ORIENTATION BEHAVIOR OF FOUR SPECIES OF WATERFOWL

FRANK C. BELLROSE

INITIAL investigations of the orientation of Mallards (*Anas platyrhynchos*) by the sun and stars were made in the fall of 1956 (Bellrose, 1958a). Since then, data from continuing experiments with this species, as well as initial experiments with Blue-winged Teal (*Anas discors*), Pintails (*Anas acuta*), and Canada Geese (*Branta canadensis*), have added materially to the information available on the orientation behavior of waterfowl.

These experiments have reinforced the original findings that waterfowl use celestial cues to fly a particular direction both by day and by night. A recent report by Matthews (1961) extends the use of the sun for direction-finding to the nonmigratory Mallards of England. Moreover, this study shows that Mallards in England orient northwestward, a direction similar to that taken by Mallards orienting to celestial cues in Illinois.

Evidence is accumulating that birds exhibit two fundamental types of compass orientation. This is shown by experiments in which birds (1) select directions similar to those taken by the species in migration, or (2) select a particular compass direction regardless of the migration direction or the direction of home.

Examples of orientation along migrational directions are: (1) Kramer's (1952) early experiments with caged starlings (*Sturnus vulgaris*) which showed orientation southwestward, the ancestral migration direction in autumn; and (2) Sauer and Sauer's (1955) experiments with caged Garden Warblers and Blackcaps (*Sylvia borin* and *S. atricapilla*) which chose the traditional migration direction of south–southwest to southwest in the autumn.

Examples of orientation to a particular compass direction are: (1) the findings of Griffin and Goldsmith (1955) and Goldsmith and Griffin (1956) that Common Terns (*Sterna hirundo*) orientated to the southeast under clear skies by day notwithstanding the place of release or the direction of their breeding sites; and (2) Bellrose's (1958a) finding that Mallards released under clear skies both by day and by night flew northward regardless of the direction of their home lake.

Another group of experiments suggests that birds can be displaced from home, yet readily determine their homeward course from celestial cues. This has been termed "goal orientation." It implies the ability of birds to recognize their latitudinal and longitudinal location in relation

to "home." Such bico-ordinate orientation would entail navigation in the strictest sense of the word.

A long series of experiments with homing pigeons by Matthews (1953a) indicated that displaced pigeons used the sun as a means of determining the home direction. In another series of experiments conducted with the Manx Shearwater (*Procellaria puffinus*) Matthews (1953b) also presented evidence that these birds, upon displacement to unfamiliar territory, flew toward their breeding grounds. Experiments with caged warblers in a planetarium convinced Sauer (1958, 1961) and Sauer and Sauer (1960) that these nocturnal migrants could determine their home direction upon being presented with a geographic shift in the star pattern.

However, Wallraff (1960) experimented with the sun orientation of pigeons (*Columba livia*), studied the experiments of others, and critically analyzed Sauer's experiments on nocturnal migration, concluding (p. 459): "It has not yet been possible to demonstrate bico-ordinate navigation on a purely astronomical basis in any animal. At present the hypothesis of sun navigation is to be regarded as disproved, at least in pigeon homing, that of star navigation as not proven."

Early orientation experiments with Mallards in Illinois showed that they performed only a one-directional type of orientation unrelated to migration direction (Bellrose, 1958a). This type of orientation was termed "nonsense" orientation by Matthews (1961: 212) because its function was not clear. This paper discusses the relationship of the initial flight direction of waterfowl to subsequent movements.

MATERIAL AND METHODS

The three species of ducks used in these experiments were trapped, for the most part, in the Illinois River valley near Havana, Illinois, in the autumn migration (Figure 1). A few Mallards and Blue-winged Teal were trapped and released in the same area in spring. The Canada Geese were trapped at the Horseshoe Lake Game Refuge near Cairo, Illinois, in mid-winter.

Many ducks were released the same day they were trapped. Others were confined in pens for periods varying from one day to two weeks. Ducks confined for more than two weeks continued to show disorientation as reported earlier (Bellrose, 1958a: 84). Ducks confined for periods longer than two weeks were subject to special experiments seeking to determine the cause of such disorientation; these results were not included here in summary appraisals.

The birds were held, until release, in pens 914 cm (30 feet) long, 183 cm (6 feet) wide, and 61 cm (2 feet) high, which were elevated 76 cm (30 inches) above the ground. The sides and top were poultry wire; the floor, one-half inch mesh hardware cloth. A metal tank 213 cm (7 feet) long, 91.5 cm (3 feet) wide, and 30.5 cm

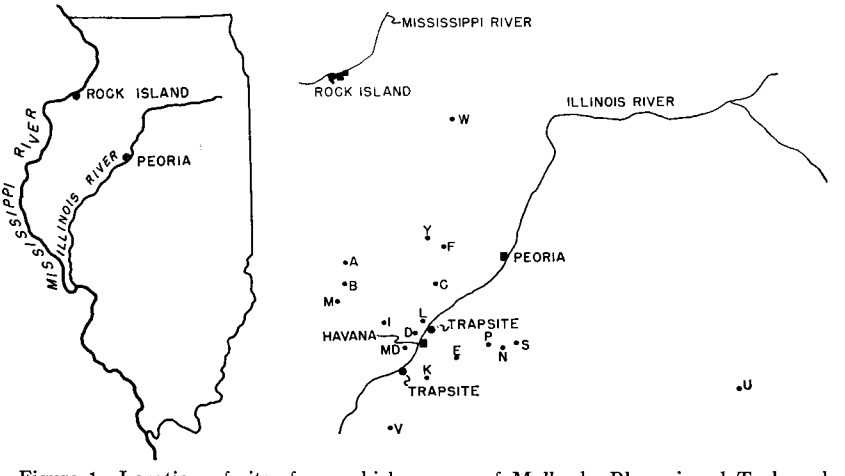

Figure 1. Location of sites from which groups of Mallards, Blue-winged Teal, and Pintails were released individually in relation to the sites where they were captured in migration in Illinois, 1956–1960.

(1 foot) deep, provided with running water, furnished drinking and bathing facilities for the birds in each pen. Food supplied to the ducks consisted of corn, wheat, and commercial duck pellets. The pens were located about 0.8 km (one-half mile) from where the Mallards were trapped and 19 km (12 miles) from where the teal and Pintails were taken.

The waterfowl were placed in crates covered with burlap, and carried in a station wagon to the release site. The birds were held in crates from 30 minutes to four hours, depending on distance traveled and number released. Releases of ducks were made from less than 1.6 km (1 mile) to over 152 km (95 miles) from where they were trapped (Figure 1). Most release points were east and west of the Illinois River valley in areas of flat agricultural land as devoid of trees, watercourses, farm buildings, and landmarks as could be found. Canada Geese were released near Ullin, Illinois, some 19 km (12 miles) northeast of the Horseshoe Lake Game Refuge and also near Wyatt, Missouri, about 29 km (18 miles) south of Horseshoe Lake.

Ducks and geese were tossed individually into the air. We observed each flight, with the aid of binoculars, until the bird was out of sight. The direction of release was usually rotated. Released birds were generally in sight from two to five minutes, but some erratic-flying individuals remained in sight for as long as 15 minutes.

The flight of each duck was plotted by one member of a two- to three-man team on a diagram provided with concentric circles for distance and radii at 22.5 degree intervals for direction. The other observer(s) followed the flight of the duck through binoculars, calling off direction and location. The flight of each Mallard was followed for 1.6 km (1 mile) or more; the flight of each Blue-winged Teal, Pintail, and Canada Goose was followed for 3 km (2 miles) or more.

The north–south and east–west alignment of fences and roads formed a grid-like pattern in the areas of release, thereby facilitating the determination of distance and direction. Distance was also determined from the elapsed time of the bird in flight, which varied from 0.8 km (½ mile) for Mallards and Canada Geese to 1.2 km (¾ mile) per minute for Pintails and Blue-winged Teal.

Releases of individual waterfowl were made at various times of the day and night. A bird's course at night was followed by attaching a pen-light device to its leg (Bellrose, 1958a: 76, 80). Under optimum visual conditions the light was observed for 3 to 5 km (2 to 3 miles), about as far as a duck could be seen during the daytime.

Birds were released under many different weather conditions, varying from combinations of subzero temperatures and snow, to warm and cloudless. An effort was made to release birds under either entirely clear or entirely overcast skies, but, on occasion, this was not feasible. When clouds were present under conditions classed as diurnal and clear, the sun was visible. A few stars were visible on the nights with 9/10 overcast, even though they were classed as overcast.

Headings taken by the waterfowl in each experiment were tabulated by 10° sectors of the compass at intervals ranging from 0.8 to 3 km from the release point. Distances that waterfowl traveled in reaching a hypothetical circle either 1.6 or 3 km (1 or 2 miles) in a straight line from the point of release were determined by a map measurer. The radius employed was 1.6 km (1 mile) for Mallards and 3 km (2 miles) for Pintails, Blue-winged Teal, and Canada Geese.

Dr. H. W. Norton, Professor of Agricultural Statistical Design and Analysis, University of Illinois, designed the mathematical treatment of the data. Mean headings of each release and of groups of releases were computed by finding the average sine and cosine with their variances and covariances. The implied average angle was then found. The significance of the mean heading was determined by standard propagation-of-error methods.

The computations were made on the Illiac, a digital computer, at the University of Illinois, Urbana.

RESULTS

GENERAL BEHAVIOR

Individual birds varied markedly in their behavior upon release. On a few occasions, Mallards and Blue-winged Teal, upon release, flew at heights of from 3 to 6 m (10 to 20 feet). Usually, however, they climbed steadily from 6–10 m to between 150–300 m. The height flown by individual birds or entire releases of birds could not always be correlated with wind, temperature, or sky condition, and the cause of variation in flight behavior was not apparent.

Upon being tossed into the air, numerous ducks showed orientation almost immediately, some veritably somersaulting into a specific direction at the terminus of the throw. Others hovered on beating wings for three to five seconds before pursuing a particular course. However, most individuals displaying orientation flew in the propelled direction for 200 to 300 m before changing their heading. This was especially evident among those orienting ducks which were released in a southerly direction, for they executed a fish-hook flight path bringing them back past the observers.

The directness of the flight of the released bird was usually sufficient to indicate whether the bird was oriented or disoriented. An oriented bird flew a fairly direct course, seldom deviating over 20° after once

TABLE 1

THE LENGTH OF FLIGHT PATH TO A POINT 1.6 KM FROM RELEASE SITE FOR MALLARDS AND 3.2 KM FOR BLUE-WINGED TEAL, PINTAILS, AND CANADA GEESE, 1956–1960*

Species	*Diurnal*			*Nocturnal*		
	Clear	*Overcast*	*Difference*	*Clear*	*Overcast*	*Difference*
Mallard	20.6	45.5	24.9	25.5	43.3	17.8
Blue-winged Teal	25.3	35.3	10.0	21.0	32.2	11.2
Pintail	19.4	47.0	27.6	20.9	55.5	34.6
Canada Goose	25.7	53.3	27.6	23.4	44.2	20.8

* Figures express per cent of flight above airline distance.

establishing a definite heading. On the other hand, a disoriented bird shifted headings repeatedly, usually between 45° and 90° and frequently as much as 180°. Some disoriented ducks passed repeatedly over or near the release point even when observers were in plain sight.

Usually, a duck or goose released under clear skies by day or by night pursued an oriented course while those released under overcast skies by day or by night pursued a disoriented course. However, there were some important exceptions to this general rule, most of which applied to Blue-winged Teal; these will be discussed later.

DISTANCE TRAVELED

The distance traveled by waterfowl in reaching an "airline" distance of 1.6 km (Mallard) or 3 km (Blue-winged Teal, Pintail, Canada Goose) from the release point are compared for clear and overcast skies in Table 1.

Under clear skies in the daytime, Mallards and Pintails flew shorter distances to reach a given point than did Blue-winged Teal and Canada Geese. On the other hand, at night under clear skies, Blue-winged Teal and Pintails flew a more direct course than did Mallards and Canada Geese (Table 1).

Overcast skies by day and night resulted in most waterfowl flying more tortuous paths, almost 25 per cent farther than the flight paths under clear skies. The flight paths of Blue-winged Teal under overcast skies were exceptional in that they were only about 10 per cent longer than those under clear skies (Table 1).

FLIGHT HEADINGS

A perusal of the flight headings of the four species of waterfowl tested showed an appreciable variation in the response of each species to celestial cues, as well as to environmental factors. Therefore, the results of experimental releases of waterfowl to appraise flight direction are given species by species.

TABLE 2

FLIGHT HEADINGS OF FOUR SPECIES OF WATERFOWL GROUPED AS TO TIME OF DAY AND SKY CONDITIONS, 1956–1960

Species	*Light period*	*Sky*	*Number in sample*	*Mean heading*	*Standard deviation*	*Chi-square value*
Mallard (*Anas platyrhynchos*)	Diurnal	Clear	336	355	1.7	533.5
" " "	Diurnal	Overcast	255	70	14.9	13.9
" " "	Nocturnal	Clear	93	351	3.6	134.8
" " "	Nocturnal	Overcast	43	316	26.0	3.9
Blue-winged Teal (*Anas discors*)	Diurnal	Clear	169	280	7.6	46.8
" " " "	Diurnal	Overcast	88	294	38.0	1.3
" " " "	Nocturnal	Clear	169	317	3.6	158.8
" " " "	Nocturnal	Overcast	81	291	9.4	25.9
Pintail (*Anas acuta*)	Diurnal	Clear	35	269	6.6	94.0
" " "	Diurnal	Overcast	12	132	48.5	0.4
" " "	Nocturnal	Clear	31	291	3.7	143.9
" " "	Nocturnal	Overcast	9	314	24.0	6.7
Canada Goose (*Branta canadensis*)	Diurnal	Clear	35	202	6.3	90.4
" " " "	Diurnal	Overcast	18	259	26.4	2.0
" " " "	Nocturnal	Clear	14	213	9.0	21.8
" " " "	Nocturnal	Overcast	16	201	44.5	3.0

Mallards.—Data on the flight headings of 336 Mallards were obtained from 23 separate releases under clear skies in the daytime. The Mallards showed a strong inclination to fly north, as shown by the mean (Figure 2 and Table 2). The very low standard deviation indicates that the headings were very significantly grouped around an approximate mean of 355°.

Under overcast skies by day, the distribution of 255 headings in 19

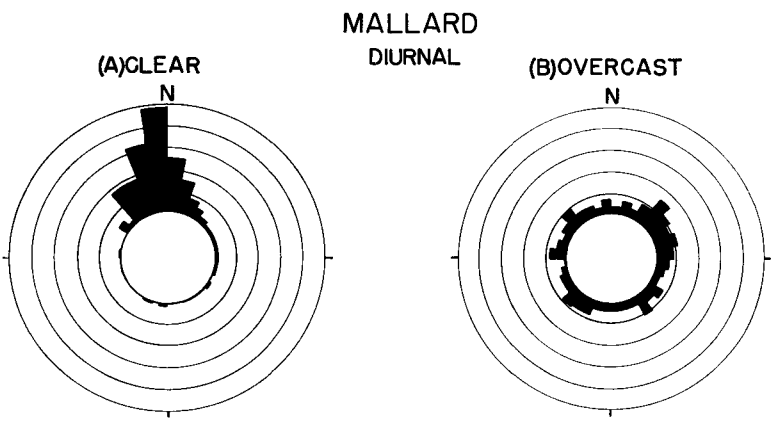

Figure 2. The flight headings of Mallards by day under (A) clear and (B) overcast skies, 1956–1960. Data plotted by 10 degree sectors.

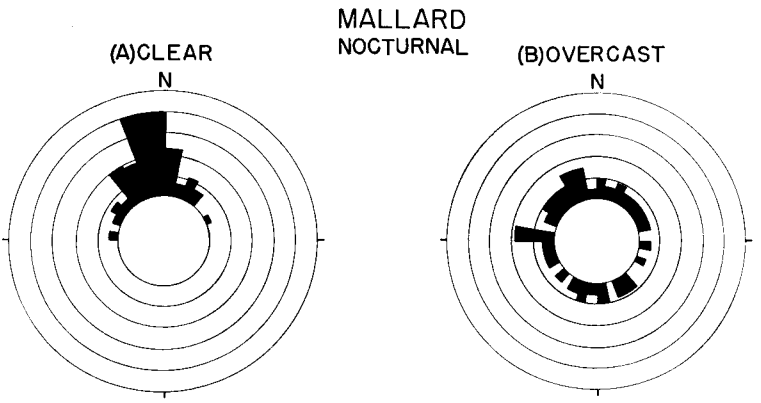

Figure 3. The flight headings of Mallards at night under (A) clear and (B) overcast skies, 1956–1960. Data plotted by 10 degree sectors.

releases indicated a much greater variation in flight directions (Figure 2 and Table 2) than under clear skies. However, the standard deviation implies a slight significance of the mean heading under overcast skies by day.

When releases were made at night, the results (Figure 3) were similar to those obtained from daytime releases. Under clear nocturnal skies, Mallards flew northerly courses, the mean direction of which was only 4° to the west of that for all diurnal releases under clear skies. All individual headings under overcast skies, when grouped by 10° sectors, showed a marked directional variation (Figure 3 and Table 2). The standard deviation of the mean implies no significance to the mean heading found under nocturnal overcast skies. Thus, data obtained from Mallards released since the spring of 1957, when combined with earlier data, revealed almost the same directional orientation for the Mallard as reported in a previous paper (Bellrose, 1958a).

Mean headings. However, when the flight pattern of each release group of Mallards is examined separately (Figures 4 and 5, and Tables 3–6), one finds a certain degree of conformity among the headings taken by individuals in certain groups. The mean headings of each release show details of flight direction not evident when all the releases are combined.

Group headings of Mallards under diurnal clear skies (Figure 4a and Table 3) show only one group with flight directions quite distinct from the 22 other, closely bunched groups.

This aberrant group (released at M, 15 November 1957) flew a heading of 137° with a standard deviation of 16.7° (Table 3), indicating a significant directional grouping by individuals of the release. This unusual

TABLE 3

RESULTS OF EACH RELEASE OF MALLARDS UNDER CLEAR SKIES DURING THE DAY, 1956–1960

Release point (See Fig. 1)	*Date*	*Time (Central Standard)*	*Number plotted*	*Cloud cover*	*Wind direction*	*Wind velocity (MPH)*	*Home bearing in degrees*	*Mean heading in degrees*	*Standard deviation in degrees*	*Distance flown to reach one mile*
E	11-13-56	1600–1800	30	0	S	25–30	315	356	4.4	1.12
P	11-27-56	1600–1750	20	0	S	15	290	337	4.0	1.18
S	12- 4-56	1050–1250	26	0	S	5–10	282	348	3.8	1.15
M	12- 7-56	1450–1600	14	0	NW	10–15	100	354	7.0	1.38
E	1-10-56	1350–1500	21	0	N	10	315	348	2.3	1.11
F	1-10-56	1650–1800	15	5	NW	2	190	343	4.9	1.14
E	1-18-57	1100–1200	8	0	W	10–12	315	346	16.8	1.32
E	2- 1-57	1400–1500	9	0	NNW	10	315	352	7.5	1.29
M	11-15-57	1400–1550	14	5	S	15–20	100	137	16.7	1.45
E	11-19-57	1350–1450	10	1	W	20–25	315	27	20.7	1.42
K	11-22-57	1600–1800	16	2	WSW	10	5	345	10.4	1.50
U	11-22-57	1200–1450	22	6	WSW	20	103	358	3.0	1.14
L	11-25-57	0950–1050	10	0	SSW	10	80	19	13.4	1.31
L	11-25-57	1000–1100	11	0	SSW	10	80	356	8.6	1.35
E	11- 4-59	1050–1200	16	5–8	SSW	20	315	6	6.6	1.39
B	11-10-59	1400–1600	16	4	SSW	20–25	112	9	5.5	1.17
E	11-19-59	1450–1650	15	3–7	SE	2–3	315	7	7.4	1.34
L	12-23-59	1100–1300	16	9–10	SE	10–15	80	346	3.2	1.26
C	12-31-59	1150–1350	20	1–2	—	0	180	356	4.8	1.18
W	10-27-60	1600–1650	3	0	—	0	185	305	11.8	1.50
C	11- 3-60	1550–1600	6	0	SW	5	180	357	25.7	1.70
W	11-17-60	1500–1650	13	9–10	S	25	185	342	13.0	1.27
C	11-23-60	1400–1450	5	0–1	—	0	180	21	8.9	1.30

flight heading could not be related to wind direction or the place of release. A previous release of Mallards at the same site on 7 December 1956, resulted in a mean flight heading of 354°, typical for a release under clear skies.

The only phenomenon that may relate to this southeast flight heading was a duck migration in southern Illinois which was reported under way in mid-morning. No migrating ducks were visible at the release site some 64 km (40 miles) west of the Illinois River in the central part of the state.

The headings of each group of Mallards released under clear nocturnal skies (Figure 4b and Table 4) showed no deviation from a northerly direction. There was no relationship between migration of ducks and a change in heading. On the nights of 26 November 1957, and 19 November 1958, there was a departure of ducks from the Illinois River valley, yet Mallards released on those nights flew the customary northerly heading.

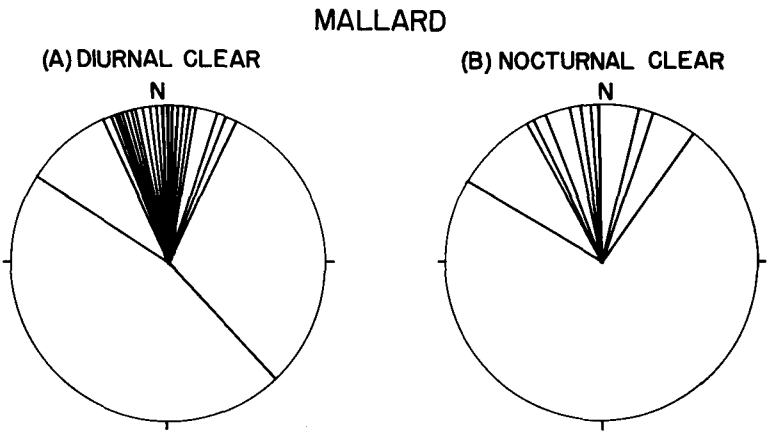

Figure 4. The mean flight headings taken by each group of Mallards released under clear skies (A) diurnally and (B) nocturnally in Illinois, 1956–1960.

Releases of individual Mallards under overcast skies by day resulted in group headings (Figure 5a and Table 5) which suggested a greater degree of directional orientation than when individuals of all groups were considered together (Figure 2b).

Of the 19 releases made under overcast skies by day, 9 had mean headings which were statistically significant at a standard deviation of less than 21° (Table 5). Four headings were in the north to northeast sector, four in the south to east–southeast sector, and one in the west.

TABLE 4

RESULTS OF EACH RELEASE OF MALLARDS UNDER CLEAR SKIES AT NIGHT, 1956–1960

Release point (See Fig. 1)	*Date*	*Time (Central Standard)*	*Number plotted*	*Cloud cover*	*Wind direction*	*Wind velocity (MPH)*	*Home bearing in degrees*	*Mean heading in degrees*	*Standard deviation in degrees*	*Distance flown to reach one mile*
E	11-27-56	1950–2000	4	0	S	10–15	315	358	4.8	1.15
E	12- 3-56	1950–2100	12	0	SE	5	315	334	6.3	1.17
E	1-18-57	1950–2050	8	0	SW	5	315	18	13.4	1.09
K	2-14-57	2000–2100	7	0	E	7	5	331	10.2	1.22
E	3-13-57	2250–2300	5	0	S	5–10	315	347	13.0	1.05
K	4- 9-57	2000–2100	10	5	—	0	5	36	24.6	1.68
E	4- 9-57	2100–2200	10	7	—	0	315	355	11.7	1.47
E	4-10-57	2000–2150	12	6	S	10	315	338	9.6	1.55
P	11-26-57	1950–2100	12	0	SE	10	290	353	2.8	1.07
B	11-19-58	2000–2100	9	0	SSW	5	112	13	10.4	1.24
M	10-10-60	2100–2150	4	0	—	0	100	300	15.4	1.25

TABLE 5

RESULTS OF EACH RELEASE OF MALLARDS UNDER OVERCAST SKIES BY DAY, 1956–1960

Release point (See Fig. 1)	*Date*	*Time (Central Standard)*	*Number plotted*	*Cloud cover*	*Wind direction*	*Wind velocity (MPH)*	*Home bearing in degrees*	*Mean heading in degrees*	*Standard deviation in degrees*	*Distance flown to reach one mile*
P	11-20-56	1600–1800	10	10	N–NW	10	290	102	21.3	1.70
E	11-28-56	0800–0900	10	10	NW	10–15	315	274	19.4	1.81
S	11-28-56	1400–1600	13	10	NW	15–20	282	351	25.7	2.58
P	11-12-57	1500–1700	17	10	SE	15–20	290	71	27.0	1.66
S	11-20-57	1400–1600	15	10	W–SW	17	282	36	13.7	1.68
L	11-21-57	1300–1400	10	10	W–SW	10–15	180	17	20.2	1.73
S	11- 3-59	1300–1500	18	10	—	0	282	0	48.8	2.53
S	11- 6-59	1400–1600	21	10	NW	15	282	44	14.9	1.54
M	11-12-59	1400–1600	28	10	ENE	15	100	234	50.5	1.89
L	12-28-59	0900–1100	16	10	ESE	5	180	358	15.0	1.46
MD	12-29-59	1450–1600	5	10	NNW	15–18	45	144	26.2	1.45
D	2- 8-60	1150–0200	17	10	SW	15	75	264	39.4	2.63
D	2-24-60	1300–1400	11	10	NE	15	75	157	42.7	1.70
E	2-24-60	1500–1600	10	10	NE	15	315	118	13.7	2.24
E	10-19-60	1000–1100	11	10	N	20	315	112	7.5	1.52
E	10-21-60	0950–1100	5	10	SSW	10	315	327	107.0	1.82
E	11- 8-60	1650–1750	5	10	S	15	315	100	27.1	3.36
E	11- 9-60	0850–1000	13	10	N	15–20	315	176	20.2	1.93
E	11-22-60	1100–1300	19	10	NW	8	315	100	17.1	3.28

There were southward migrations of Mallards on the same day in which all four releases showed southeast headings. However, there were also southward movements of Mallards on the same day that two of four releases flew northeastward.

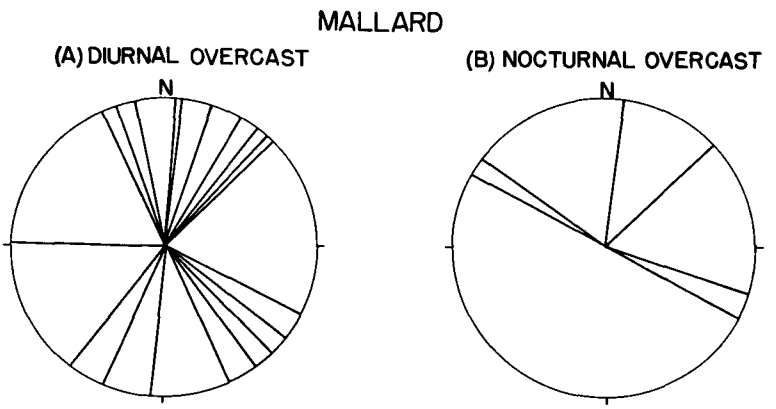

Figure 5. The mean flight headings taken by each group of Mallards released under overcast skies (A) diurnally and (B) nocturnally in Illinois, 1956–1960.

TABLE 6
RESULTS OF EACH RELEASE OF MALLARDS UNDER OVERCAST SKIES AT NIGHT, 1956–1957

Release point (See Fig. 1)	*Date*	*Time (Central Standard)*	*Number plotted*	*Cloud cover*	*Wind direction*	*Wind velocity (MPH)*	*Home bearing in degrees*	*Mean heading in degrees*	*Standard deviation in degrees*	*Distance flown to reach one mile*
E	11-26-56	1950–2000	5	9–10	N	8	315	117	46.5	1.40
E	11-28-56	1950–2000	6	10	NW	15	315	296	34.2	1.42
E	11-29-56	1950–2100	9	10	SSW	4	315	0	52.7	1.70
E	12-17-56	2100–2300	10	10	NW	5–10	315	117	49.6	1.55
E	12- 5-57	1950–2100	10	10	S	10–15	315	319	16.6	1.43
E	12-16-57	2000–2100	8	9–10	E	5–10	315	269	34.9	1.46

Only one mean heading under overcast skies at night was significant (Table 6). It was to the northwest.

Attraction of the home lake. Several releases of Mallards were made under clear skies and by day from two sites, 5 km (3 to 4 miles) north–northwest of the traps where the ducks had been captured. One site was on a bluff overlooking the Illinois River valley, the other site was a bottomland field about midway between the bluff and river (Figure 6). Lake Chautauqua, where the traps were located, was 2.4 km (1.5 miles) from the nearest release site and 3.8 km (2.5 miles) from the farthest site.

The lake, about 11.2 km long and 1.6 km wide, was in full view of the released ducks. Yet, despite the nearness of such a large body of water, all but 5 of the 36 ducks flew away from it (Figure 6). The course away from the lake led over a 21 m bluff topped with trees and then over prairie farmland. The five Mallards that did not follow suit flew eastward on a heading that would gradually return them to lakes in the Illinois River valley.

The headings that most Mallards took away from the lake were in a northerly direction, but covered a sector extending from 315° to 40°.

Ten Mallards, released from the bluff release site on an overcast day (21 November 1957), showed no movement toward the lake even though their flight paths were scattered over a large sector of the compass.

Because ducks flew away from the lake when released north of it, several releases were made under clear skies on the south and east side of Lake Chautauqua (Figure 7). We wished to determine their behavior when, after flying north, they arrived at their home body of water. A 30 m tower, south of the east shore of the lake, enabled the observer to see most of the ducks from their release to their "goal."

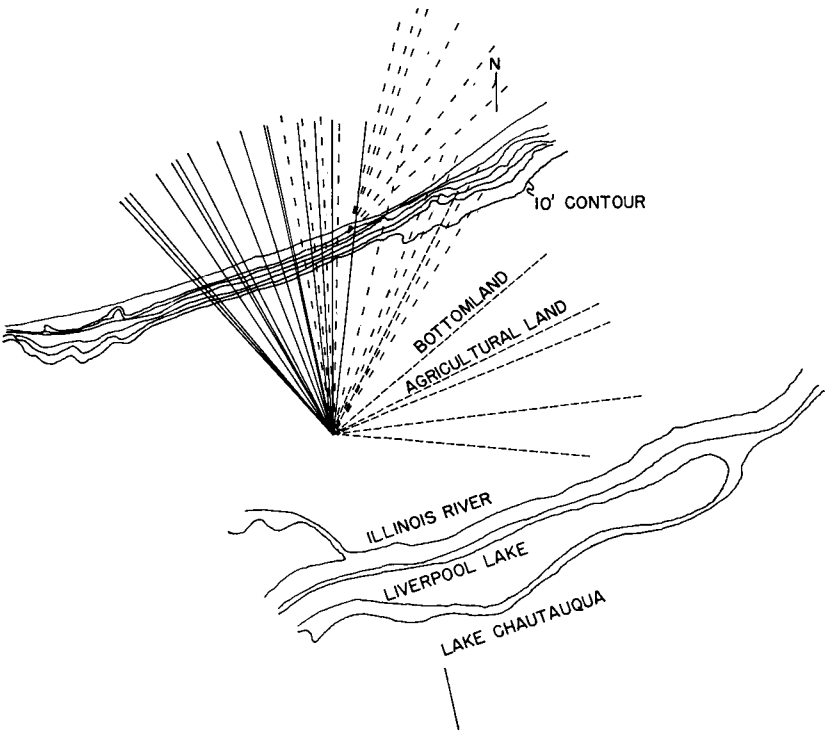

Figure 6. The individual flight headings taken by 36 Mallards released 4.8 to 6.4 km (3 to 4 miles) from the place of trapping and 2.4 to 4 km (1.5 to 2.5 miles) from Lake Chautauqua, which was clearly visible. Releases made on 25 November 1957 and 23 November 1959.

Upon release 0.8 or 1.6 km from the lake, almost every Mallard pursued a northerly course, flying about 15 m above the ground, until the lake was reached. The Mallards appeared not to recognize landmarks, for they flew out over the open water as if to continue the same heading. However, upon passing over flocks of ducks, most birds circled back to join the flocks on the water (Figure 7). Two individuals ignored the lake and resting ducks to continue their course across the lake until lost to view. Three Mallards started north at different times, but all swung west to join flocks of Mallards flying out to feed in nearby cornfields.

Five Mallards were released on a clear night from the south side of the 30 m tower. The birds immediately turned north, gradually losing altitude until they landed 0.75 to 1.6 km away in the lake. For a short time, the lights attached to their feet revealed them swimming about in random fashion.

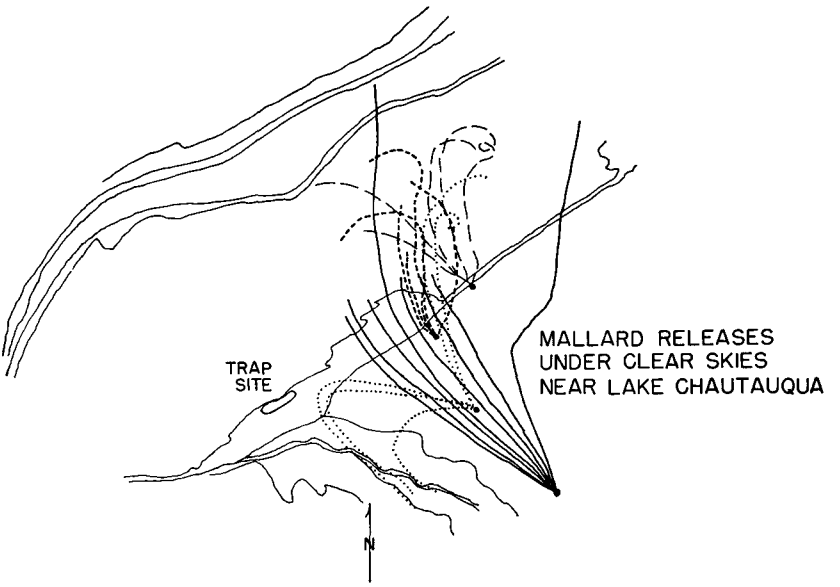

Figure 7. The flight paths of 23 Mallards released to the south of Lake Chautauqua on 4 and 30 December 1957, 22 December 1959, and 26 November 1960.

Attraction of unfamiliar lakes. Five groups of Mallards were released 1.6 km south of two artificial lakes (C and W, Table 3). For the most part, these ducks flew north from the release site and passed over the lakes without stopping. All those that flew across the lakes continued on a northward course until lost to view.

The best-charted release of this type was made on 31 December 1959, 1.6 km south of Canton Lake, when observers at both the release site and lake traced the flight paths of 20 Mallards: 8 of these passed to the west of the lake which, though visible, failed to attract them; 12 arrived at the lake, 8 of them continuing in a northwesterly direction; 2 individuals circled part of the lake several times before turning east and then back south; 2 others alighted on the lake.

When the 2 sitting Mallards were flushed 30 minutes later, they flew west of the lake 0.8 km, climbing to 300 m. Next, they swung east for 1.6 km, flying parallel to the south edge of the lake. Then they turned 90° to the south and were soon lost to sight.

On a previous release of 210 Mallards, 13 November 1952, at the University Airport, Champaign (Bellrose, 1958a: 86), an incident occurred that also suggests a reorientation of Mallards southward following an initial flight northward. Here 26 of the 210 Mallards that flew north alighted on a pond on the university golf course about 3.2 km north

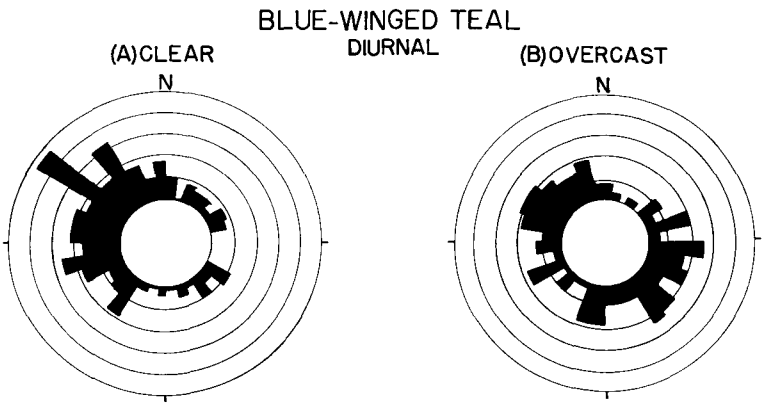

Figure 8. The flight headings of Blue-winged Teal by day under (A) clear and (B) overcast skies, 1957–1960. Data plotted by 10 degree sectors.

of the point of release. These ducks were inadvertently flushed 30 to 60 minutes later and flew south, reaching an altitude of 30 m as they passed a radar tower from which visual and radar observations of the experiment were being made. They continued in a southerly direction until out of sight, about 3 km from the point of observation.

Blue-winged Teal.—Thirteen releases of 169 Blue-winged Teal were made under diurnal clear skies (Table 2). Most of the headings taken (Figure 8a) were distributed over 100°, about twice the spread found for Mallards under similar conditions. Nevertheless, the standard deviation and Chi-square values indicate (Table 2) that the mean heading

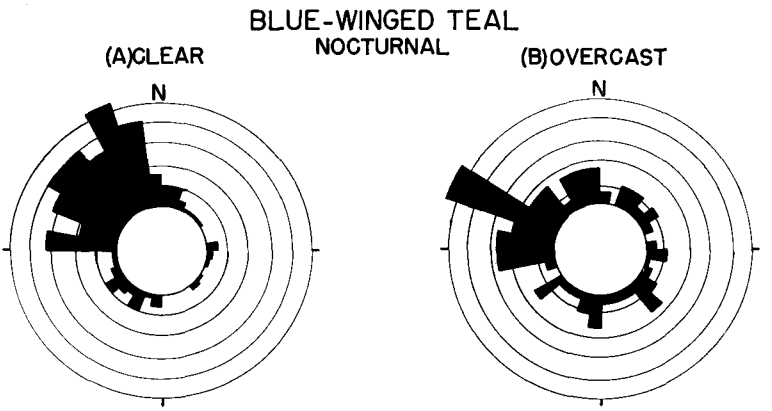

Figure 9. The flight headings of Blue-winged Teal at night under (A) clear and (B) overcast skies, 1957–1960. Data plotted by 10 degree sectors.

TABLE 7
RESULTS OF EACH RELEASE OF BLUE-WINGED TEAL UNDER CLEAR SKIES BY DAY, 1957–1960

Release point (See Fig. 1)	*Date*	*Time (Central Standard)*	*Number plotted*	*Cloud cover*	*Wind direction*	*Wind velocity (MPH)*	*Home bearing in degrees*	*Mean heading in degrees*	*Standard deviation in degrees*	*Distance flown to reach one mile*
E	9-16-57	1300–1400	8	0	NW	10–15	250	322	6.2	2.39
U	9-23-57	1050–1250	21	0	NW	10–15	275	334	8.1	2.80
M	9-24-57	1200–1400	19	0	S	20	135	220	35.0	2.50
M	9-25-57	1300–1400	15	0	SW	10	135	267	11.3	3.15
E	9-26-57	1000–1100	8	0	E	10–15	250	294	9.4	2.43
S	9-26-57	1400–1500	14	4	E	15	255	275	9.1	2.79
F	10- 2-57	1450–1600	15	0	E	10	195	190	13.4	2.30
V	10- 4-57	1400–1600	13	0	NE	10	10	276	9.1	2.48
Y	10- 7-57	1600–1700	8	3	NE	4	190	274	10.7	2.73
A	10- 7-57	1750–1800	6	5	—	0	155	119	114.2	2.63
S	10-11-57	1400–1550	20	5	NNE	5	255	152	11.7	2.89
S	9-27-59	1300–1500	12	3–4	S	20	255	331	11.8	2.36
M	10- 6-60	1600–1700	10	0	N	15	135	340	7.1	2.86

is significant. The mean heading of 280° is 75° to the west of the Mallards' mean heading for diurnal clear conditions.

Under overcast skies by day (Table 2 and Figure 8b), 88 Blue-winged Teal showed considerably less orientation than under clear skies. The high standard deviation indicates that little significance can be attached to the mean heading.

At night under clear skies, the headings of 169 Blue-winged Teal were significantly grouped about the mean (Table 2 and Figure 9a). As shown by standard deviation and Chi-square values (Table 2), the headings at night were grouped more compactly than those by day.

The mean heading of Blue-winged Teal under overcast skies at night has significant standard deviation and Chi-square values (Table 2). The reason for this significant mean heading in three releases may be found in the fact that a few bright stars shone faintly in the zenith. These releases were placed in the overcast category because Mallards under similar nocturnal sky conditions showed no evidence of oriented flight.

Orientation to the south. Mean headings of each release of Blue-winged Teal (Figures 10 and 11) show some diverse directional flights not apparent in the mass of data. Under diurnal clear skies, two groups flew to the southeast, one to the south, and one to the southwest (Figure 10a). Of these four aberrant mean headings, standard deviation data in Table 7 suggest that only two are statistically significant. One release of

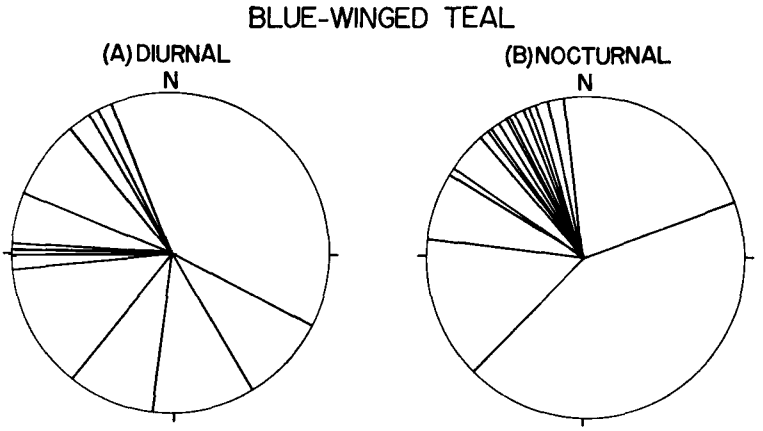

Figure 10. The mean flight headings taken by each group of Blue-winged Teal released under clear skies (A) diurnally and (B) nocturnally in Illinois, 1957–1960.

15 teal (at release point F of Figure 1 on 2 October 1957) showed that the individuals flew similar headings centering around 190°. The other release of 20 teal (at release point S on 11 October 1957) showed individuals grouped around a heading of 152°.

Of the two aberrant mean flight headings (71° and 225°) shown in Figure 10b, for nocturnal clear skies, only one (at release point B on 28 October 1958) was statistically significant (Table 8). The 14 teal in this release flew similar headings to the southwest.

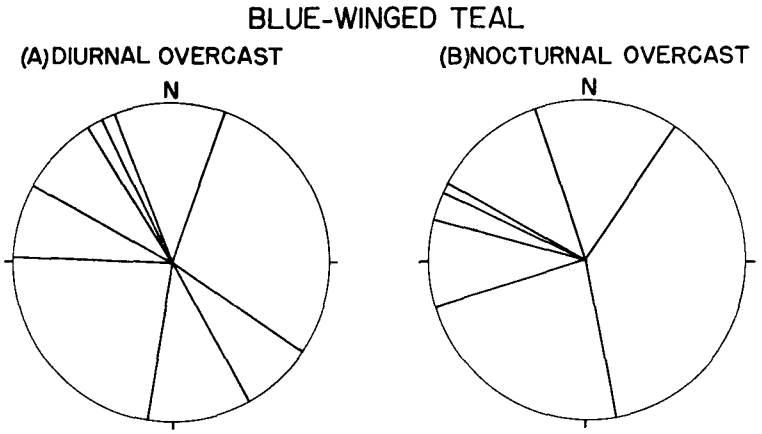

Figure 11. The mean flight headings taken by each group of Blue-winged Teal released under overcast skies (A) diurnally and (B) nocturnally in Illinois, 1957–1960.

TABLE 8
RESULTS OF EACH RELEASE OF BLUE-WINGED TEAL UNDER CLEAR SKIES AT NIGHT, 1957–1960

Release point (See Fig. 1)	*Date*	*Time (Central Standard)*	*Number plotted*	*Cloud cover*	*Wind direction*	*Wind velocity (MPH)*	*Home bearing in degrees*	*Mean heading in degrees*	*Standard deviation in degrees*	*Distance flown to reach one mile*
E	9-18-57	2050–2200	17	0	SE	5	250	323	3.9	2.28
M	9-25-57	1900–2050	10	0	E	4	135	344	24.9	2.92
P	9-30-57	2050–2200	19	0	—	0	253	303	6.5	2.85
E	10- 1-58	2000–2150	10	0	S	4	250	333	3.9	2.37
P	10- 1-58	2200–2300	9	0	S	3	253	319	11.9	2.48
B	10- 8-58	1900–2100	18	0	S	10–15	143	304	11.0	2.47
E	10-13-58	2000–2100	8	0	S	5–10	250	332	7.3	2.64
P	10-13-58	2150–2250	8	0	S	5–10	253	339	12.7	2.48
B	10-28-58	2000–2150	14	0	N	5	143	225	11.4	2.82
B	11-19-58	2000–2150	9	0	SW	10	143	353	43.2	2.99
S	10- 9-59	2100–2250	8	0	—	0	255	278	2.4	2.37
E	4-21-60	2100–2300	13	0	S	10–15	250	332	3.8	2.26
E	4-28-60	2100–2200	5	6–7	S	10	250	340	5.6	2.19
E	9- 9-60	2300–2450	9	1	N	5	250	71	32.6	3.28
S	9-23-60	2100–2200	5	4–5	SE	5	255	327	7.6	2.50
M	10-10-60	2100–2200	3	0	—	0	135	323	56.8	2.53
E	10-19-60	1950–2000	4	0	NW	10	250	349	21.9	2.23

Six of the nine headings under overcast skies by day (Table 9) were statistically significant. All three headings to the southeast (Figure 11a) were significant as well as three of the five in the west to northwest sector.

Orientation from only a few stars. Under overcast skies at night, four of the seven headings (Table 10) were statistically significant. Three of these headings were in the west–northwest sector, the other in the north–northwest sector (Figure 11b) of the compass. When three of these releases were made, only a few stars were visible. The flight directions of the two releases in the fall were very similar to the general direction taken by most teal under clear skies. Although the flight direction was still similar to that for clear skies, individuals in the single release made in April flew in a more north–northwesterly direction than did those in the fall.

Probably the Blue-winged Teal that oriented northwestward used astral cues to determine direction. However, the sky conditions prevailing at the time of the three releases provided limited astral cues.

When teal were released on 3 October 1957, a few stars of the constellation Cygnus were visible in the zenith and the moon shone through a thin layer of clouds on the south horizon. Again, when teal were first

TABLE 9
RESULTS OF EACH RELEASE OF BLUE-WINGED TEAL UNDER OVERCAST SKIES BY DAY, 1957–1959

Release point (See Fig. 1)	*Date*	*Time (Central Standard)*	*Number plotted*	*Cloud cover*	*Wind direction*	*Wind velocity (MPH)*	*Home bearing in degrees*	*Mean heading in degrees*	*Standard deviation in degrees*	*Distance flown to reach one mile*
S	10- 9-57	1350–1500	5	10	N	10	255	150	15.4	3.57
E	10- 9-57	1550–1700	9	10	NW	10	250	171	13.8	3.86
S	10-21-57	1050–1350	12	10	SE	15–20	255	332	15.9	2.68
P	11- 7-57	1500–1700	16	10	SSE	10	253	270	15.5	3.00
I	10- 7-58	1650–1700	8	10	S	15	145	19	35.5	3.63
S	10- 2-59	1450–1550	9	10	SE	10	255	296	10.4	3.41
E	10- 6-59	1300–1450	4	10	SW	18	250	326	30.2	3.52
S	9-25-59	1700–1800	9	10	S	15	255	337	24.9	3.13
S	9-30-59	1600–1750	16	9–10	N	10	255	124	6.9	2.27

released on 18 September 1959, the constellations Cygnus and Lyra could be seen in the small patch of clear sky in the zenith, but midway through the release the stars of these constellations were obscured by the thickening overcast. Yet, the moon, about 25° above the east horizon, shone through the overcast indicating that the overcast was high and not very dense. Flight paths of the ducks before and after the last stars faded from sight were very similar.

As teal were being released individually on the night of 28 April 1960, a bank of clouds moved across the sky from the northwest to the southeast. All but 5 per cent of the sky was obscured by the time 8 of the 10 birds had been released. Then the only stars visible were slightly southeast of the zenith. In spite of the steady reduction in astral cues, all individuals flew a direct, northerly course.

Shift in direction. A number of teal released in the fall under clear skies pursued a given heading for 1.6 to 5 km before abruptly changing direction by 80° or more. Among the daytime releases of 164 ducks, 19 showed this pronounced change in heading. Under nocturnal conditions, 29 of the 175 ducks providing data showed a similar sharp shift in flight path.

Of the 47 Blue-winged Teal that suddenly shifted flight direction by 80° or more under clear skies, 23 took headings from west or northwest to south, 12 from north to west, 9 from west to north, and 3 from north to east.

Flight direction versus migration. Data in Tables 7–10 suggest some relationship between the southward orientation of Blue-winged Teal (in

TABLE 10
RESULTS OF EACH RELEASE OF BLUE-WINGED TEAL UNDER OVERCAST SKIES AT NIGHT, 1957–1960

Release point (See Fig. 1)	*Date*	*Time (Central Standard)*	*Number plotted*	*Cloud cover*	*Wind direction*	*Wind velocity (MPH)*	*Home bearing in degrees*	*Mean heading in degrees*	*Standard deviation in degrees*	*Distance flown to reach one mile*
S	10- 3-57	2000–2150	10	9–10	ENE	6	255	292	8.9	2.80
E	9-22-58	1900–2050	15	10	SE	5–10	250	294	12.5	3.73
P	9-22-58	2100–2200	9	10	SE	5–10	253	250	41.8	3.00
E	10- 9-58	1950–2150	16	9–10	NW	25	250	168	26.0	3.64
S	9-18-59	2200–2300	17	10	SE	8	255	282	6.1	2.38
E	4-28-60	2100–2200	5	9–10	S	10	250	338	10.3	2.19
E	9- 8-60	2200–0100	10	9–10	WSW	5	250	31	19.7	3.01

contrast to the customary west–northwest orientation) and the migratory movements of ducks.

The two releases showing significant southward orientation under clear diurnal skies occurred when sizable duck flights took place. However, when a small duck flight arrived in the Illinois River valley shortly after dawn on 23 September 1957, the teal released 95 miles east of there some 4 hours later did not shift headings southward.

Only one group of teal released at night under clear skies showed a significant southerly heading (Table 8). A large duck flight occurred that night, 28 October 1958. There were several records of duck flights occurring the night previous or the night following releases of teal on a clear night, yet with lack of direct concurrence, a northwesterly orientation took place.

Experimental teal did not respond with a southerly heading the night of 19 November 1958, even though a large departure of Mallards from the Illinois River valley occurred at sunset (Table 8).

Three of nine groups of teal released under overcast skies by day flew significant southeast headings (Table 9) and on all three occasions, duck flights took place. No duck flights occurred within 24 hours of the other six releases, three of which were statistically significant and showed northwest headings.

The one release showing southward orientation under overcast skies at night (Table 10) was not statistically significant, but a teal migration did occur that night.

Pintails.—Under clear skies both by day and night, Pintails showed orientation to the west or west–northwest (Figure 12). The mean head-

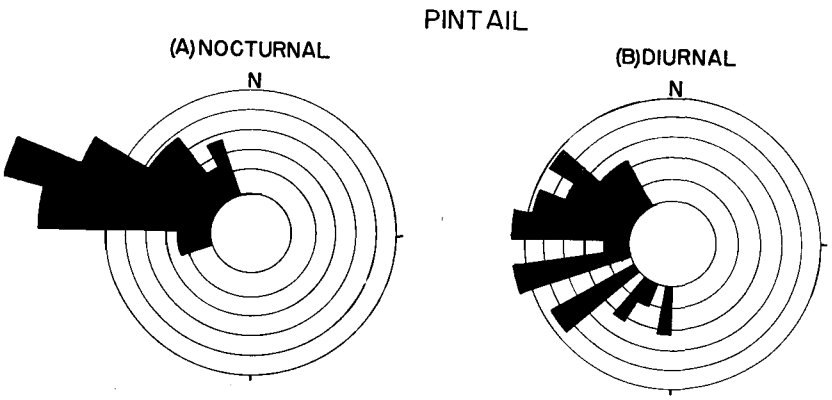

Figure 12. The flight headings of 30 Pintails released under clear skies at night (A) and 35 Pintails released under clear skies by day (B), 1960. Data plotted by 10 degree sectors.

ings taken by Pintails were 11° to 28° west of those taken by Blue-winged Teal (Table 2). As with the teals, Pintails displayed more uniform headings under clear skies at night than by day (Table 2). The standard deviations for Pintails, Blue-winged Teal, and Mallards under clear skies at night were almost identical (Table 2) suggesting that these species had a comparable ability in determining direction under favorable sky conditions.

Twelve Pintails released singly under overcast skies by day 19 October 1960, showed a marked change in flight paths with a worsening in weather conditions. At the start of the release, heavy black clouds at an altitude of 270–300 m covered the entire sky. The wind was from the north at 24 km per hour. Light rain was falling and the temperature was 13°C (55°F). Under these conditions, the first four Pintails flew in a somewhat meandering path toward the north.

Then the wind velocity increased to 41 km per hour and the temperature dropped about 6°C (10°F) in 5 to 10 minutes. The sky remained covered with dark clouds. With the acceleration in wind velocity and drop in temperature, each released Pintail began to climb higher in the sky. The next four ducks headed toward the southeast in a much straighter flight path. The next two Pintails flew a northwesterly heading, while the last two birds resumed a southeasterly flight heading. The standard deviation (Table 11) for this release seems too large to be significant, a result of the first four Pintails flying north.

Large and extensive duck flights occurred throughout this day (19 October 1960) all the way from the plains of the Dakotas to Arkansas. Near the release site two flocks of migrating Mallards were observed

TABLE 11
RESULTS OF EACH RELEASE OF PINTAILS UNDER CLEAR AND OVERCAST SKIES, 1960

Light period	*Sky cover*	*Release point*	*Date*	*Time (Central Standard)*	*Number plotted*	*Wind direction*	*Wind velocity (MPH)*	*Home bearing in degrees*	*Mean heading in degrees*	*Standard deviation in degrees*
Diurnal	Clear	E	9-27	1500–1700	12	NE	10–15	315	276	6.7
"	"	M	10- 6	1550–1650	10	N	15	315	225	9.0
"	"	E	10-14	1400–1550	13	—	0	315	293	7.3
"	Overcast	E	10-19	0900–1000	12	N	25	315	132	48.5
Nocturnal	Clear	S	9-23	2000–2100	7	—	0	255	307	8.6
"	"	E	9-29	2100–2200	10	NE	5	315	286	3.0
"	"	M	10-10	1950–2050	9	—	0	135	291	7.2
"	"	E	10-19	2000–2050	5	N	5	315	282	12.0
"	Overcast	E	9-29	1950–2100	9	S	5	315	314	24.2

flying through the base of the dark clouds 30 minutes after the last Pintail had been released.

Another instance of a southward orientation occurred in a release of 10 Pintails on 6 October 1960, but in this case the release occurred under clear skies by day. The mean heading was 225° with a standard deviation of 7.16, which was statistically significant (Table 11).

The single release of nine Pintails under overcast skies on the night of 29 September 1960, appeared to show a degree of orientation to the west–northwest (Table 11). The sky was completely covered by clouds at 900–1,200 m. A light overcast occurred over one-third of the sky in contrast to the dark clouds over the remaining area. Although the Pintails showed some confusion in flight by circling, they flew a mean heading of 314° with a significant Chi-square value (Table 2). While we could not see any stars, it is possible that the Pintails were able to see some stars through the thinner clouds.

Canada Geese.—Canada Geese, which were released both diurnally and nocturnally under clear skies, showed significant mean headings to the southwest (Table 2). An analysis of the flight headings of each goose released under clear skies (Figure 13a and b) showed that most of the headings were grouped in a 60° sector. The flight directions remained southwestward (Figure 13) whether the geese were released northeast of Horseshoe Lake, near Ullin, Illinois, or south of there near Wyatt, Missouri.

The 18 geese released under overcast skies by day (Figure 14a) and the 16 geese released under overcast skies at night (Figure 14b) flew in

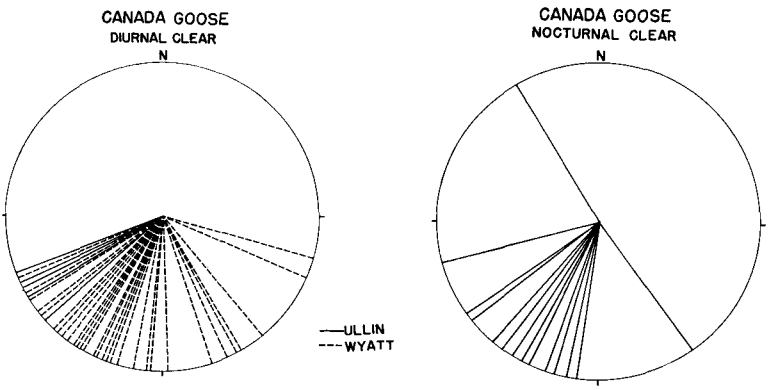

Figure 13. The flight headings of 35 Canada Geese (left) released under clear skies by day, 5 near Ullin, Illinois and 30 near Wyatt, Missouri on 28, 29, and 30 January 1958, and 4 February 1959; and (right) the flight headings of 14 Canada Geese released under clear skies at night near Wyatt, Missouri, 29 January 1958 and 4 February 1959.

numerous directions. This resulted in mean headings that were not significant (Table 2).

A group of five geese (not shown) was transported from Horseshoe Lake to Puxico, Missouri, some 96 km (60 miles) to the west. Four geese, when released individually from a knoll overlooking the Mingo National Wildlife Refuge, flew to the south away from the lake on the refuge. The

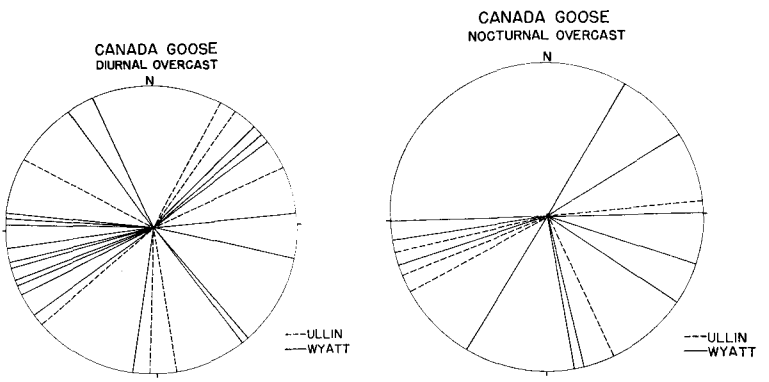

Figure 14. The flight headings of 18 Canada Geese (left) released under overcast skies by day at Ullin, Illinois, 28 January 1958 and Wyatt, Missouri, 29 and 30 January 1958; and (right) the flight headings of 16 Canada Geese released under overcast skies at night near Ullin, Illinois, 28 January 1958, and Wyatt, Missouri, 29 January 1959 and 13 January 1960.

fifth goose flew toward a flock of geese on the lake. These geese had started calling in response to calls from the birds being released.

ORIENTATION IN SASKATCHEWAN

Ducks released in orientation experiments in central Saskatchewan, 1,900 km (about 1,200 miles) northwest of central Illinois, show an initial fixed flight direction similar to that found in Illinois.

On 4 September 1962, Mr. J. B. Gollop of the Canadian Wildlife Service, took 54 Pintails some 80 km (50 miles) west of the trapping site near Kindersley, Saskatchewan. He released them singly and in pairs from about three hours before sunset to one-half hour after sunset under a sky that was at first hazy and then clear.

Within 15 seconds of release, regardless of the direction faced, 90 per cent of the Pintails flew northwest for one to four minutes. Then, a large number turned east for two to four minutes before again turning back to west or northwest.

Gollop released 40 Mallards 6.4 km (4 miles) west of the slough where they were trapped on 6 September 1962. The sky was again hazy at first and then clear during the release period, 1030 to 1330 hours. Within 10 seconds of their release as pairs, practically all Mallards oriented to the northwest. This direction was maintained for four to five minutes. Mallards that were still under observation were then observed to turn east and southeast and return to the slough where trapped.

DISCUSSION

Mallards, Blue-winged Teal, Pintails, and Canada Geese followed more direct paths and had a greater uniformity of flight headings under clear skies than under overcast skies. This finding convincingly supports the thesis that these birds use the sun and stars for guidance in determining direction.

The headings flown under clear skies by all four species of waterfowl were quite distinct from each other. These headings varied from north for Mallards, to northwest for Blue-winged Teal, to west for Pintails, and southwest for Canada Geese (Table 2).

Under clear skies there were no significant differences between the diurnal and nocturnal mean headings of Mallards, but in the other three species of waterfowl the nocturnal mean headings were slightly north of the diurnal mean headings (Table 2). Flight headings were significantly more uniform for Blue-winged Teal and Pintails at night than they were for these species by day. The flight headings of Mallards on clear nights were grouped almost as compactly as those of Blue-winged Teal and Pintails under similar conditions, but Mallard flight headings were grouped

more compactly by day than by night (Table 2). Their diurnal flight headings were more closely grouped than those of the Blue-winged Teal and Pintails.

One reason for the greater scattering of Blue-winged Teal and Pintail flight headings under clear skies by day was the greater propensity for releases of these species to head southward. Under clear skies by day only 1 in 23 Mallard releases showed a southward heading (Figure 11), but 2 of 13 Blue-winged Teal releases showed a significant southeast heading, and 1 in 3 Pintail releases showed a southwest heading.

The relation of the mean flight headings of the four species of waterfowl to the direction taken in their fall or spring migration is quite variable.

Band recoveries indicate the flight paths followed by waterfowl migrating through Illinois from their breeding grounds in the north to their wintering grounds in the south. Mallards pursue a heading of between 135° and 145° when migrating to Illinois from their principal breeding grounds in Saskatchewan. In Illinois they shift to a heading of 180° to 195° to reach their main wintering grounds in the swamps of Arkansas and Louisiana.

Blue-winged Teal also pursue a heading of from 135° to 145° when migrating to central Illinois. Upon leaving Illinois, about 44 per cent of the teal fly a heading of 140° to 160° for their wintering grounds in Venezuela and Colombia; about 26 per cent fly a heading of 160° to 180° and 7 per cent take a heading of 200° to 210° (Bellrose, 1958b: 27, 28).

Pintails take a heading of 125° to 135° in order to reach Illinois from the south-central Canadian plains where they breed. Some Pintails continue along the same heading to the southeast Atlantic Coast, but most take a heading of 190° to 200° to the coastal marshes of Louisiana and east Texas.

Few band recoveries are obtained in the spring, but these few reported recoveries, when combined with visual observations, suggest that Mallard, Blue-winged Teal, and Pintail flights in the spring are the reverse of those in the autumn.

Canada Geese take a heading of 200° to 210° when migrating from James Bay to their wintering grounds in southern Illinois. The initial flight direction of oriented geese (Table 2) is very similar to that taken in fall migration.

However, the oriented flight headings taken by Mallards were about 30° to the north of the reverse direction of their autumn migration to Illinois. The oriented headings were 10° west of the direction of their spring migration to Illinois.

The back azimuth of fall migrating Blue-winged Teal is similar to the

mean heading of teal released under clear skies at night. For reasons already discussed, the nocturnal heading of teal is considered the most representative of the species orienting under clear skies. The back azimuth of fall migrating Pintails is about 20° north of the mean heading of this species under nocturnal clear skies.

The initial orientation of Mallards and Pintails was unrelated to either the fall or spring direction of migration. However, the mean heading of Blue-winged Teal under clear skies at night was similar to a reversal of their direction in the fall migration. The mean heading of Canada Geese under clear skies was similar to the direction of their fall migration. Matthews (1961: 225) also concluded: "It is doubtful whether there is much in common between the present orientation tendency and reverse migration." Such a thesis seemed tenable on the basis of Drost's (1949) reporting of bands recovered from birds many miles in the "wrong" direction a few days after release. He suggested that this might be a short-term reaction set up by the stress of trapping and handling.

In a recent article, Sauer (1961: 234) referred to reverse migration in birds as being induced by trapping, partially cloudy skies, and various other conditions. Although waterfowl may initially fly a fixed direction as a result of stress, it is obvious that their flight is not necessarily a reversal of their migratory direction.

ASTRAL GUIDANCE

There was evidence that Blue-winged Teal and probably Pintails were able to determine direction from the presence of only a few stars in the zenith. On two occasions the only stars visible to us were in the constellation of Cygnus, and on one other occasion stars were visible in both Cygnus and Lyra. The most important stars were Deneb, the brightest star in the constellation Cygnus, and Vega, a star in the constellation Lyra. Because of their exceptional brilliance (magnitude 1.3 and 0.1, respectively) and their position in the sky, Deneb and Vega were the last stars to disappear in the thickening overcast on 18 September 1958.

Whether the few stars visible in Cygnus and Lyra were sufficient for the teal and Pintails to determine direction, or whether other stars were used which were apparent to them but invisible to us, is conjectural.

However, supporting evidence that only a few stars may be necessary for direction-finding comes from Sauer (1961: 237). He found, in preliminary tests, that the conspicuous triangle of stars formed by Deneb, Vega, and Altair, served as an important orientation pattern for birds. Sauer also stated that various combinations of the parts of this triangle

with other constellations seemed sufficient for birds to establish proper migration direction.

Because the distance is greater through the atmosphere from the zenith to the horizon, the farther a star is from zenith, the fainter it appears. For example, a star has about the same brilliance from zenith to 45°. At 75° from zenith, a star is 1¾ times fainter; at 86° it is 6¼ times fainter; and at 89° it is 15 times fainter (Norton and Inglis, 1954: 42) than it was at zenith.

Because of limited visibility, it would be advantageous for migratory birds to use for their celestial cues only those stars of, or approaching, the first magnitude that appear between the zenith and 45° declination along the birds' routes of migration. Circumpolar constellations which have the advantage of continuous visibility above the horizon have the disadvantages of obscurity from haze, atmospheric absorption of brilliance, and possessing stars of low magnitude.

HOME DIRECTION

A perusal of the mean flight headings of each release of Mallards, Blue-winged Teal, and Pintails, in relation to the bearings of the site of their capture shows no tendency for these ducks to head toward "home" on their migration route. It is obvious that at the beginning of their flight, Mallards and teal were unable to ascertain their displacement geographically regardless of the distances (1.6 to 153 km) involved. Canada Geese released both north and south of their winter home, oriented initially in the same fixed direction, to the southwest.

INITIAL FIXED DIRECTION

The tendency initially to fly a fixed direction under clear skies appears innate. This trait is so strong, in fact, that rather than alter their fixed directional flight, Mallards have flown away from their home lake. Other Mallards after flying a mile or two northward have passed over small lakes without alighting even though no other water areas were visible. The only factor that abruptly terminated the directional flight of most Mallards was their decoying to resting flocks of waterfowl.

The initial innate flight direction appears to play a basic role in waterfowl behavior. It must serve a highly useful function because it is present in such a dominant and characteristic form in all waterfowl tested to date. Moreover, it has also been found in the Common Tern by Griffin and Goldsmith (1955). Since three waterfowl and one tern species represent a large proportion of those species in which initial flight headings have been studied, it seems evident that similar flight behavior will be found among many more avian species.

Experiments by Kramer, Hoffmann, Sauer, and others with birds in circular cages show that birds use celestial cues either to orient in the direction of migration or to a goal for which they were trained. Displacement experiments, on the other hand, show a different type of orientation.

The initial fixed direction of orientation taken by displaced birds is probably the first step in determining either the direction of home or the direction to be taken in migration. Home may be an area of prolonged use on the breeding grounds, on a migration route, or on the wintering grounds. An innate response to celestial cues provides a means for birds to leave a point of stress most quickly and yet provides time and space for further cognizance of terrestrial and celestial cues.

It is suggested that it would take more time for a bird to determine where it "wants" to go than the few seconds birds actually take in selecting the fixed directional course taken. Furthermore, it appears logical to assume that a bird needs the passage of time or space to obtain sufficient celestial cues to determine the direction of home, or the direction of migration from the point of release.

Birds released in displacement experiments have not had the advantage of a continuous feedback of environmental cues benefiting birds flying from home or departing in migration. Only one cue is immediately available to a displaced bird upon release: a directional cue from the sun or stars. I think that a fixed directional course is taken until other cues become available for reorientation.

REORIENTATION OF INITIAL FLIGHT DIRECTION

There is evidence that some waterfowl do orient in their accustomed migratory direction a short time after release. There are three different areas of evidence suggesting a subsequent change in initial northward flight: (1) the southward flight of some Mallards after they had alighted on water to the north of the release site; (2) the shift in flight headings of 7 per cent of the released Blue-winged Teal from northwest to south, such an abrupt change in headings usually occurring after 1.6 to 6.4 km (1 to 4 miles) of direct flight; and (3) the southward migration of juvenile Blue-winged Teal removed to lakes 80 to 112 km (50 to 70 miles) from the trap site (Bellrose, 1958b: 22–31).

The juvenile teal were released in November and December after the species had migrated from Illinois. Recoveries of banded teal indicated that those juveniles flew along customary flyway routes without the guidance of adults (*op. cit.*: 25–27). The remarkable speed southward made by a few juvenile teal indicates that some of these birds became oriented in the correct migration direction within a few hours. For

example, one juvenile teal released late in the afternoon of 10 November 1954, was killed two days later in Florida. Two juveniles released in mid-afternoon, 22 November 1955, were shot on 24 November on Mobile Bay, Alabama (Bellrose, 1958b: 25).

It is difficult to envision juvenile teal using anything other than celestial cues to fly such long distances in the proper direction in such a short time. If this is true, then Blue-winged Teal, which initially use celestial cues to fly northwestward over land, must alter direction to fly southward during the autumn.

Homing pigeons also show a reorientation of initial flight directions. Individual releases of homing pigeons were made by Wallraff (1960: 452) at four equally spaced points near Wilhelmshaven, Germany. Under clear skies, most of the pigeons flew toward the east and southeast even though these headings did not lead the pigeons from two of the release sites toward home. However, most of the pigeons that initially flew away from home did eventually get home.

Band Recoveries Show Subsequent Movements

Band recoveries from a small proportion of the ducks released also indicate that the majority of the experimental birds eventually migrated south of Illinois in autumn, in the customary manner of the species. However, band recoveries suggest little as to when or where the change in directions occurred because most of the recoveries were made more than two weeks after the ducks were released.

Some bands that were recovered in less than two weeks did indicate a change in the initial flight direction. Two Blue-winged Teal were recaptured at the trap site the day following release; they had been released at different times 24 km (15 miles) to the northeast of the trap site. A Mallard released 16 km (10 miles) north of Lake Chautauqua and last observed flying north was recaptured back at the same place one week later. A number of band recoveries were received from the vicinity of Lake Chautauqua, south of the release sites, one to two weeks after release. An exception was a Pintail which was observed on 6 October 1960, flying southwest under overcast skies from its release point near Macomb, Illinois. This Pintail was shot on 12 November 1960, in Wisconsin 384 km (240 miles) northeast of the release site.

British Versus American Mallard Orientation

Matthews (1961: 223) thought that the northwest headings taken by Mallards in England were of short duration. He presented evidence showing that the longer a Mallard was in sight, the greater the spread in its flight headings. Moreover, subsequent band recoveries from these ducks indicated that a random distribution developed not far from the release

sites. Surprisingly, Matthews found that 83 per cent of all the band recoveries obtained were within 48 km (30 miles) of the release sites weeks and even months later.

Until our visual contact ceased 1.6 to 2.4 km (1 to 1½ miles) from the release point, we observed that the headings of Mallards released under clear skies in Illinois became more grouped, the farther the birds proceeded from the release point. As previously noted, Mallard band recoveries indicate an eventual migration southward (Bellrose, 1958a: 87).

Mallards in England are largely sedentary; those in Illinois are migratory. This difference may explain why English Mallards remained in the area where their initial orientation drive abated, while those in Illinois, within a similar period of time, resumed migration.

SOUTHWARD ORIENTATION

Under clear skies 5 of the 71 releases of ducks and under overcast skies 7 of the 43 releases showed significant southward headings. The 7 releases under overcast skies apparently represented a fixed angle response to the wind and can be omitted from further consideration.

It seems doubtful, however, that wind caused the southward heading of the 5 releases under clear skies. First, a statistical appraisal showed no response of flight headings to wind vectors under clear skies. Second, although three of the five winds were from the north, one was from the east, and one from the south.

The evidence suggests that the southward headings under clear skies occurred as a result of celestial cues. If this is true, why did only a few releases fly southward while the majority of the releases flew northward?

DISPOSITION TO MIGRATE AND DIRECTIONAL FLIGHT

Possible explanations for variations in orientation behavior may lie in the bird's disposition to migrate (*Zugdisposition*) and the weather conditions which initiate migratory behavior. Ducks either not disposed to migrate or not triggered by the proper weather conditions would have a greater tendency to stay in the area than to leave in migration. They may, therefore, respond to an initially stronger stress motivation than to a secondary migratory drive.

Ducks in disposition to migrate and triggered by suitable weather conditions may respond to a stronger migratory drive than to a stress motivation. When they possess a stronger migratory drive than stress tendency, ducks might orient southward immediately. Individuals not physiologically in a migratory state might pursue an escape drive heading until fear subsides and a suitable water area is found. Depending upon the suitability of the new habitat, the ducks may or may not remain in the new area until the migratory drive asserts itself.

Banding and waterfowl censuses have shown us that Mallards remain in Illinois much longer than do Blue-winged Teal. The individual Mallard remains about 21 days, the individual teal considerably less. Therefore, the Blue-winged Teal probably responds more readily than Mallards to migratory motivation; this may account for teal orienting southward more frequently than Mallards.

The frequent agreement between migratory movements of ducks in Illinois and their southern orientation lends credibility to the thesis that orientation direction is related to migratory disposition and weather conditions. As previously discussed, the evidence suggesting a relationship between migratory duck flights and southward orientation is fairly convincing for the Blue-winged Teal but less convincing for the Mallard.

ACKNOWLEDGMENTS

I am most grateful to Dr. H. W. Norton, University of Illinois, for the statistical consultation; to Mr. Philip Norton for processing the data; to the staff of the Digital Computer Laboratory of the University of Illinois for the use of their facilities; to Dr. William Hamilton, III, of the California Academy of Sciences and Dr. Klaus Hoffmann, Princeton University, who read the manuscript and made helpful suggestions; to Dr. Thomas G. Scott and Mrs. Wendy K. Patton, Illinois Natural History Survey, for their editorial assistance; to Mr. Robert Crompton and Mr. Howard Crum, Field Assistants, Illinois Natural History Survey, for trapping the ducks and providing zealous assistance in handling and releasing the birds.

SUMMARY

1. Releases of wild-trapped Mallards, Blue-winged Teal, Pintails, and Canada Geese were made from 1.6 to 153 (1 to 95 miles) from the trapping sites.

2. Most of the releases of ducks were made to the east and west of the Illinois River valley in areas of level farmland as devoid of trees, watercourses, and buildings as could be found in central Illinois. Canada Geese were released to the northeast and south of Horseshoe Lake in extreme southern Illinois where they had been trapped.

3. Waterfowl were released individually and flight paths of Mallards, Blue-winged Teal, Pintails, and Canada Geese were traced for 1.6 km (1 mile) or more. At night the flight paths of these birds were traced by attaching a pen-light device to one leg of each bird.

4. The flight behavior soon after release usually indicated whether a bird was oriented or disoriented. An oriented bird usually flew a fairly direct course; a disoriented bird usually flew a tortuous course. Under overcast skies, Mallards, Pintails, and Canada Geese flew about 25 per cent farther than they did under clear skies to reach the same point. However, Blue-winged Teal flew only 10 per cent farther under overcast skies than under clear skies.

5. Mallard flight headings under clear skies, both diurnally and nocturnally, embraced a span of about 50° between north–northeast and north–northwest. Under overcast skies, Mallard headings by day and by night showed no statistically significant direction when all the releases were combined.

6. Several releases of Mallards were made within sight of the lake where they had been captured. Yet when released only 2.4 or 4.0 km (1.5 or 2.5 miles) north of the lake, most birds persisted in flying northward headings away from the lake.

7. Released south of their "home" lake and near the trap site, most Mallards flew north over the lake until attracted to flocks of resting ducks. Two birds ignored even these resting flocks of Mallards and flew north across the lake until out of sight.

8. Mallards released south of two artificial lakes unfamiliar to them flew north over or near the lakes without being noticeably attracted to them. Two Mallards that alighted on one lake flew south when flushed later. This recalled an early experiment in which 26 Mallards of 210 released at the University Airport alighted on a pond two miles north of the release site. When flushed, they, too, flew south as a flock.

9. Blue-winged Teal also showed better orientation under clear than under overcast skies, but the difference was not as pronounced as for Mallards. The headings at night were much more uniform than those during the day. The headings under clear skies at night were to the northwest, about 35° to the west of those taken by Mallards.

10. Blue-winged Teal showed a greater tendency to fly southward than did Mallards. More southward movements occurred under overcast than under clear skies. Most, but not all, southward movements were associated with duck flights in Illinois. Headings to the south were more scattered than those to the north, but, nonetheless, southward headings were hardly the result of chance.

11. Pintails showed a directional grouping of flight paths under clear skies. The headings nocturnally were twice as uniform as those diurnally. The nocturnal mean heading of Pintails was 26° to the west of that taken by teal.

12. An increase in wind velocity and a drop in temperature during a release of Pintails under a heavy overcast sky apparently resulted in some of the birds orienting southward. A duck flight was observed 30 minutes after the last Pintails were released.

13. Canada Geese exhibited more compactly grouped directional headings when released under clear skies both by day and by night than under overcast skies. Their mean flight headings were to the southwest, some 78° south of the mean nocturnal heading of Pintails.

14. The initial fixed-direction flight of Mallards and Pintails was not parallel with either their fall or spring direction of migration. Blue-winged Teal in the autumn oriented in the reverse direction to their migratory direction at that time. Canada Geese initially flew in a direction similar to their southward migration.

15. On two occasions Blue-winged Teal, and on one occasion Pintails, apparently determined direction from only a few stars in Cygnus and Lyra. Because of haze and atmospheric absorptions, stars near the horizon would not be as visible to birds as stars in the zenith.

16. There was no relation between the initial flight heading taken by waterfowl and the location of their migratory or winter home.

17. The initial fixed flight direction taken by waterfowl under clear skies appears to be an important and characteristic behavior pattern which has survival value.

18. There is some evidence that the initial fixed-direction flight is only the first stage in determining the migration direction. Some birds have changed to a migration heading within a few miles or a few hours after release.

19. An innate response to celestial cues provides birds with the most expedient means of leaving an area of stress and still provides time and space for further cognizance of terrestrial and celestial cues. It seems apparent that birds would require more than a few seconds to determine their displacement from home or the proper direction of migration.

20. The initial flight headings in English Mallards deteriorated. Most of the birds were found weeks and even months later within 30 miles of the release sites. Mallard flight headings in Illinois did not show this deterioration, and band recoveries indicated a resumption of southward migration.

21. A few releases of ducks showed statistically significant mean southward headings under clear skies. Celestial cues probably account for the southward headings.

22. The variation in flight direction under clear skies may result from variations in the disposition of waterfowl to migrate and in the weather conditions which trigger migration.

23. The first drive of captured waterfowl may arise from stress which leads them in a direction entirely different from their migratory direction. After fear subsides, they may again come under a migratory motivation which returns them south in autumn. Under certain conditions, the migratory motivation may assert itself on or shortly after release.

LITERATURE CITED

BELLROSE, F. C. 1958a. Celestial orientation by wild Mallards. Bird-Banding, **24**: 75–90.

BELLROSE, F. C. 1958b. The orientation of displaced waterfowl in migration. Wilson Bull., **70:** 20–40.

DROST, R. 1949. Verkehrte Zugrichtungen als Beispiele einer "Zugscheu." Pp. 255–260 *in Ornithologie als Biologische Wissenschaft.* Heidelberg.

GOLDSMITH, T. H., AND D. R. GRIFFIN. 1956. Further observations of homing terns. Biol. Bull., **111:** 235–239.

GRIFFIN, D. R., AND T. H. GOLDSMITH. 1955. Initial flight directions of homing birds. Biol. Bull., **108:** 264–276.

KRAMER, G. 1952. Experiments on bird orientation. Ibis, **94:** 265–285.

MATTHEWS, G. V. T. 1953a. Sun navigation in homing pigeons. J. Exp. Biol. **30:** 243–267.

MATTHEWS, G. V. T. 1953b. Navigation in the Manx Shearwater. J. Exp. Biol., **30:** 370–396.

MATTHEWS, G. V. T. 1961. "Nonsense" orientation in Mallard *Anas platyrhynchos* and its relation to experiments on bird navigation. Ibis, **103:** 211–230.

NORTON, A. P., AND J. G. INGLIS. 1954. Norton's star atlas and telescopic handbook, 12 edit. London, Gall and Inglis. 55 pp. and maps.

SAUER, E. G. F. 1958. Celestial navigation by birds. Sci. Amer., **199:** 42–47.

SAUER, E. G. F. 1961. Further studies on the stellar orientation of nocturnally migrating birds. Psychologische Forschung, **26:** 224–244.

SAUER, E. G. F., and E. M. SAUER. 1955. Zur Frage der nächtlichen Zugorientierung von Grasmücken. Revue suisse de Zoologie, **62:** 250–259.

SAUER, E. G. F., AND E. M. SAUER. 1960. Star navigation of nocturnal migrating birds; the 1958 planetarium experiments. Cold Spring Harbor Symposia on Quantitative Biology, **25:** 463–473.

WALLRAFF, H. G. 1960. Does celestial navigation exist in animals? *Ibid.*, **25:** 451–461.

Illinois Natural History Survey, Urbana, Illinois.