw pile. This time she flushed at about ten feet. As she became accustomed to the tractor she allowed it to approach to within a few feet before flushing. When I visited the nest on the evening of May 24, after it had been moved four times, it had ten eggs which were quite far along into incubation. As we came up to the site on foot she flushed at about twenty feet.

The amount of disturbance that nesting ducks can stand without deserting is variable and seems to be greatest where disturbance is recurring so that the bird becomes conditioned to it and where cover is scant.

Disappearance of eggs.--During the course of this study nests of laying and incubating birds were found. When revisited a few days later a nest of a laying hen normally had a larger number of eggs than when first found. Nests of incubating birds normally had the same number of eggs. This, however, was not always the case and the loss of eggs from an unknown cause was frequent. In twelve instances I found a dwindling number of eggs. Data on these nests of individual incubating hens are given in Table 14 which shows the size of clutch when the nest was first found as compared with the

size of clutch when the nest was revisited a few days later.

The frequency of egg loss during the incubation period (short of complete destruction) is probably far greater than these data seem to indicate. This is because very few of the 593 nests found during the study were allowed to continue to destruction or hatching.

The eggshell carrying behavior of the hen probably accounts for part of the disappearance of eggs.

SUMMARY

1. On warm evenings following arrival, mallard and pintail pairs cruise the nesting meadows in low circling flights. These flights are curtailed by low temperatures.

2. Cruising flights over nesting meadows may precede egg laying by four or more days.

3. The only part of nest construction which preceeds the laying of the first egg is the scraping of the nest bowl.

4. Nesting material is gathered by the hen from her position on the nest. I have found no evidence that surface-feeding ducks ever carry nesting material from distances beyond their reach from the nest.

5. When located in heavy grass the surface-feeding ducks pull surrounding vegetation over their bodies to form a concealing canopy over the nest.

6. Normally, one egg is deposited by the hen each day until the clutch is completed.

TABLE 14 REDUCTION OF CLUTCH SIZE OF 12 NESTS DUE TO UNKNOWN CAUSES

		Number of Eggs in Clutch					
Species	Day Found	2nd Day	3rd Day	4th Day	6th Day	7th Day	12th Day
Pintail	7				4		
Pintail	7					4	
Pintail	7	5					
Pintail	8		7				
Gadwall	10				9		
Shoveller	11	10					
Shoveller	6	5					
Shoveller	12	9					
B-w Teal	10						6
B-w Teal	11		5				
B-w Teal	7			6			
B-w Teal	9					7	

7. Laying mallard, pintail, and gadwall hens usually go to the nesting meadows during the first four hours of daylight. Shoveller and blue-winged teal hens go to the meadows to lay later in the morning.

8. The drake accompanies the laying hen to the nesting meadow, waits for her at some near-by loafing place and often makes low flights over the meadow where she is located on her nest.

9. Mallard, pintail and gadwall drakes abandon their hens shortly after the clutch is completed. Shoveller and blue-winged teal drakes remain paired with their hens later into the incubation period.

10. As in many other species of birds, ducks will sit for long periods past normal incubation time on dead or infertile eggs before abandoning them.

11. Only occasional prenuptial courtship of surface-feeding ducks is seen at Delta because most of the birds are paired when they arrive and are already in their nuptial period. Thus, during the first three weeks of the nesting season, very little courtship activity is seen.

12. Late in the nesting season "teasing flights" of renesting courtship of mallards, pintails, and gadwalls are common. The incitement call of this courtship can be induced in incubating hens by disturbing them and keeping them off their nests.

13. The emitting of the incitement call on disturbance is

apparently the first stage of courtship leading to re-pairing and renesting. It is not common in shovellers and blue-winged teals. The drakes of these species remain with their hens far into the incubation period and for this reason unpaired hens are less common than in mallards, pintails, and gadwalls.

14. It was found that shoveller and pintail hens retrieved eggs from outside the nest by pulling them into the nest with the under side of their bills. They were not always able to differentiate between whole eggs and broken eggs.

15. Broken eggshells were removed from the nest by hens. The shells were carried in the bill and taken to water. One shoveller hen pushed each shell under the water and waited on the water until the shell sank.

16. The tendency to carry shells to water apparently accounts for the eggshells commonly found on the bottom of dried up sloughs and ditches in late summer.

17. Eggs often disappear from nests during the incubation period. These eggs are apparently removed by the hen following breakage by the hen or by a predator.

18. Some ducks will allow their nests to be moved during the incubation period without deserting. It is a common practice among Manitoba farmers to move nests found in fields during farm operations.

CHAPTER VII

RENESTING

One afternoon in early May a mallard hen stood on the rim of a prairie pond. Floating seeds and water insects broke the blue water before her. Her crop full, she preened her feathers, ran her oily bill the length of each long wing shaft, and stretched.

In the adjoining meadow was her nest, filled with twelve large eggs--nearly ready to hatch. Taking off from her feeding place she circled the meadow in wide sweeps and then dropped down a hundred yards from her nest site. She stood, eyed the expanse around her, made another short flight to within ten feet of her nest. This time she alerted as a whistle and streak of moving grass betrayed a gray gopher's dash from the spot.

The hen allowed a full minute to elapse before making a final flight to inspect her riddled nest. She walked the last four feet, along a traveled route, stood on the edge before the broken shells and egg-smeared down. The squirrel had destroyed and scattered the nest and had eaten part of the eggs.

This mallard hen in her first nesting attempt of the year was one of many females which lose their [illegible]s to predators. Such predation upon duck nests has been the subject of study by many workers and in many places. Some who

have contributed much to our present store of knowledge are Kalmbach (1937:19), Kalmbach (1938:610-623), Kalmbach (1939: 591-604, Williams and Marshall (1937:41), Low (1945:45), Bennett (1938:57), and Girard (1941:242).

At Delta I found (Sowls, 1948:130) that during the years 1938, 1939, and 1940, 45 per cent of 206 nests of nine species of ducks were destroyed by skunks, crows, Franklin ground squirrels and flooding.

Bennett (1938:57-58) and Low (1945:50) have distinguished renesting attempts from first nests by smaller clutch size, less down, the general appearance of the nest, and the lateness of the season. In predation studies, Kalmbach (1937:21) classified the nests into "early" and "late season" nests, the latter group apparently representing renests. Cartwright (1944:427) and Errington (1942:170-171) discussed some of the theoretical aspects of the importance of renesting in game birds including waterfowl. Hochbaum (1944:158) pointed out the need for renesting information about ducks and suggested nest-trapping and marking of hens as a means of study.

Barnes (1948:449) described the occurrence of a banded wood duck nesting twice in one season. Angeling (1949:6) says of a mottled duck in Texas, "I observed a pair build five nests in succession and lay a total of thirty-four eggs before finally hatching a brood of nine."

A preliminary report of my Delta studies was published

(Sowls, 1949). Since that time work on the renesting problem has been continued through two more field seasons. Additional data gathered during this later period confirmed all earlier findings and answered some of the questions which were still unanswered in the spring of 1949.

During the year 1950, I concentrated on the behavior of hens after nests were destroyed during the later stages of incubation in order that this aspect of the problem could be more thoroughly treated.

Clutch Size, First Nests Versus Renests.--Lack (1947) pointed out that the tendency for clutches of renests to be smaller than clutches of first nests among ducks has been known for many years in Europe. I have already mentioned Bennett's and Low's work on clutch size.

My data on clutch size of both first nests and renests for twenty-one individual hens are given in Table 15. On analysis the apparent drop in clutch size was found to be statistically significant.

Although the average number of eggs in first clutches is statistically greater then the average number of eggs in renests, the difference is not great enough to distinguish first clutches from renests.

Some known renests of gadwalls, blue-winged teals and pintails had more eggs than the first clutch of another individual of the same species. One pintail had the same size clutch in her first nest and her renest.

TABLE 15 CLUTCH SIZE OF FIRST NESTS AND RE-NESTS OF INDIVIDUAL HENS

Species	Number Eggs First Nest	Number Eggs Second Nest	Number Eggs Third Nest
Mallard	10	9	
Pintail	10	9	
	10	8	8
	10	7	
	9	8	7
	9	7	
	9	6	
	9	4	
	8	8	
	8	7	
	8	7	
	8	6	
	7	6	
	7	5	
Gadwall	11	9	
	10	9	
	8	5	
Shoveller	12	9	
	12	8	8
B-w Teal	12	10	
	10	9	

In Table 16 I have broken the nesting season into three arbitrary parts and included under each part of the nesting season all clutches known to be full sets of eggs. It is readily apparent that a decrease in size occurs in all species as the season advances.

Bennett's "normal" nests of the blue-winged teal averaged only 9.5 eggs. One blue-winged teal at Delta in 1948 had more eggs (ten) in her second nest than Bennett's average for all first nests. The other teal in this study had about the same number of eggs (nine) in her second nest as Bennett's average first clutch in a species where clutches of twelve or more are common. The above instances may indicate that many of what Bennett called "normal" nests were already renests.

The accumulated evidence appears to show that clutch size is not a valid criterion for distinguishing initial attempts from renests. Many renests by present standards would fall into the category of initial attempts. Low (1945:50) recognized this in the redhead and suggests that his classification of renests does not include all of the renests but only those of which he was certain.

There are other complicating factors which may be inherent in all duck-nesting studies. For example, the number of eggs in a nest may not represent the actual number laid by the hen. A reduction of the clutch occurrs when (1) a predator removes an egg, (2) the hen removes an egg broken

TABLE 16 DIFFERENCES IN CLUTCH SIZE DURING THE EARLY, MIDDLE AND LATE PERIODS OF THE NESTING SEASON

Species	Completed By May 15		Completed May 15-June 15		Completed after June 15	
	No.	Ave.	No.	Ave.	No.	Ave.
Mallard	23	10.0	25	8.3	3	9.1
Pintail	45	9.0	46	7.1	14	7.0
Gadwall	--	--	17	10.5	10	9.5
Shoveller	--	--	15	10.8	14	8.5
B-w Teal	--	--	54	10.6	42	8.8

by a predator, (3) the hen is disturbed at laying time and drops an egg away from the nest, and (4) another hen adds an egg to the owner's nest as occasionally happens.

Appearance, First Nests Versus Renests.--Some renests were as well constructed and as well concealed as other first nests. In some cases there was no noticeable change in appearance between first nests and renests. In two or three gadwall nests there was just as much down in the second nest as in the first. In the case of both blue-winged teal nests and mallard nests I could distinguish some reduction of down, but it was not great. In the case of pintails, the species for which I have the most data, there was a noticeable decrease in the amount of down in some renests when compared with the first nest of the same individual. However, without having seen and recorded the first nest, it would have been impossible to say whether or not the nests were first attempts or renests (Figure 35).

One of the difficulties in distinguishing renests by appearance is that in order to do so one would have to compare all nests at the same stage of incubation because down and other materials accumulate gradually.

Renesting Interval.--The time between the destruction of the first nest and the laying of the first egg in the second nest might well be called the renesting interval. That this time varies with the stage of incubation had been described for other groups of birds than waterfowl. Stieve (1918)

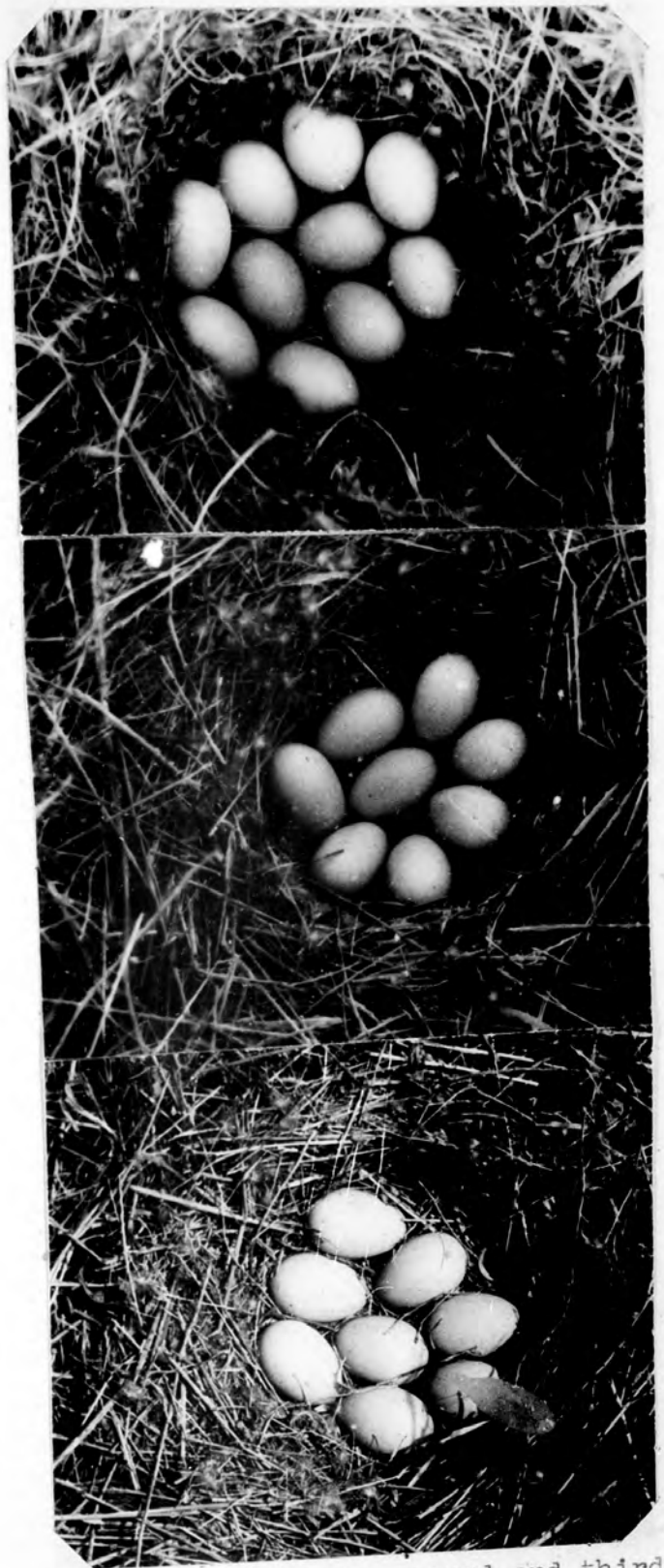


Figure 55 First, second and third nests of pintail 47-604106 for 1948.

studied the anatomical basis of the relaying capacity of the jackdaw in Poland. Laven (1940:131) discussed Stieve's findings in terms of its meaning to renesting. Laven says that when the first clutch is destroyed shortly after the first laying period, relaying occurs more promptly than when the first clutch is well advanced in incubation. The remaining follicles, after cessation of laying, are soon resorbed. For a time, however, the larger follicles are capable of being rebuilt. Later in incubation they are so regressed that they can no longer be used for replacement purposes, and thereafter the smaller follicles must go through a construction process. Accordingly, relaying takes longer.

For the ringed plover, a two-brooded species, Laven (1940:132) in Germany found an increase in length of renesting interval after nests were destroyed but also found a shortening of the interval again in the very late stages of incubation. When the stage of incubation of the first clutch was 6-12 days, the renesting interval was 5-6 days. When incubation was advanced to 14-21 days, the interval was 11-20 days. When a clutch was 26 days incubated, however, the interval was only 6-7 days. Laven points out that this indicates a renewed regular growth of the follicles toward the end of the incubation period in this species which normally raises two broods a year.

Not all groups of birds show a lengthening of the renesting interval as the incubation-stage-at-destruction

advances. Nice (1937:111) found that the renesting interval in song sparrows is usually five days. This is compatible with the short incubation period of this species (12-15 days) and with the fact that it normally lays three or more clutches a year.

Data gathered at Delta on the renesting interval between twenty-four first and second duck nests are plotted graphically in Figure 36.

All hens waited at least three days before renesting. For each additional day of incubation at the time of destruction of first nest, these hens waited an average of 0.62 day before beginning to lay their second clutches.

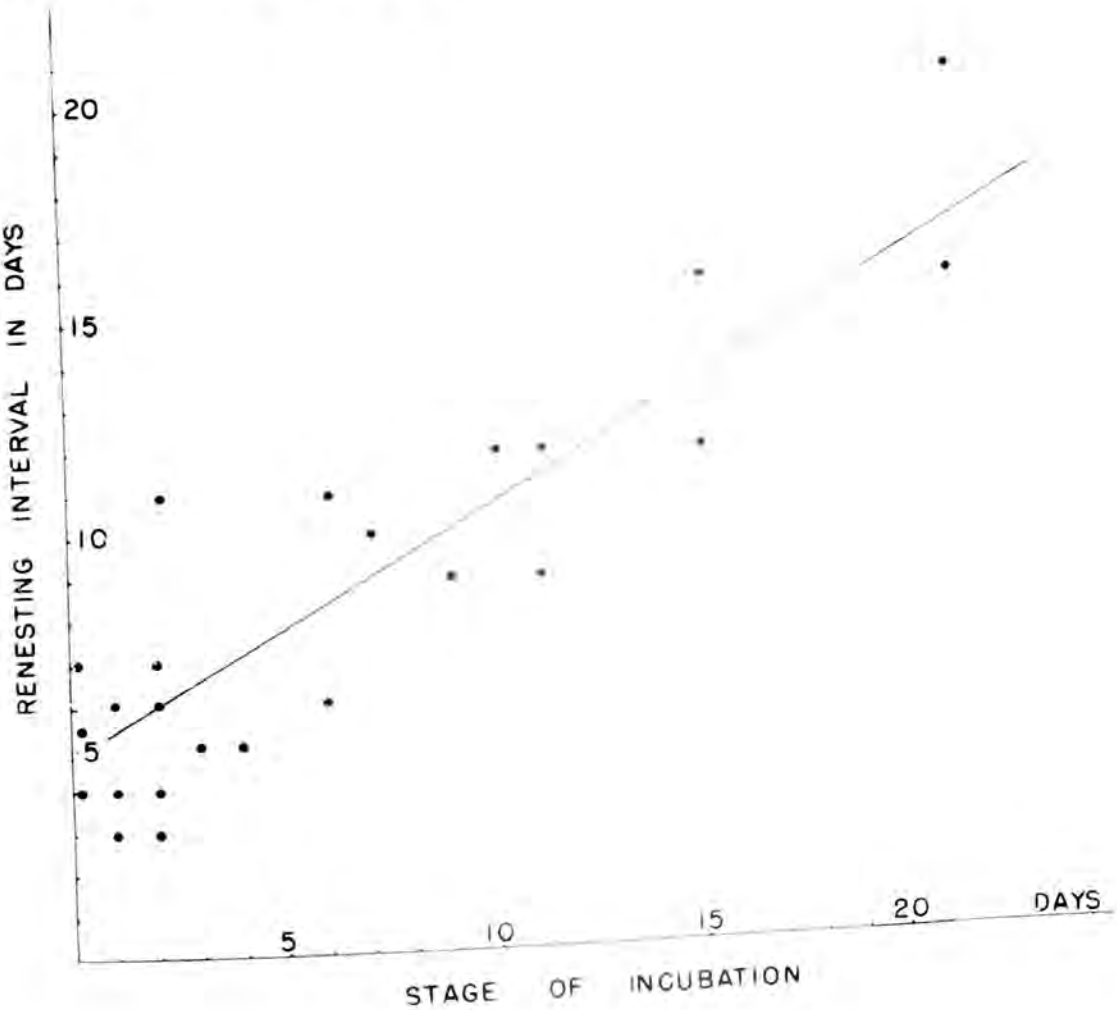
Continuous Laying.--All data so far presented have dealt with the renesting which follows the destruction of a complete clutch after incubation has begun. When nests are destroyed during the laying period another situation exists.

Information on this phase of renesting behavior has been more difficult to obtain because hens are hard to capture and mark during the laying time. When laying, a hen's attachment to her nest is weaker than it is during incubation, and disturbance often causes desertion. The robbing of a nest each day to determine how many eggs a hen will lay continuously has not been successful in the field due to heavy predation which in all cases terminated experiments.

In 1949 three records of continuous laying in the wild were obtained. A blue-winged teal hen was captured and

FIGURE 36 REGRESSION OF LENGTH OF RENESTING INTERVAL ON STAGE OF INCUBATION AT DESTRUCTION OF FIRST NEST

$S_\epsilon = 2.32 \quad \hat{Y} = 4.44 + 0.644X$



marked on May 24 after she had laid five eggs. One egg was warm when I found the nest. The eggs were taken from her at this time. On June 2 the same hen was found on a new nest fifty yards from the first nest site. At that time she had nine eggs, but continued laying until she had a clutch of thirteen. The number of eggs found on June 2 indicated that the hen had continued laying in her new nest the day following the destruction of her first nest. Thus, a total of eighteen eggs were laid continuously.

The same year continuous laying was noted twice in the shoveller. On May 20 a banded hen was flushed from her nest where she had laid one egg. She abandoned her nest and moved eighty yards and began a new nest, this time laying twelve eggs. The first egg in this later nest was laid the day following abandonment of the first nest.

It is an interesting side-light here that this individual hen, who was well known to me, nested for four consecutive years on the study area and that all four of her first nests, each of which had a complete clutch, held twelve eggs.

The other record of a shoveller laying continuously in 1949 was of a banded hen found on June 27 with four fresh eggs. She then abandoned her nest and continued to lay in another nest 150 yards away on June 28. This time she produced a clutch of six eggs. This late-season nest was probably a second renest since the clutch was small.

It seems likely from these observations, that con-

tinuous laying is the usual thing when nests are broken up during the laying period, and that there is no renesting interval.

Further observations concerning continuous laying were made by autopsy. In Figure 26 the reproductive system of a laying hen has been shown. A shell was about to be deposited on an egg in the oviduct. Other eggs in various stages were in the process of development. Several ovulated follicles were visible and the largest one (indicated by an arrow) was probably the source of the egg about to be laid. This mallard hen had laid four eggs when she was killed. Contrast this condition with the reproductive system of a gadwall hen which was collected after having laid ten eggs (Figure 37). Although there is one egg still to be laid, there are no new eggs coming on at the rate that was indicated in Figure 26. Apparently this hen had just come to the nest to lay her eleventh and final egg, as no eggs in the nest were warm when this hen was collected at 7 A.M. Clutch size in gadwall nests found in these studies never exceeded eleven eggs. This bird was collected on June 19, 1950.

Figure 38 shows the regression of the follicle cluster in a pintail hen that had been incubating her clutch for four days. The follicles were considerably reduced as regression of the follicle cluster was in progress.

From this anatomical evidence it seems likely that

Figure 37 Reproductive system of a gadwall hen which had laid ten eggs. The eleventh and last egg was about to be laid.

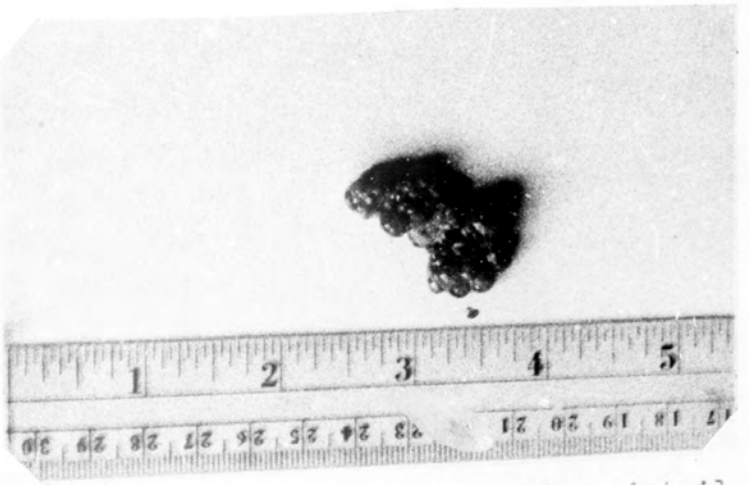


Figure 38 Follicle cluster of a pintail hen which had been incubating for four days.

continuous laying could not occur if the nest is destroyed at the time that the last egg is about to be laid and definitely not during the incubation period. Just when in the laying period clutch size is determined is unknown. But it is evident that regression of follicles and their increase again to egg-laying size is a rapid one.

The lengthening period of the renesting interval as the ovaries regress during the incubation period is consistent with anatomical data existing on domestic fowl. Aside from the fact that the smaller ova have more growing to do than the larger ones, the rate of growth of the larger ova has been found to be faster. Of this Riddle (1916:388) says, "...the rate of growth is not uniform, or continuous, and may be divided into a number of periods. In a previous study I found some evidence that the growth period in the fowl is not a steady, unbroken one--not even among the larger continuously growing ova of a functioning ovary; but at a certain point the rate quite suddenly changes to a rate apparently eight to twenty times faster than before; and further, that the change in rate normally occurs five to eight days before ovulation, and when the ova have reached a diameter of about 6 mm."

Renesting After Loss of Brood.--In 1949 and in 1950 I made an effort to determine what happened to a hen after her brood was taken from her.

In order to answer this question I nest trapped and

marked ten hens and left them to incubate their eggs. Then, just as the young had hatched and were dry enough to leave the nest, they were taken from the hen. The proceedure was carried out with six pintails, three blue-winged teals and one mallard. Of this group two of the pintail hens were known to renest following loss of brood. One waited for a period of eighteen days and then laid a clutch of three. Her first clutch had been seven. The second one waited for sixteen days and produced a clutch of eight. Her first clutch had been ten.

From these observations we see that some hens will renest even after their eggs have hatched and the brood is destroyed. How long after hatching a hen will do so is unknown. Variation between early-season brood-loss and late-season brood-loss may be considerable. This is also unknown.

Location of Renests.--The locations of first nests and renests of thirty-three hens are plotted in Figure 39. Of these hens, all but one had located their second nests within a relatively short distance from their first nests. The maximum, minimum and average distances between first nests and renests of thirty-three hens of five species are given in Table 17. Only one hen moved over seven hundred yards. This bird was a pintail which located her second nest fifteen hundred yards from her first nest. In this case rising marsh waters flooded the area around the site of the first nest so that the hen was forced to move.

FIGURE 39. LOCATIONS OF FIRST NESTS AND RENESTS OF 31 HENS OF 5 SPECIES, 1947 — 1950.

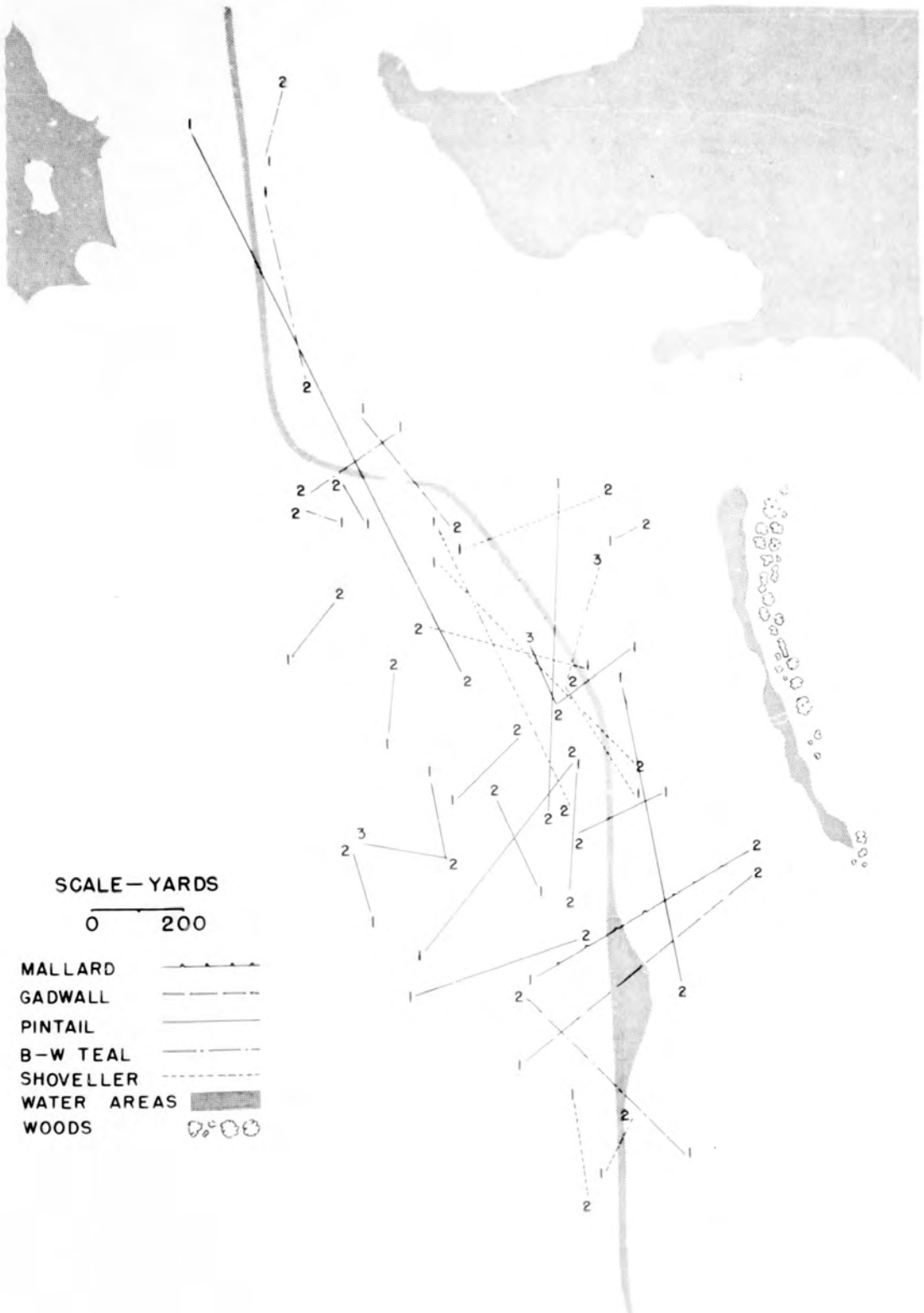


TABLE 17 DISTANCES IN YARDS BETWEEN DIFFERENT NESTS OF THE SAME HEN DURING THE SAME YEAR

Species	Number of Hens	Maximum Distance	Minimum Distance	Average Distance
Mallard	1	700	700	700
Gadwall	3	600	45	320
Pintail	15	1500	85	282
Shoveller	7	765	135	355
B-w Teal	5	405	135	270

It is of interest to note that the pattern of nest sites in Figure 39 (first nests and renests in a single year) is similar to the pattern of nest sites in Figure 7 (nests of returning hens, two or more years).

Number of Unsuccessful Hens which Renest.--How many unsuccessful hens renest is unknown. The fact that only 42 of our 220 marked hens were known to do so does not mean that the others did not. I have no doubt that there were renests on the study area which I did not discover. This is clearly indicated by the fact that 6 of my 42 renest records came about through seeing a brood with a marked hen rather than by finding the second nests. Other hens probably nested outside the study area; still others may not have renested at all.

Low (1945:48) in his study of the redhead divided the nesting season into ten-day periods and showed the number of hens in each of these periods which terminated their breeding efforts due to nest failures.

Laven (1940:141) in his study of the ringed plover in Germany says that one pair produced four additional layings after the loss of its first clutch, while other pairs in the area produced one clutch and departed when that was lost. He also points out that great variation between individuals and birds of different ages must be expected.

That some pairs of ducks wander following nest destruction may account for the large gatherings of pairs which one often

sees on the breeding grounds late in the nesting period. As has been mentioned, this may follow changes in environment of first nesting. Arthur S. Hawkins and I saw such a gathering of pairs and lone hens of gadwalls, pintails, mallards and blue-winged teals at Whitewater Lake, Manitoba, on June 26, 1946. For three springs I have seen such gatherings of pintails south of the study area at Delta. Similar flocks have been observed by Stoudt and Davis (1948:134) who say, "Apparently the South Dakota area had a large number of either transient or non-breeding birds on the transects during the first week in June and these consisted mainly of pintails, mallards and shovellers....It may be that this state has more than her share of non-breeding birds which may consist of either infertile or sexually immature ducks or bachelor drakes....The fact that 135 pairs of pintails were seen on Transects F and B in June and only four broods were found in July illustrates the need for future studies along these lines."

Renesting and Inventory Counts.--The presence of birds of undetermined status as described above may confuse the counting of breeding pairs for inventory purposes. Smith and Hawkins (1948:62) ask the question, "How many times during the season does the population of an area renew itself; i.e., what is its turnover rate? If a given drake defends his territory against all other drakes of his kind for only two weeks and the nesting period for the species spans six weeks, there is the theoretical possibility that the area appraised

at ten pairs per section had a total season's population of thirty pairs (three turnovers)."

To what extent this wide span of nesting is accounted for by late first nesters and to what extent by renesters who failed earlier is not known. Considering the ducks' persistence to renest, however, it seems likely that a large number of the late nesters are merely the same birds which failed earlier. Hence, rather than having a "turnover" of hens, we have an extension of the nesting season brought about through renesting.

Persistence in Renesting, Variation between Species.--Not all species exhibit the same persistency to renest following the destruction of their first nests. The measurement of this comparative persistency is not easily made, however, owing to several factors. The number of hens marked in the renesting study was not the same for all species. The time of season in which they were marked too was not always the same. Many hens were probably marked for the first time when they were already on their second nests. Mallards were difficult to handle, deserted readily and did not offer good opportunity for comparison.

In my studies I repeatedly found that of all species, the pintail was the most persistent renester and the blue-winged teal the least persistent renester. Of sixty-two pintail hens marked I obtained definite renesting records on nineteen or 30 per cent. Two of these were known to renest a second time

following destruction of their second nest. It was the pintail which gave me positive information that renesting does not only follow nest destruction but will sometimes follow destruction of a hatched brood.

In the five years of my study I nest-trapped and marked eighty-eight blue-winged teal hens. Of this number only five or about 6 per cent were known to renest. This sample of marked hens was even larger than the number of marked hen pintails, but the renesting number was only about one sixth as great.

Only one renesting mallard was recorded of twenty hens marked. Of thirty-three shovellers marked, only seven renested. One of these, however, was persistent enough to renest twice in one year. This shoveller and two pintail hens were the only three individuals in my study known to do this. The gadwall was a persistent renester and 25 per cent of sixteen gadwalls marked were known to renest. For these three species just mentioned, a relatively small amount of data was obtained. Although only one mallard was known to renest, I am certain from dates of nesting, that they readily do so.

Importance of Renesting to Production.--Williams and Marshall (1937:41) working at Bear River, Utah, found that 70 per cent of the duck eggs found hatched successfully. Sowls (1948:130), however, working at Delta, found that only 35 per cent of nests found hatched successfully. Thus we see that there is a variation in early-season nest losses

between regions and between years.

In 1940 heavy early-season nest losses at Delta resulted from spring floods. In 1946 spring fires wiped out all early nests over large parts of the Delta marsh and only renesting could have maintained population numbers that year. In 1950 spring plowing on the Portage plains took an abnormally heavy toll of pintail nests during the peak of the nesting season.

Evidence that early losses are compensated for by renesting is evident from an analysis of nesting data. To interpret such data we might set an arbitrary date after which all nests started would be considered renests. For the Delta marsh area I would set this date for mallards and pintails at May 20. (This date would vary with early and late years but would be safe for the latest season I have seen at Delta). From Figure 25 it is evident that 53 per cent of all mallard nests and 25 per cent of all pintail nests in 1949 were started after this date and would therefore be considered renests. In 1950, 46 per cent of the mallard and 47 per cent of the pintail nests were begun after May 20 and would be, therefore, renests. I believe that this is a conservative interpretation. As has been pointed out earlier, these figures do not include renests of marked hens which renested after my disturbance of the first nest. Furthermore, nests destroyed very early in incubation and nests destroyed during the laying period could have led to renestings which would have been begun before this date.

For the later nesting blue-winged teal I would set the arbitrary date after which all nests begun could be considered renests at June 24. Figure 23 then shows us that 12 per cent of the blue-winged teal nests found in 1949 were renests and in 1950, 30 per cent were renests.

I believe that the data on the gadwall and shoveller given in Figure 24 are insufficient for such an analysis.

During the spring of 1950 I determined from embryo dating of eggs found in early season nests that a large hatch of mallards and pintails would occur during the period between June 6 and June 12. This prediction was fulfilled when the majority of early-collected eggs hatched in the Delta incubator during this period. Contrary to the prediction that large numbers of pintail and mallard broods would appear in the wild, no broods were seen until July 5. At least a half dozen observers had been in the field during this time. I believe that only on the basis of early and heavy nest loss can this lack of early broods be explained.

Analysis of brood data on the dates of hatching within arbitrarily set periods would give us an estimate of the percentage of young which resulted from renesting. In my study I was unable to gather enough brood data to do this.

Although we cannot determine, from the data now available, the percentage of thwarted hens which renest and the percentage of production which results from renesting, it is

clear that renesting at Delta is of major importance in maintaining the waterfowl population there.

SUMMARY

1. Ducks have but one brood a year but readily renest if their first nest is destroyed. While the extent of nest destruction has been thoroughly studied in the United States and Canada, the details of the renesting phenomenon have, previous to this study, received slight attention.

2. In 1946 a study to answer basic questions in regard to renesting in ducks was started at the Delta Waterfowl Research Station at Delta, Manitoba. Hens were captured on their nests, banded, feather-marked, their nests robbed, and hens released. After this operation the area was watched for renesting birds.

3. Of 220 birds so trapped, 42 were known to renest again. Of the 42 renesters, three hens were known to have three nests during one season. Two of these were pintails and one was a shoveller.

4. Although the average number of eggs in first clutches is statistically greater than the number of eggs in renests, the difference is not great enough to distinguish first clutches from renests. Some renests have as many or more eggs than other first nests.

5. Renests cannot safely be distinguished from first nests by their appearance. Many renests look like first nests.

6. The time between the destruction of the first nest and the laying of the first egg in the second nest (the renesting interval) varies with the stage of incubation at which the nest is destroyed. The farther advanced incubation is, the longer the hen waits before renesting.

7. Continuous laying without a renesting interval occurs if the first nest is destroyed during the early part of the laying period. A renesting interval is probably required before laying again if nest destruction occurs on the day the last egg of the first clutch is due to be laid.

8. Two pintails whose young were taken from them after hatching renested following the robbing of their young. Thus, renesting may follow the destruction of a hatched brood.

9. The percentage of unsuccessful hens which renest has not been determined. In this study some may have renested outside the study area and some may not have renested at all.

10. Hens located their renests in the vicinity of their first nests. All hens located their renests within seven hundred yards of their first nests except one pintail which moved fifteen hundred yards to renest.

11. Of the five species studied the pintail was the most persistent renester and the blue-winged teal the least persistent.

12. Inventory counts made by the transect method are complicated by the renesting phenomenon in that birds counted

as breeders at one time may be counted as breeders again at a later time when they are in reality renesters that have failed earlier.

13. Renesting varies in its importance to production with locality and year depending on the extent of nest loss. In some areas during some years it may account for nearly the entire production in that area.

14. The number of nests found which were renests was estimated by considering all nests begun after an arbitrarily set date as renests. The arbitrary date for mallards and pintails at Delta was May 20. For blue-winged teal it was June 24. Thus, in 1949 it was estimated that at least 33 per cent of all mallard nests, 20 per cent of all pintail nests and 12 per cent of all blue-winged teal nests were renests. In 1950 at least 46 per cent of the mallard nests, 47 per cent of the pintail nests and 30 per cent of the blue-winged teal nests were estimated to be renests.

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APPENDIX

Common and Scientific Names of Plants, Birds and Mammals Mentioned in the Text.

Plants*

Common Name	Scientific Name
Common cattail	Typha latifolia
Pondweed	Potomogeton sp.
Brome grass	Bromus sp.
Whitetop	Scolochloa festucacea
Kentucky bluegrass	Poa pratensis
Quackgrass	Agropyron repens
Yellow cane, phragmites	Phragmites communis
Skunk grass	Hordeum jubatum
Cordgrass	Spartina pectinata
Sedge	Carex sp.
Hard-stem bulrush	Scirpus acutus
Soft-stem bulrush	Scirpus validus
Willow	Salix sp.
Cottonwood	Populus deltoides
Bur oak	Quercus macrocarpa
Pigweed	Chenopodium sp.
Wild mustard	Brassica sp.
Boxelder	Acer Negundo
Red osier dogwood	Cornus stolonifera
Bladderwort	Utricularia
Snowberry	Symphoricarpos occidentalis
Red-berried elder	Sambucus pubens
Goldenrod	Solidago sp.
Aster	Aster sp.
Canada thistle	Cirsium arvense
Sow thistle	Sonchus arvensis

Birds**

North American Species

Common Canada goose	Branta canadensis canadensis
Common mallard	Anas platyrhynchos platyrhynchos

* Plant nomenclature is from: Fernald, Merrit Lyndon. 1950. Gray's manual of botany. Eighth Ed., American Book Co.

**Names of North American species follow the American Ornithologists Union Check-list of North American Birds. Ed. 4, 1931 and supplements.

New Mexican duck	Anas diazi novimexicana
Mottled duck	Anas fulvigula maculosa
Common black duck	Anas rubripes tristis
Gadwall	Anas strepera
Baldpate	Mareca americana
American pintail	Anas acuta tzitzihoa
Green-winged teal	Anas carolinensis
Blue-winged teal	Anas discors
Shoveller	Spatula clypeata
Wood duck	Aix sponsa
Redhead	Aythya americana
Canvasback	Aythya valisineria
Lesser scaup duck	Aythya affinis
Snowy owl	Nyctea scandreca
Barn owl	Tyto alba pratincola
Eastern crow	Corvus brachyrhynchos brachyrhynchos
Western crow	Corvus brachyrhynchos hesperis
Carolina chickadee	Parus carolinensis carolinensis
Eastern robin	Turdus migratorius migratorius
American redstart	Setophaga ruticilla ruticilla
Eastern song sparrow	Melospiza melodia melodia
Eastern snow bunting	Plectrophenax nivalis nivalis

European Species*

Grey lag goose	Anser anser
Ringed plover	Charadrius hiaticula
European jackdaw	Corvus monedula
English robin	Erithacus rebecula

Mammals**

Mink	Mustela vison
Long-tailed weasel	Mustela frenata
Striped skunk	Mephitis mephitis
Woodchuck	Marmota monex
Richardsons ground squirrel	Citellus richardsonii
Franklins ground squirrel	Citellus franklinii
Pocket gopher	Thomomys talpoides
Meadow mouse	Microtus pennsylvanica
White-tailed deer	Odocoileus virginianus

* Names of European species are taken from Witherby, H. F., F.C.R. Jourdain, Norman F. Ticehurst and Bernard W. Tucker, 1939. The handbook of British birds. Witherby, London.
**Species names of mammals follow: Anderson, Rudolph Martin. 1946. Catalogue of Canadian Recent Mammals. Bull. 102, Nat. Mus. Can.