

THE ORIENTATION OF DISPLACED WATERFOWL IN MIGRATION

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FIELD experiments designed to test the ability of birds to navigate over unfamiliar territory may be placed in either of two principal categories: (1) those in which homing pigeons (*Columba livia*) or wild birds are released at varying distances from their home loft or nest site to evaluate their ability to orient toward home, and (2) those in which wild birds are artificially displaced in their migration by space, time, or both.

This paper reports on studies made experimentally with waterfowl, the objective of which was to ascertain the ability of the birds to orient themselves when displaced artificially in some manner. To this end, three different groups of experiments were made, namely: (1) the delay of south-bound juvenal Blue-winged Teal (*Anas discors*) in central Illinois until all individuals of the species had left the state; (2) the transplantation of adult and juvenal Mallards (*Anas platyrhynchos*) from central Illinois to Utah; and (3) the release of hand-reared Wood Ducks (*Aix sponsa*), some of which were transplanted from Illinois to Indiana and Wisconsin.

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O. D. McKeever, formerly of the Indiana Department of Conservation, was instrumental in determining the homing results of Wood Ducks raised in Illinois and released in Indiana. Dr. Robert McCabe, of the University of Wisconsin, determined the homing of Wood Ducks released at Madison, Wisconsin.

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PREVIOUS INVESTIGATIONS

Most of the investigations involving the transplanting of birds by time, place, or both have been conducted in Europe. A review of the more pertinent experiments on this problem is presented as an aid in evaluating the data of the present study.

On the Baltic sea coast at Rossitten in East Prussia, Schuz (1934) released 73 young storks (*Ciconia ciconia*) which had been detained until the middle of September, one to two weeks after the last of the local storks had left. Most of the young storks followed the normal migration route for the species, that is, southeastward toward the Black Sea. However, some flew slightly farther west than normal, as determined from recoveries in Greece and Crete; in addition, the flight of three individuals was quite aberrant, for they migrated southwestward through the Alps into Italy.

Additional experiments were made by Schuz (1949) in which young storks from East Prussia were released in western Germany, at Essen and Frankfurt, after the departure of the local storks. Although storks native to western Germany migrate southwestward, those released at Frankfurt flew southward to the Alps, and those released at Essen flew southeastward through the Alps into northern Italy. The direction taken by the transplanted storks bore a greater similarity to that followed by their parents than to that followed by the storks indigenous to the release area.

Ruppel and Schuz (1949) transplanted young and old Hooded Crows (*Corvus corone cornix*) from Rossitten to Frankfurt, Germany, in April, late enough so that the few individuals which infrequently winter there had already departed northward. Most of the released birds moved northeastward, but a number of individuals flew in other directions. Inasmuch as the Hooded Crow's normal migration route is to the northeast, most of the birds flew in the accustomed direction without the benefit of local birds to guide them.

Perdeck (1953) captured about 5,500 young and adult Starlings (*Sturnus vulgaris*) in fall migration at Texel, Netherlands, and transported them to three release points in Switzerland. Subsequent band recoveries indicated that young Starlings continued to migrate southwestwardly similar to the original direction of flight. However, the old birds were prone to fly northwestwardly to their normal winter quarters.

In North America, Rowan (1946) conducted a study of delayed migration in young Common Crows (*Corvus brachyrhynchos*). In early November of 1940, he released 54 young birds at Tolfield, Alberta, after all indigenous crows had departed. Of the 31 individuals reported, all but two were in the general direction of their wintering quarters.

McIlhenny (1934:331) shipped 276 ducks of unspecified species from Avery Island, Louisiana, to various points on the Pacific Coast where they were released. Of the 49 band recoveries eventually received, 40 were from the Mississippi Flyway, and 9 from the Pacific Flyway. He also sent 164 banded ducks to the Atlantic Coast, from which a total of 41 recoveries was received. Two recoveries were from the Atlantic Flyway, the other 39 from the Mississippi Flyway. Unfortunately, McIlhenny made no distinction between band recoveries of the same season and subsequent ones.

Williams and Kalmbach (1943:169) reported that 213 ducklings were shipped from Delta, Manitoba; Lower Souris National Wildlife Refuge, North Dakota; and Malheur National Wildlife Refuge, Oregon, to areas outside of their native flyways. Of the eight band recoveries received, only one was not from the flyway where released. However, six of the recoveries were for the same year as released, and only two recoveries were from the subsequent year.

METHODS

Detention Experiments.—Blue-winged Teal for the detention experiments were obtained by bait-trapping in Mason County, Illinois, during August and September, 1952 through 1955. These ducks were then in migration from their breeding grounds in the northern plains of the United States and the prairie provinces of Canada to their wintering grounds in northern South America. Adult teal were banded and released at the trap site, but juveniles were placed in pens on the Chautauqua National Wildlife Refuge, near Havana, Illinois. Juveniles were separated from adults on the basis of the characters of the cloaca and tail feathers.

The Blue-winged Teal juveniles were banded and released on lakes from 20 to 70 miles away from the trap sites (Table 1). They were not released until observations indicated that the last of the migrating teal had departed from central Illinois 10 to 40 days previously. Most of the Blue-winged Teal had left Louisiana by the time of the later releases. State-wide waterfowl censuses made in Louisiana by Richard Yancey (personal communication) of the Louisiana Wildlife and Fisheries Commission revealed that in the fall of 1953, Blue-winged Teal numbers dropped from 180,000 on September 15 to only 1,850 on November 1; 500 remained during the winter. In 1954, Yancey found that Blue-winged Teal declined from 76,000 in mid-October to 4,000 on November 1, and he found none by December 1. In 1955, Blue-winged Teal in Louisiana declined from 233,000 in mid-October to 11,000 by the first of November and none was found by the middle of that month.

Control data for comparison with experimental data were obtained from bandings of Blue-winged Teal in Mason County, Illinois, from 1949 through 1952. As is customary in banding operations, these birds were released the same day they were trapped and banded.

Transplantation Experiments.—Mallards for transplantation to Utah were trapped on the Chautauqua National Wildlife Refuge, near Havana, Illinois, in early November, 1953. On the basis of cloacal characters drakes were separated into adults and juveniles. They were placed in pens until a sufficient number was at hand for shipment. On November 13, the Mallards were placed in crates on a stake truck, and the trip west started at 4:00 p.m. The Mallards arrived at their destination, 1,150 miles to the west, in the Great Salt Lake Basin of Utah early in the morning of November 16. Only a few ducks died en route. Adult Mallard drakes, numbering 470, were released at Utah's Ogden Bay Refuge, near Hooper. Juvenal Mallard drakes, numbering 425, were released at the U. S. Fish and Wildlife Service's Bear River Migratory Bird Refuge, 25 miles north of Ogden Bay, near Brigham City.

Control data for this experiment were provided by previous Mallard bandings at the Chautauqua National Wildlife Refuge in Illinois and the Bear River Migratory Bird Refuge in Utah.

Homing Experiments.—In 1944 young Wood Ducks were artificially reared at the Survey's Havana field laboratory for transplanting to other places. The eggs were collected from Wood Duck boxes erected in Mason County, Illinois. A report on the artificial hatching and rearing of the young has been published by Hanson (1951).

Juvenal Wood Ducks were banded and transplanted, when three to six weeks old, from Havana, Illinois, to the Jasper-Pulaski Game Preserve near Medaryville, Indiana, the University of Wisconsin Arboretum near Madison, Wisconsin, and the Tribune Farm near Wheaton, Illinois. Ninety-five ducklings were taken to the Jasper-Pulaski Game Preserve on August 7, 1944, and confined for one week before release. One hundred ducklings were taken to Madison on August 4, 1944, and were released there on August

14, 18, 22 (McCabe, 1947:105). Twenty ducklings were released at the Tribune Farm on July 20, 1944.

Control material for this experiment consisted of 90 hand-reared Wood Ducks, released within a few miles of where they were raised, on Quiver Creek, Mason County, Illinois, September 8 and 16, 1953.

The results obtained from experimental releases of Blue-winged Teal, Mallards, and Wood Ducks were determined from band recoveries. Recoveries received the same season as the bandings are termed *direct*; those received in subsequent seasons are termed *indirect*. Bands recovered from control groups of ducks provided a means of evaluating experimental results.

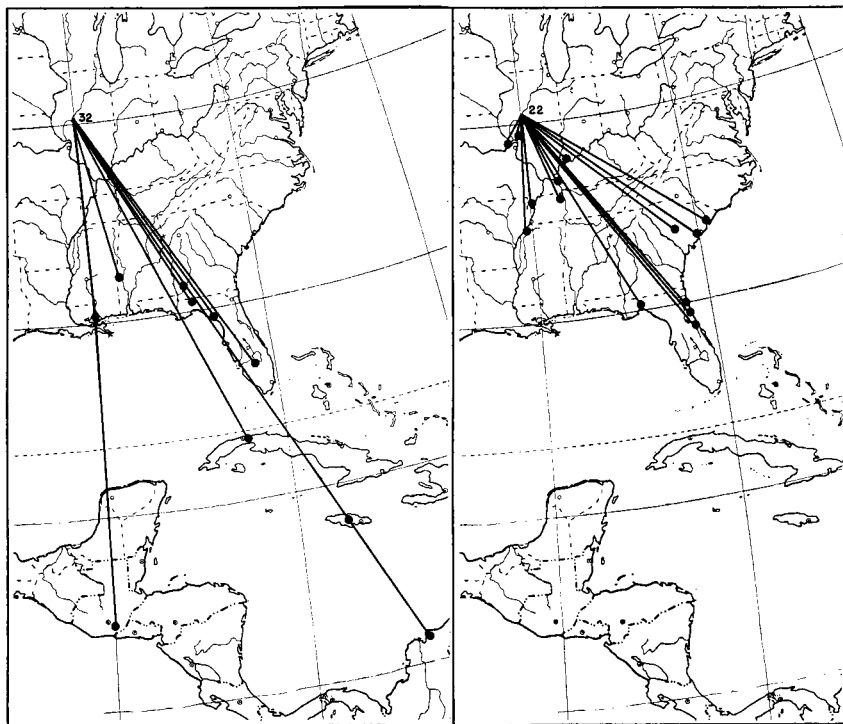


FIG. 1. (*left*) Direct band recoveries of juvenal Blue-winged Teal which were detained in fall passage until November 11, 1952.

FIG. 2. (*right*) Direct band recoveries of juvenal Blue-winged Teal which were detained in fall passage in Illinois until November 30, 1953.

EXPERIMENTS WITH DETAINED TEAL

Direct band recoveries from juvenal Blue-winged Teal detained until November 11, 1952, at Lake Chautauqua National Wildlife Refuge in Mason County, Illinois, show (Fig. 1 and Table 2) a movement to the southeast

TABLE 1
NUMBERS OF JUVENAL BLUE-WINGED TEAL RELEASED IN CENTRAL ILLINOIS AT INTERVALS
AFTER THE DEPARTURE OF THE SPECIES FROM THE STATE, 1952-1955

Date	Release Lake	Number Released	Number of Direct Recoveries	Per Cent Recovered
Nov. 11, 1952	Chautauqua	393	43	10.9
Nov. 30, 1953	Chautauqua	343	38	11.1
Nov. 10, 1954	Springfield	100	11	11.0
Nov. 23, 1954	Decatur	70	6	8.6
Dec. 1, 1954	Springfield	70	6	8.6
Nov. 22, 1955	Springfield	50	4	8.0
Dec. 8, 1955	Springfield	45	3	6.7

and south. Thirty-two recoveries were made within a radius of 25 miles of the release point, and 10 recoveries were from more distant points.

In 1953, Blue-winged Teal juvenile were detained at Lake Chautauqua until November 30, when they were released there. Direct band recoveries (Fig. 2 and Table 2) indicated that there was a greater movement to the east-southeast than in the previous year. Nevertheless, six recoveries were in a southeasterly direction from the point of release, two from a southerly direction, and two from a southwesterly direction.

Juvenal Blue-winged Teal were released at Lake Springfield on November 10 and December 1, 1954, and at Lake Decatur on November 23 of that year. Recoveries later that year show (Fig. 3 and Table 2) a great deal of individual variation in movement of birds from these release points. Although one juvenile moved north 75 miles, and two flew east, and one west, most of the recoveries were to the southeast with smaller numbers from the south and southwest.

Direct recoveries from releases of juvenal teal on November 22 and December 8, 1955, at Lake Springfield show a movement to the east-southeast, southeast, and south (Fig. 4 and Table 2).

A principal reason for the spread of release dates from November 10 to December 8, was to determine if the course of migration followed by the juvenal teal changed with the sun's decreasing declination as fall progressed. Such a possibility was indicated by the greater proportion of recoveries from the east-southeast from the release made on November 30, 1953, as compared to recoveries from the release made on November 11, 1952. However, subsequent data (Table 2) indicate that there was no correlation between the course followed by juvenal teal and the sun's changing declination.

Experimental Versus Control Recoveries.—A comparison of direct recoveries from detained juvenal Blue-winged Teal (Table 2) with control data from teal banded during their normal passage through central Illinois (Fig. 5 and Table 3) is most astounding. It shows that juveniles of the Blue-winged Teal, without guidance from adults, migrated southward along routes normally used by the species, and that the proportion of recoveries along each route from experimental birds was almost identical to recoveries from control birds (Tables 2 and 3).

TABLE 2
DIRECTION OF FLIGHT TAKEN BY JUVENAL BLUE-WINGED TEAL DETAINED IN AUTUMN
MIGRATION IN CENTRAL ILLINOIS, 1952-1955. (BASED UPON DIRECT BAND RECOVERIES)

Date of Release	0 to 90°	90 to 100°	100 to 110°	110 to 120°	120 to 130°	130 to 140°	140 to 150°	150 to 160°	160 to 170°	170 to 180°	180 to 190°	190 to 360°
Nov. 10, 1954							2	1	1	1	1	5
Nov. 11, 1952								7		3		
Nov. 22, 1955								1		3		
Nov. 23, 1954	2	1					2	1				
Nov. 30, 1953					2	2	4	1	1	1	1	2
Dec. 1, 1954				1				1	3			1
Dec. 8, 1955						1	1			1		
Total	2	1	1	2	2	3	9	12	5	9	2	8
Per Cent	3.7	1.9	1.9	3.7	5.6	16.7	22.2	9.3	16.7	3.7	14.8	

The routes by which Blue-winged Teal customarily migrate from central Illinois to their winter home appear to combine in three major "trunk lines." The principal course is southeastward through Florida and Cuba to Colombia and Venezuela (Fig. 5). The next most important course appears to be almost due south to the Delta region of Louisiana, and thence across the Gulf of Mexico to Central America. A third course, apparently used by only a small proportion of teal, lies in a southwesterly direction to the coast of Texas.

Rate of Movement.—Not only did juveniles of the Blue-winged Teal exhibit individual traits as to direction of flight, but also in speed of flight. Some teal departed from the point of release almost immediately while others remained in the release area for as long as a month.

Band recoveries which indicate the fastest rate of movement by juvenal Blue-winged Teal after being detained in migration are shown in Fig. 6. Some of their speeds are indeed remarkable. One juvenile released late in the afternoon of November 10, 1954, was killed 2 days later in Florida. Two juvenal teal released in mid-afternoon of November 22, 1955, were killed together on November 24, on lower Mobile Bay, Alabama.

On the other hand, local band recoveries indicated that some of the detained juveniles stayed near the release point for 19 days in 1952 and 15 days in 1953. Field observations revealed 10 teal near the release site at Lake Chautauqua on November 28, 1952, 17 days after their release, and six were still there on December 1, but none was seen thereafter.

In 1953, Lake Chautauqua froze over on December 15, 16 days after the teal were released. For two weeks following the freeze-up, four banded teal were seen feeding along the margin of an open creek, about two miles from the release point.

The extended stay of some of the juvenal Blue-winged Teal in the area of

release would indicate either a loss in their desire to migrate or confusion as to where to migrate as a result of their prolonged detention.

Effect of Other Ducks.—It may be argued that the juvenal teal followed other species of ducks in migration. This is most unlikely. Banding data reveal that only two other species of waterfowl which frequent Illinois commonly migrate to the southeast, namely, the Pintail (*Anas acuta*) and Ring-necked Duck (*Aythya collaris*). These species were not present at Lake Springfield or Lake Decatur at the time of or immediately following the releases there. Pintails and Ring-necked Ducks were present in the Lake

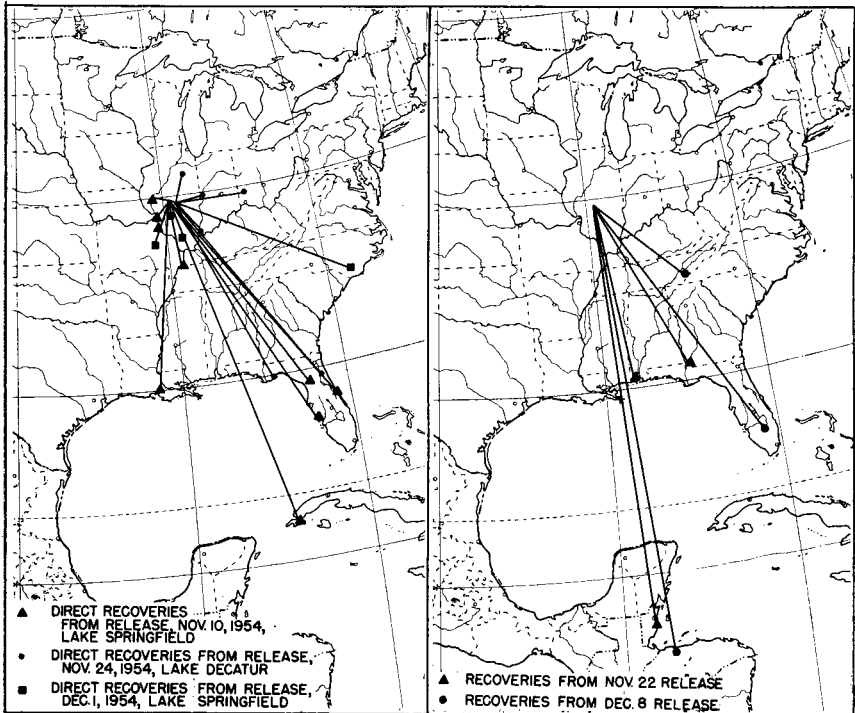


FIG. 3. (left) Direct band recoveries of juvenal Blue-winged Teal which were detained in fall passage until November 10, 24, and December 1, 1954.

FIG. 4. (right) Direct band recoveries of juvenal Blue-winged Teal detained in fall passage in Illinois until November 22 and December 8, 1955.

Chautauqua area only at the time of the November 11, 1952, release. Mallards have made up the bulk of the duck populations whenever and wherever juvenal teal have been released. Thousands of band recoveries from Mallards trapped in central Illinois demonstrate that the bulk of this species migrates almost due south to Reelfoot Lake, Tennessee; Stuttgart, Arkansas; and

northern Louisiana. Fewer than 1 per cent of Illinois-trapped Mallards migrate east-southeast to South Carolina.

Furthermore, the exacting degree to which juvenal teal prorated their flight over the routes used by the species (Tables 2 and 3) makes it inconceivable that the detained teal followed other species of ducks. If they had, most of the band recoveries would have occurred between 170 and 190 degrees, rather than between 140 and 160 degrees.

Effect of Wind Direction.—It may be argued that the detained teal “drifted” in a southeasterly or southerly direction because of air mass movements. However, a study of the daily weather maps of the U.S. Weather

TABLE 3

DIRECTION OF FLIGHT TAKEN BY ADULT AND JUVENAL BLUE-WINGED TEAL BANDED WHILE IN FALL MIGRATION THROUGH MASON COUNTY, ILLINOIS, 1949–1952. (BASED UPON DIRECT BAND RECOVERIES)

Banding Period	0 to 90°	90 to 100°	100 to 110°	110 to 120°	120 to 130°	130 to 140°	140 to 150°	150 to 160°	160 to 170°	170 to 180°	180 to 190°	190 to 360°
September, 1949 through 1952	8	2				2	11	19	8	10		8
Per Cent	11.8	2.9				2.9	16.2	27.9	11.8	14.7		11.8

Bureau reveals a lack of correlation between wind direction and movements of the detained juvenal teal. To restrict the period in which weather might have influenced the direction of flight, only those movements which were charted within five days after release were considered.

In 1952, one juvenal teal was killed 700 miles to the south four days after release. The day after release, the winds between central Illinois and the Gulf of Mexico were light and northeasterly. On the following four days, the winds were light and southerly.

During the five days following the release of Blue-winged Teal on November 30, 1953, winds were light to moderate and were almost entirely from the southeast and south during this period. One juvenile flew southwestward 125 miles, one southward 275 miles, two south-southeastward 215 and 300 miles, and three flew southeastward 300, 960, and 960 miles, respectively.

From the release made on November 10, 1954, two detained teal flew 112 miles south-southwest overnight. Another teal flew 930 miles southeast in two days. Winds on November 11, were from the south at light velocities in the sector affecting the first two teal. In the region southeast of Illinois winds were from the south or east. On November 12, winds in that region were largely from the northeast.

From the release made on November 24, 1956, two teal flew east 140 and 270 miles in two days. One teal flew southeast 152 miles in four days. Winds on November 24 were 11 to 16 miles per hour from the west. On November 25 and 26, winds were still in the northwest and west from light to moderately strong.

Two teal flew south 150 miles overnight from the release made on December 1, 1954. At that time, winds were from the north at 11 to 16 miles per hour.

Two teal flew south-southeast 675 miles during a two-day period following their release

on November 23, 1955. On November 24, winds in this region were light from the northwest; on November 25, these were light from the east.

It would appear from these records that winds were adverse as often as they were favorable to a southward movement of experimental birds. Winds

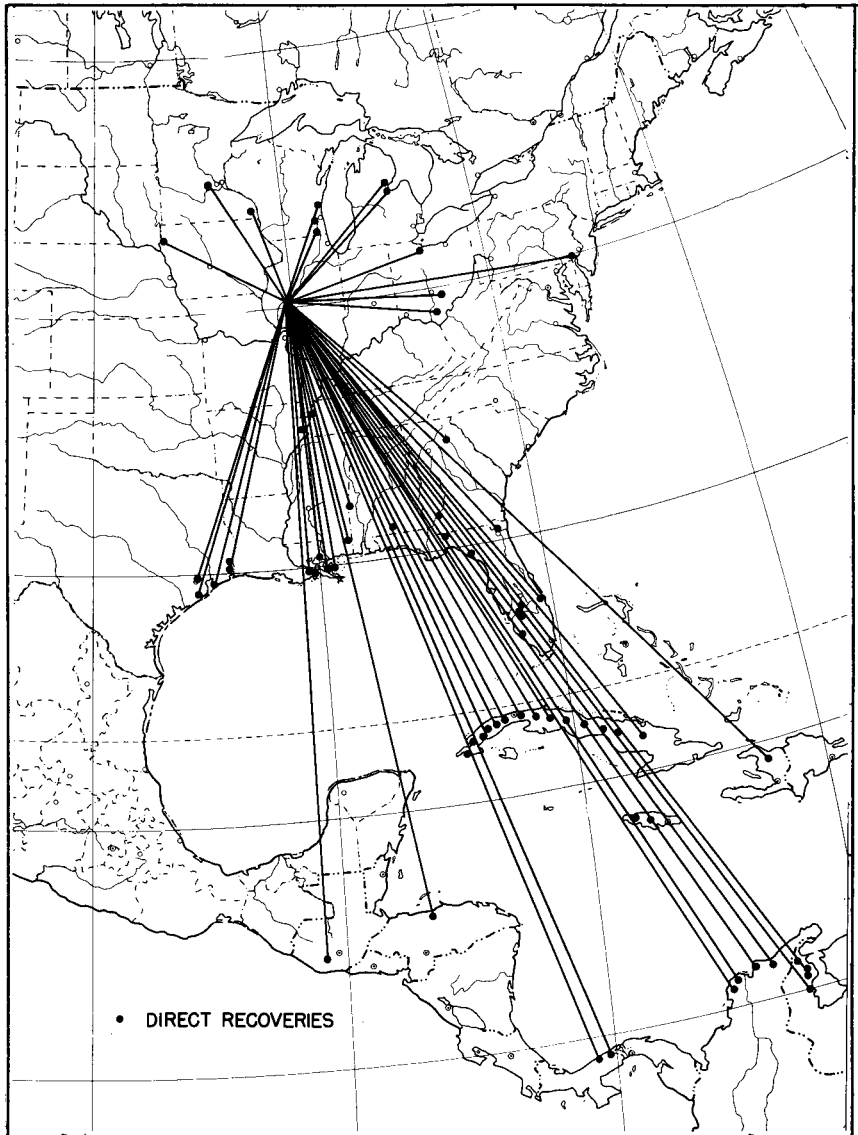


FIG. 5. Direct band recoveries from Blue-winged Teal banded during fall passage in Mason County, Illinois, September, 1949, through September, 1952.

were largely adverse for movements made after releases in 1952, 1953, and November 10, 1954. Winds were favorable for movements made following the releases of teal on November 23 and December 1, 1954. Although the direction was favorable, winds were so light following the release on November 23, 1954, as to be of doubtful influence.

The only decisive movement of detained teal which might be attributed to weather is the aberrant flight of two birds to the east concurrently with moderate west winds.

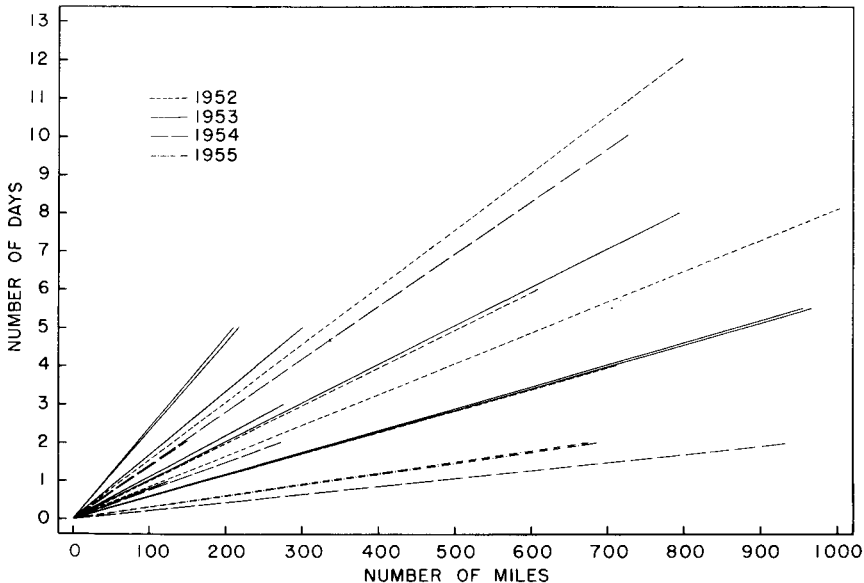


FIG. 6. The rate of migration by detained juveniles of the Blue-winged Teal as shown by band recoveries selected for their speed.

Field Observations.—Observations in the field substantiate banding data that Blue-winged Teal juveniles migrate south without adults to guide them. In trapping Blue-winged Teal during September at Delta, Manitoba, Arthur S. Hawkins of the U.S. Fish and Wildlife Service found the proportion of juveniles to be extremely high in relation to adults. In September of 1950 he trapped 133 juveniles per adult; in the same month of 1952, he caught 61 juveniles per adult. During this period, Hawkins observed Blue-winged Teal depart to the southward between sunset and darkness, usually in flocks numbering from 10 to 40 individuals. According to Hawkins, the low proportion of adults in the population at the time of departure would have made it impossible for every flock to contain even one adult. In the darkness, it would seem highly improbable that flocks remained in contact with each other.

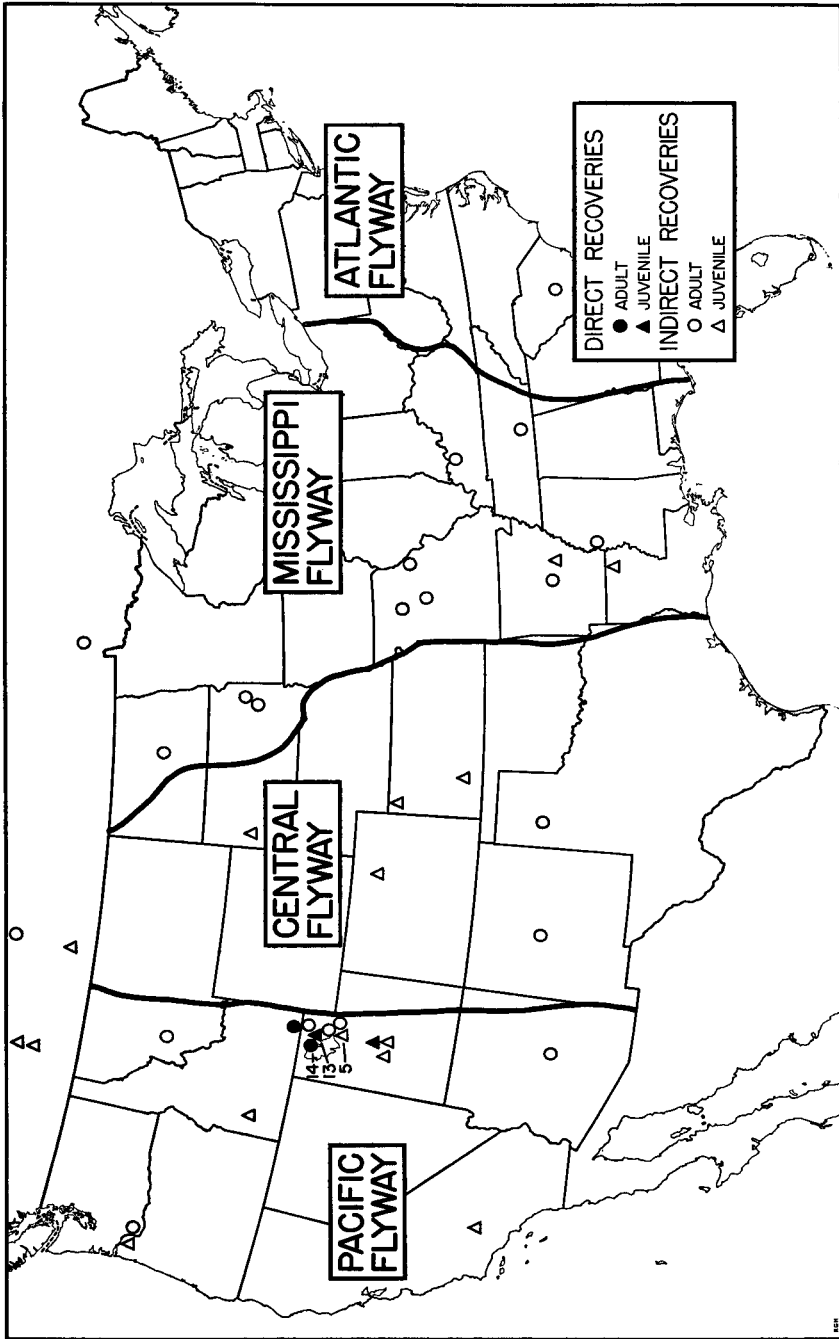


FIG. 7. Band recoveries from adult and juvenile drake Mallards trapped in Illinois and released at the Ogden Bay Refuge and the Bear River Migratory Bird Refuge, Utah, on November 16, 1953. The outline of the flyways represents a combination of both biological and political flyways to avoid the overlapping of the biological and the rigid outlines of the political.

Behavior in Pens.—The activity of captive teal also indicated a migratory incentive and an orientation response at the time the sun set. Throughout the day, during October and November, the teal dispersed through the pens, but as sunset approached they gathered in a compact group at the south end of the pens. Mallards which were held in similar pens at the same time never exhibited this behavior.

EXPERIMENTS WITH TRANSPLANTED MALLARDS

Direct and indirect band recoveries from adult and juvenal Mallard drakes transplanted from Illinois and released at two different points in Utah on November 16, 1953, are shown in Fig. 7. With only two exceptions, all of the 29 direct recoveries, both adults and juveniles, were in the Great Salt Lake Basin. These three recoveries were not far outside the Basin: One adult was killed about 100 miles north; and one juvenile was taken about 150 miles south of the Bear River Migratory Bird Refuge. During the subsequent two hunting seasons, 19 recoveries of birds liberated as juveniles were recorded, and 21 of birds liberated as adults. There was a marked difference between the migration movements of adults and juveniles during the fall months of 1954 and 1955 (Fig. 7). Among adults, one recovery was in the Atlantic Flyway, 12 in the Mississippi, two in the Central, and six in the Pacific. The indirect recovery in South Carolina undoubtedly represented a bird which previously had migrated through Illinois to the Atlantic Flyway. Among recoveries of Mallards transplanted as juveniles, two were in the Mississippi Flyway, five in the Central, and 12 in the Pacific.

Band recoveries from Mallards native to the Bear River Migratory Bird Refuge, Utah (Van Den Akker and Wilson, 1949:365), show that few individuals normally migrate east of the Pacific Flyway. Van Den Akker and Wilson report that, among 145 direct recoveries, only 13 were taken outside the Pacific Flyway: two were in Colorado, one in Illinois, two in Iowa, two in Nebraska, one in New Mexico, one in Oklahoma, and four in Wyoming. Among 75 indirect recoveries, they recorded only five outside the Pacific Flyway, two from Colorado and three from Wyoming, both states adjacent to Utah.

Indirect recoveries from thousands of Mallards banded in central Illinois indicate that fewer than 4 per cent of these birds have been taken west of the Mississippi Flyway in the Central and Pacific Flyways.

It is obvious that Mallards from Illinois did not attempt to return to the Mississippi Flyway during the same season they were released in Utah. They also failed to follow the migration pattern of Mallards banded in Utah. During the first hunting season, Illinois-captured Mallards released in Utah did not migrate southward as did Utah-banded Mallards (Van Den Akker and Wilson 1949:365).

The failure of Mallards from Illinois to move far from the point of release in Utah during the first fall is attributed either to an awareness of their displacement in longitude, or to confusion resulting from the unfamiliar landscape.

If they recognized they were displaced over 1,000 miles to the west, the large displacement may have induced the Illinois Mallards to remain *in situ*. Recent studies by Matthews (1953*a*, 1953*b*, 1955) suggest that birds may have an internal chronometer that would enable them to determine longitude.

However, it is entirely possible that the transplanted Mallards were so confused by the mountains and other unfamiliar landscape features that they remained in the area of release longer than the indigenous Mallards.

The lack of direct band recoveries for the experimental Mallards south of Utah suggests that the birds wintered in the Great Salt Lake Basin or the Snake River Valley, 100 miles to the north, in Idaho, an important wintering area for Mallards in the Pacific Flyway.

From the distribution of indirect band recoveries of the experimental Mallards (Fig. 7) it is assumed that in the spring migration they moved north with Mallards of the Pacific Flyway to breeding grounds in Alberta and Saskatchewan. Although there is some intermingling of Mallards from the Mississippi, Central, and Pacific Flyways on their breeding grounds in Saskatchewan and Alberta, those from the Pacific Flyway generally breed farther west than those from the Mississippi Flyway (Aldrich, *et al.*, 1949:4). Probably few of the experimental Mallards came into contact with Mississippi Flyway Mallards on the western breeding grounds. However, on the breeding grounds, the displaced Mallards were much closer to their former haunts than they would have been anywhere else in the Pacific Flyway.

The return of about two-thirds of the adult and one-third of the juvenal experimental Mallards to the Mississippi Flyway (Fig. 7) suggests that the proximity of the breeding areas resulted in these birds' finding their way back. Because of the greater return of adult than juvenal Mallards to the Mississippi Flyway, it is believed that topographic features were used by the adults as navigation cues in returning to the Mississippi Flyway.

It can be safely assumed that adult Mallards have a greater knowledge of topographic features of the breeding grounds than yearlings. It seems reasonable to assume that displaced adults, while moving from breeding areas to molting areas, and during pre-migration flights would more likely come upon and recognize previous haunts than would the displaced juveniles.

EXPERIMENTS WITH WOOD DUCKS

Recoveries and sight observations of banded hand-reared Wood Ducks are shown in Fig. 8. Direct recoveries show that most of the juveniles were killed in October and November within 25 miles of the point of release.

Because the ducklings were released near Madison, Wisconsin; Medaryville, Indiana; Wheaton and Havana, Illinois, in mid-summer, it is apparent that most of them remained near the release site until late in the fall migration period. Only two birds moved northward after release; these two, released near Havana, moved 70 miles up the Illinois River valley (Fig. 8).

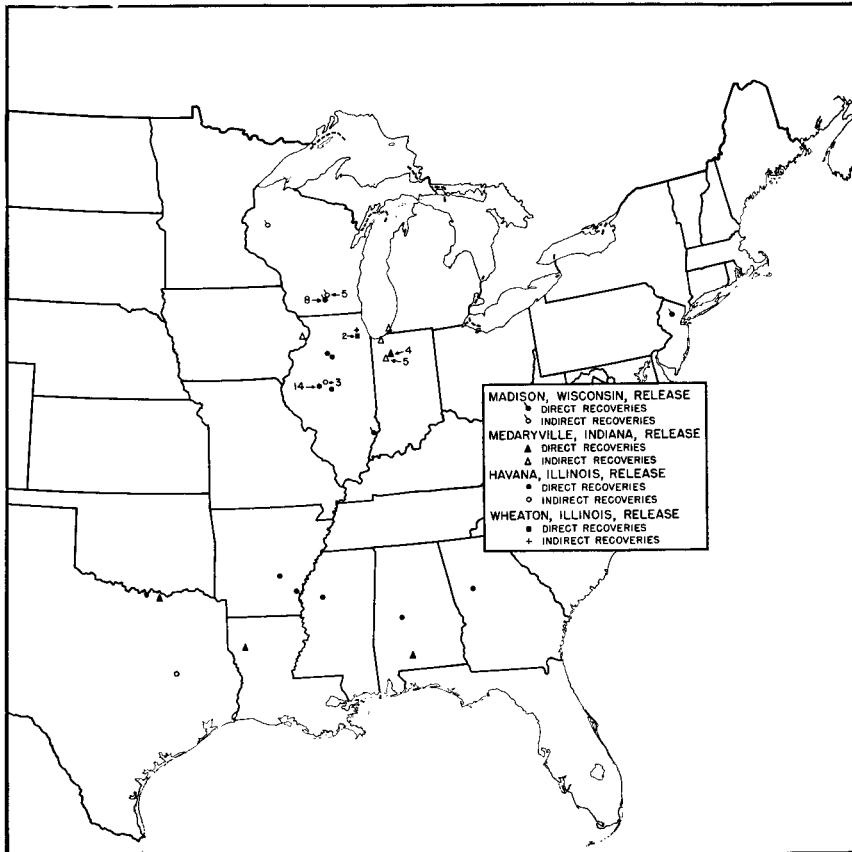


FIG. 8. Recoveries and sight observations of banded hand-reared Wood Ducks released near Madison, Wisconsin; Medaryville, Indiana; and Wheaton, Illinois, in 1944, and Havana, Illinois, in 1953.

McCabe (1947:106) observed that most of the 100 transplanted ducks had left the Madison, Wisconsin, release site by November 3. However, he saw a few Wood Ducks during the winter, and the indications were that at least two hens wintered in the area. O. D. McKeever reported (letter, August 23, 1944) that 46 of the 95 released near Medaryville, Indiana, on July 14, were still at the site on August 15, and a total of 93, including some local Wood

Ducks, was counted on the entire Jasper-Pulaski Game Preserve. Several of the released ducks were live-trapped there up to October 2. As far as known, no Wood Ducks wintered that year in the Jasper-Pulaski area of Indiana.

Observations on 90 young Wood Ducks released on Quiver Creek, near Havana, Illinois, on September 8 and 16, 1953, revealed that numbers remained for over a month. Some remained on the release area through November, and two hens were shot there as late as mid-December. However, none was observed to winter in the area.

Bands recovered at a distance from the several release sites indicate that the majority of birds wintered in an area from Georgia to Texas (Fig. 8). Although this area embraces the general wintering ground for most Mississippi Flyway Wood Ducks, it represents a greater dispersal than that shown by bandings of wild-trapped birds in Illinois. One transplanted Wood Duck showed a pronouncedly aberrant flight; a hen released as a juvenile at Madison, Wisconsin, on July 19, 1944, was killed in Morris County, New Jersey, on November 4, 1944.

In the spring following the several releases of hand-reared Wood Ducks, live-trapping and an inspection of nesting sites revealed that a number of hens returned to their respective areas of release.

At the Jasper-Pulaski Game Preserve, near Medaryville, Indiana, O. D. McKeever (letter, June 9, 1945) captured a hen on April 7, 1945, and another on April 13, from the group which had been released there the previous summer. Four Wood Duck hens from this group were found later that spring in nesting houses, but one of these had been captured previously. McKeever believed that another nesting hen was banded but the bird was never captured. Therefore, five and perhaps six hens from those released the previous summer returned to breed. Drake Wood Ducks from this group were reported shot in the northern United States as follows: one on September 1, 1945, near Buffalo, Michigan, some 70 miles north of the Jasper-Pulaski Game Preserve; one on November 5, 1949, in Porter County, Indiana, 35 miles north of the release area; and one on November 15, 1948, at Clinton, Iowa, some 180 miles to the northwest (Fig. 8).

According to McCabe (1947:106-7) two hens from the ducks released at Madison, Wisconsin, in the summer of 1944 were found on nests the following spring, May 21 and 22, 1945. During that summer, three Wood Duck broods were seen in the area, and the hens with the broods were believed to be birds from the release which were in addition to the two found on the nest. Thus, probably five hens from the release group nested in the Madison area, but possibly two of these hens may have been those observed during the winter. A male from this group was shot on October 17, 1945, near Rice Lake, Wisconsin, about 200 miles to the northwest (Fig. 8). A Wood Duck hen returned the following spring to the Tribune farm near Wheaton, Illinois.

The three foregoing releases, as mentioned under Methods, represented Wood Ducks which were reared at Havana, Illinois, and transported near the flight stage to areas 175 to 200 miles away. The release of young Wood Ducks near Havana, Illinois, in September of 1953, represented birds which were reared there.

In the spring of 1954, at least three hens returned to the Havana area. Two were found in nesting houses on the area where they were released; one was found in a nesting house about four miles distant on the Chautauqua National Wildlife Refuge.

Hand-reared Wood Duck ducklings appear to remain on or near the area of release through late summer and early fall even when raised to flight stage elsewhere. Some of these birds appeared to be tardy about migrating southward as shown by those overwintering at Madison, Wisconsin, and birds which remained abnormally late on Quiver Creek, near Havana, Illinois. Brakhage (1953:476) reported that hand-reared Mallards may migrate somewhat later than wild-trapped Mallards; his data (p. 471) on Pintails and Redheads (*Aythya americana*) indicated no important differences in this respect.

Young Wood Duck hens exhibited a strong homing response to the area they inhabited during late summer and early fall preceding migration. Even though Wood Ducks were raised until 6 to 8 weeks of age at Havana, Illinois, there was no indication of their direct or indirect return to that area when transplanted 175 miles northeast to the Jasper-Pulaski Game Preserve in Indiana or 200 miles north to the University Arboretum at Madison, Wisconsin.

At the Delta Marsh in southern Manitoba, Brakhage (1953:472-473, 476) concluded that the proportion of hand-reared Mallards and Pintails which homed to their natal marsh was similar to that of wild-trapped birds banded on the same marsh.

Less is known about the movement of drakes among the Wood Ducks released as juveniles in Indiana, Wisconsin, and Illinois: Four indirect recoveries north of their respective areas of release, suggest a degree of homing, but one which is not as precise as that shown by hens released as juveniles. Less precise homing may have occurred as a result of the mating of these drakes on the wintering grounds with hens that homed to their own natal areas. Possibly they may have returned unmated, and wandered about seeking a mate.

DISCUSSION

The longer a duck remains in an area, the greater is its homing attachment to the area. Wood Ducks raised for six to eight weeks near Havana, Illinois, had no affinity for that area when transplanted only 175 to 200 miles away. A small proportion of Mallards which were several months old when transplanted from the Mississippi Flyway, to the Pacific Flyway, returned to their

original flyway the following fall. Adult Mallards exhibited a greater propensity to return to their original flyway than did juveniles.

The relationship between the age of a duck and its affinity for a particular geographic area would appear to be related to memory of topographic features. Wood Ducks which spent the first few weeks of their lives in pens at Havana, Illinois, had a very limited knowledge of their surroundings. They certainly had no innate cue which resulted in their return to the *natal* area. In the two or more months these birds spent in new areas prior to the fall migration, they surely became well acquainted with the topography of their foster home. The knowledge of topographic features acquired locally probably enabled the "Woodies" to return with competence to their foster home in the spring. Other environmental cues may play a role in the long-distance migration of Wood Ducks, but near their summer home memory of familiar landmarks must be uppermost. Griffin (1955:180) classifies this as Type I homing which he defines as a "reliance on visual landmarks within familiar territory and the use of exploration or some form of undirected wandering when released in unfamiliar territory."

Young mallards, several months of age, had had an opportunity to become acquainted with many topographic features of the Mississippi Flyway by the time they were trapped in Illinois during their first fall migration. Obviously, however, the topography of the breeding grounds and the Mississippi Flyway would be more firmly imprinted in the memory of the adult Mallard than in that of the juveniles. Both adult and juvenal experimental Mallards were equally exposed to the topographic features of the Pacific Flyway, and, apparently, these features become more firmly imprinted on the juvenile's than upon the adult's memory.

There can be little doubt that some birds remember visual patterns over a period of time, but the degree of visual retention appears debatable. An experiment by Skinner (1950:200-201) suggests that Common Pigeons (*Columba livia*) have an excellent retention of visual patterns. He conditioned 20 pigeons to strike a particular feature on a large translucent key upon which a complex visual pattern was projected. Groups were tested at the end of six months, one year, two years, and four years. Even after four years, the group of four tested showed immediate response. One bird struck the key within two seconds after the appearance of the visual pattern and continued to respond for the next hour. On the other hand, Matthews (1955:56) found that six visits to a particular release point were necessary before pigeons showed good orientation solely from the use of landmarks. This suggests that it may take a considerable time for birds to learn a particular landscape feature, but, once learned, it is retained for a lengthy period. Adults, therefore, would have a greater retention of landmarks than juveniles as a result of their longer association with their haunts.

Although the above discussion points up the apparent importance of topographic features and visual memory as used by waterfowl to orient themselves, it is not intended to imply that they are the only cues used by waterfowl in migration. The ability of juvenal Blue-winged Teal to migrate southward from Illinois without the guidance of adults, and over terrain never before seen by these birds, demonstrates that other environmental cues are available for determining direction of flight.

Hochbaum (1955:209) believed that: "all young waterfowl which do not join in mass migrations are inevitably destined to travel toward the equator in autumn by the dominant flow of the air mass in which they move." As shown previously such an environmental influence was not responsible for the movement of Blue-winged Teal juveniles along routes normally used by the species.

There can be little doubt that Blue-winged Teal have an innate means of determining direction. Griffin (1955:180) calls this Type II homing which he defines as "that by which birds are able to fly in a certain direction even when crossing unfamiliar territory."

The studies by Schuz (1934, 1949), Ruppel and Schuz (1949) and Rowan (1946), discussed earlier in this paper, indicate that other species of birds also possess an ability to fly in one direction over unfamiliar terrain.

The ability of waterfowl to migrate in a given direction over unfamiliar territory may be related to the use of celestial bodies or patterns as navigation cues. Studies by Kramer in Germany (1950, 1952), Matthews in England (1953*a*, 1953*b*, 1955), Griffin and Goldsmith (1955) and von Saint-Paul (1956) in the United States demonstrate that a number of species of birds use the sun as a means of orientation. However, many waterfowl migrate at night when sun orientation would have to be by considerable indirection.

Although the use of the sun for orientation has not as yet been demonstrated for waterfowl, it seems reasonable to assume that juvenal Blue-winged Teal used the setting sun, or some celestial pattern at night, to be able to migrate southward over unfamiliar territory without guidance by adults.

Probably juvenal Wood Ducks released near Madison, Wisconsin, where there was no local population, employed both Type I and Type II homing in returning to that area the following spring. The sun, or a nocturnal celestial pattern, may well have provided the cues for southward and northward migration, and visual memory of local landmarks, the cues necessary for such a display of precise homing.

Not all individual ducks, however, may have the same inherited ability to navigate. The juvenal Wood Duck, which was released at Madison, Wisconsin, and flew 775 miles east-southeast to be killed in Morris County, New Jersey (Fig. 8), was apparently almost 90 degrees off its proper course.

The two juvenal Blue-winged Teal which flew east from Lake Springfield, Illinois (Fig. 3) may have taken the wrong celestial cue.

There was no evidence in these experiments with displaced Blue-winged Teal, Mallards, and Wood Ducks of Type III homing, described by Griffin (1955:180) as allowing "the bird possessing it to choose approximately the correct direction of its home even when carried into unfamiliar territory in a new and unaccustomed direction." The Mallards transplanted from Illinois to Utah would especially qualify for the prerequisite of "unfamiliar territory in a new and unaccustomed direction," but, as previously shown, there was no indication of a direct movement toward the Mississippi Flyway.

SUMMARY

1. Experiments were made with Blue-winged Teal, Mallards, and Wood Ducks to ascertain their ability to orient themselves when displaced artificially in some manner. Juvenal Blue-winged Teal were delayed in autumn migration until the species had left Illinois, and, in some cases, the United States. Mallards were transplanted in November from central Illinois to central Utah, 1,150 miles to the west. Wood Ducks hand-reared to flight stage in Illinois were released in Illinois, Wisconsin, and Indiana.

2. Blue-winged Teal were trapped in Mason County, Illinois, during September, 1952 to 1955, the adults banded and immediately released, while the juveniles were placed in pens. The juveniles were banded and released on November 11, 1952; November 30, 1953; November 10 and 23, and December 1, 1954; and November 22 and December 8, 1955.

3. A comparison of recoveries from Blue-winged Teal banded during their normal fall passage through Illinois with recoveries from the detained juveniles, revealed similar directions of migration for both groups. Some of the detained juveniles migrated to the southern part of the United States within a few days after release, but others remained near the release site for two or more weeks. There is ample evidence that detained birds did not follow other ducks to reach their destination, nor were air movements responsible for their southward flight.

4. Data on flock sizes and age ratios of Blue-winged Teal at Delta, Manitoba, suggest that many flocks depart in southward migration without adults to guide them.

5. Direct recoveries of bands from 470 adult drake Mallards and 425 juvenal drakes, trapped in Illinois and released, respectively, at the Ogden Bay Refuge and the Bear River Bird Refuge in Utah in November, showed no movement toward the Mississippi Flyway. Practically all direct recoveries were in the Great Salt Lake Basin.

6. Indirect recoveries after the breeding season revealed that about two-

thirds of the adult Mallards returned to the Mississippi Flyway, whereas two-thirds of the juveniles remained in the Pacific Flyway.

7. Some Wood Ducks hand-reared at Havana, Illinois, were released locally and others were transplanted to Madison, Wisconsin, Medaryville, Indiana, and Wheaton, Illinois. All groups remained in the release area through late summer and into early autumn. Some of them were tardy in migrating southward, and a few remained over winter.

8. Young Wood Duck hens exhibited a strong homing response to the area they inhabited prior to their fall migration. There was no indication of the return of any transplanted Wood Ducks to their natal home.

9. The longer a duck remains in an area, the greater its homing attachment to the area. This suggests that increased propensity to home with increasing age is related to memory of topographic features. Homing on the basis of visual landmarks within familiar territory and exploration in unfamiliar territory has been classed by Griffin (1955:180) as Type I orientation.

10. Not all waterfowl migrate by means of Type I. Blue-winged Teal have an innate means of determining direction as shown by the southward migration of juveniles over unfamiliar territory. This has been classed by Griffin (1955:180) as Type II orientation.

11. There was no evidence in these experiments of what Griffin (1955:180) calls Type III orientation. This has been described as the ability of a bird to choose the correct direction of its home when transplanted to unfamiliar territory and direction.

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