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CELESTIAL ORIENTATION BY WILD MALLARDS

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Because waterfowl migrate long distances during both day and night it was concluded that they would make excellent subjects for investigation of celestial orientation in birds. From November 1956 to March 1957, wild Mallards (Anas platyrhynchos) were released during the day and night under various sky conditions, and their initial flight directions were recorded. An earlier release of Mallards at Champaign, Illinois, on November 13, 1952, provided supplementary data.

MATERIALS AND METHODS

The Mallards used in these experiments were wild-trapped in the Illinois River valley. Those taken during the fall were captured at the Chautauqua National Wildlife Refuge near Havana, Illinois, while those captured during the spring were trapped at Crane Lake, 25 miles south of Havana.

The majority of the Mallards trapped in mid-fall were considered to be in migration. Most of those trapped late in the fall were undoubtedly winter residents.

Thousands of recoveries from Mallards previously banded at the Chautauqua National Wildlife Refuge indicated a pronounced homing to that area during the fall migration. Therefore, it was thought that the ducks trapped there might return when released at a point away from the area.

Releases of Mallards were made from 11 to 95 miles east and west of the Illinois River valley (figure 1) on relatively level agricultural land. At most release points there were no water-courses or prominent landmarks for the Mallards to follow. Because large water areas were to be found mainly in the Illinois River valley, most of the released Mallards were required to fly there to find a suitable water area. A small number of the released birds did not fly at all or lit in fields within 1 mile of the point of release. For the most part, these were birds with wings which had become injured in trapping or handling. Birds that failed to fly 1 mile or more were excluded from consideration.

¹The writer was ably aided in this study by Robert Crompton, Field Assistant, Illinois Natural History Survey. Drs. Thomas G. Scott, William G. Starrett and the Editorial Committee of the Wildlife Research Section of the Survey reviewed the paper and helped materially.

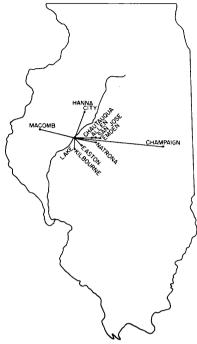


Fig. 1. The areas in which wild Mallards were released to test their orientation ability under clear and overcast skies by day and night.

Each bird was tossed into the air at random and observed with binoculars until out of sight. The course of each flight was plotted at least 1 mile on a diagram of concentric circles to provide for measurement of distance and straight lines every $22\frac{1}{2}$ degrees (figures 2, 3) for determination of direction. Because of the north-south and east-west alignment of roads and the grid-like 40-acre fields in the region, it was possible to chart the flight direction of each duck fairly accurately. At night, the passage of cars on two highways and the lights of farm houses were used to judge distance.

Releases of ducks were made at various hours of the day and night (Table I). A light was attached to the leg of each duck released at night in order to facilitate the recording of the direction of flight. This penlight device (figure 4) measured $2\frac{1}{2}$ inches in length and weighed about one-half ounce. It was attached with masking tape which disintegrated in water, thereby relieving the bird of this encumberance.

It was possible to observe a duck with a pen-light at night almost as well as during the day; the darker the night, the more readily the moving light could be traced. Under all nocturnal sky conditions, it was possible to observe lighted Mallards for at least 1 mile, and, on most occasions, for several miles.

The flight direction of each released duck was determined by the direction of a straight line from the release site to the point where the bird reached a distance of 1 mile.

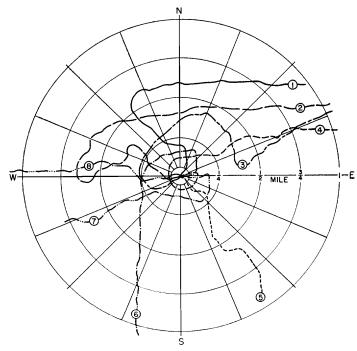


Fig. 2. The movement of 8 Mallards within a 1-mile radius of the release point at Allen Station under overcast skies, November 20, 1956.

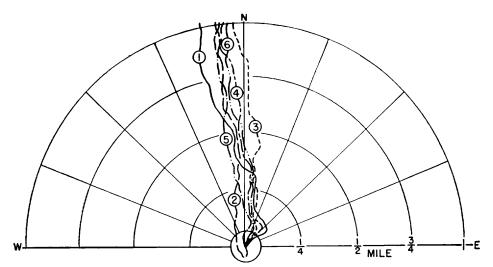


Fig. 3. The movement of 6 Mallards within a 1-mile radius of the release point near Easton, Illinois, under clear skies, January 10, 1957.

TABLE I

The initial direction of flight taken by wild-trapped Mallards transported

					APPEAL OF A Parameter and Association (ASS APPEAR AND ASS ASS ASS ASS ASS ASS ASS ASS ASS AS	Re	elation			
						to	Lake	Sam-	W	ind
Light	Sky				Release	Cha	utauqua	ple	Direc-	Velocity
Period	Conditions	Da	te	Hour	Point	Miles	Degrees	Size	tion	mph
Diurnal	Clear	1956								
		Nov.	13	4- 5 PM	Easton	11	314	28	\mathbf{s}	19
		Nov.	27	4- 5 PM	Natrona	22	294	18	\mathbf{S}	17
		Dec.	4	10-11 AM	Emden	28	285	25	\mathbf{s}	10
		Dec.	7	2- 3 PM	Macomb	33	100	16	NW	11
		1957								
		Jan.	10	1- 2 PM	Easton	11	314	21	NNW	13
		Jan.	10	4- 5 PM	Hanna City	25	202	15	NNW	8
		Jan.	18	11-12 N	Easton	11	314	8	W	11
		Feb.	1	2- 3 PM	Easton	11	314	9	NW	11
	Overcast	1956								
		Nov.	20	4- 5 PM	Allen Station	15	292	11	SSE	11
		Nov.	28	9-10 AM	Easton	11	314	12	WNW	16
		Nov.	28	2- 3 PM	San Jose	25	276	13	WNW	17
Nocturnal	Clear	1956								
		Nov.	27	7- 8 PM	Easton	11	314	4	s	17
		Dec.	3	8- 9 PM	Easton	11	314	12	ESE	7
		1957								
		Jan.	18	8- 9 PM	Easton	11	314	11	SSW	8
		Feb.	14	8- 9 PM	Kilbourne	12	180	6	E	8
		Mar.	13	9-10 PM	Easton	11	314	5	\mathbf{S}	15
	Overcast	1956								
		Nov.	26	7- 8 PM	Easton	11	314	5	NNW	13
		Nov.	28	7- 8 PM	Easton	11	314	6	NNW	17
		Nov.	29	7- 8 PM	Easton	11	314	10	ssw	8
		Dec.	17	8- 9 PM	Easton	11	314	5	NW	15

TABLE I (continued)

from Lake Chautauqua to areas 11 to 33 miles distant, November 1956-March 1957

	The second seco	Perc	centage	e of Du	cks T	aking l	Particu	ılar Dir	ection	s (Deg	rees)	of Flig	ht		
221/2	45	$67\frac{1}{2}$	90	$112\frac{1}{2}$	135	157½	180	2021/2	225	2471/2	270	2921/2	315	3371/2	0
7.1	7.1											3.6	10.7	17.9	53.6
												5.6	22.2	44.4	27.8
12.0	4.0												8.0	52.0	24.0
12.5													6.3	56.2	25.0
		4.8												47.6	47.6
	6.7												13.3	46.7	33,3
			12.5			•			12.5				12.5	37.5	25.0
33.3													11.1	44.5	11.1
	9.1	97.9	0.1	0.1		10.0		0.1		0.1	0.1				
	9.1	27.2	9.1	9.1		18.2		9.1 8.3	16.7	9.1 16.7	9.1 8.3	8.3	41.7		
	15.4	7.7	7.7		7.7		15.4	7.7	7.7	10.7	15.4	0.0	41.7	7.7	7.7
	10.4		1.1		1.1		1.7.4	1.1	1.1		10.4				1.1
															100.0
												8.3	33.3	41.7	16.7
												0.0	00.0	**	10.1
36.4	18.2													9.0	36.4
												16.7	33.3	50.0	
														40.0	60.0
	20.0	20.0		20.0			20.0	20.0							
	16.7						16.7				32.2		16.7	16.7	
20.0	10.0	10.0	10.0			10.0					10.0	10.0	20.0		
20.0	20.0			20.0		20.0	20.0								

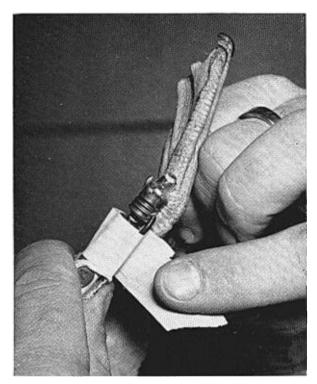


Fig. 4. The pen-light, attached to the Mallard's leg by masking tape, was used to trace the flight at night.

The length of the flight within 1 mile of the release point was recorded by using a map measurer to trace the flight pattern.

Data were obtained in flights of 240 Mallards, released on 20 occasions (Table I). Most of the releases were made under four sky conditions: (1) diurnal with clear skies; (2) diurnal with overcast skies; (3) nocturnal with clear skies; and (4) nocturnal with overcast skies. Additional releases of ducks were made under changing sky conditions or when the birds had been held captive for lengthy periods; these conditions produced certain variables in the data, and are, therefore, discussed separately.

OBSERVATIONS

Celestial orientation by wild mallards was apparent in the data (Table I). Directional grouping of flights was more evident under clear skies than under overcast skies (Table II). The chi-squares for observations made under clear conditions were highly significant for grouping; the chi-squares for observations under overcast conditions showed no significant directional grouping of flights. Figures 2 and 3 show examples of the movement of individuals under clear and overcast skies during the day.

TABLE II The chi-square values of the directional grouping of Mallards made from unfamiliar places in central Illinois under clear and overcast skies, November 1956 to March 1957.

Light Period	Sky Condition	Number of Observations	Chi-Square*
Diurnal	Clear	140	496.3
	Overcast	36	12.4
Nocturnal	Clear	38	85.9
	Overcast	26	12.7

^{*}With 15 degrees of freedom, in each case. Values exceeding 37.7 are significant at the level of one in one thousand.

Under overcast skies, the initial directions of flight for all birds released showed almost a random movement for both day and night (figure 5).

Under clear skies, during day and night, Mallards from all releases exhibited a marked proneness to fly to the north and northward (figure 6). Data from release points east of the Illinois River valley at Easton, west at Macomb, and north at Hanna City (Table I) show the same directions of flight toward the north and northwest.

Time of day, although not completely explored, appeared to have no effect upon the initial flight headings of the Mallard (Table I). If the released birds determined direction in relation to a fixed angle to the sun, then the direction of flight would shift with the changing position of the sun. The direction of flight proved to be consistent whether releases were made in midmorning or in late afternoon, thus indicating that the Mallard has a capability of correcting for or ignoring the changing position of the sun.

The direction of the wind at low to moderate velocities (Table I)

had little influence on the flight headings of the Mallards.

Over a period of months (Table I), Mallards released under clear skies followed the same general northward flight. When the ducks released in mid-fall flew north, it was suspected that those released in the spring might fly south. However, there was no reversal in flight direction in the spring.

The presence or absence of a moon had no effect upon the northward orientation of ducks at night. On the clear nights of November 27 and December 3, 1956, there was no visible moon (Table I), while the moon was approaching fullness on January 18, February 14, and March 13, 1957. On all of these nights, with constellations visible, Mallards oriented northward (Table I). On the night of December 17. a high overcast blotted out most constellations, but the moon was sufficiently strong to shine brilliantly through the clouds. Nevertheless, the Mallards which were released that night flew in diverse directions.

Partly cloudy skies during the day had a disorienting effect upon the released Mallards only when the sun was temporarily obscured by clouds (Table III). When the sun was visible the birds oriented northward, but within moments after its disappearance behind a cloud, the released mallards began to fly in a disoriented manner.

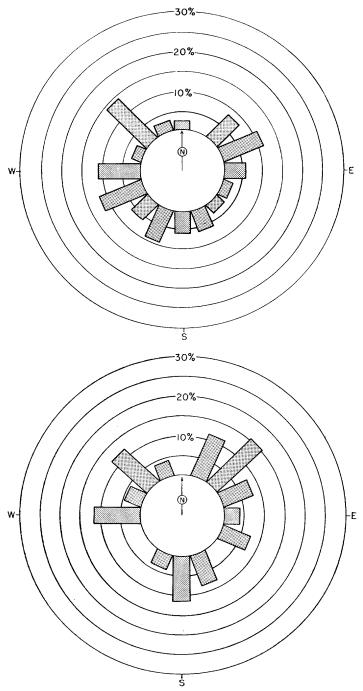


Fig. 5. The initial flight direction of all Mallards released under overcast skies during (a) day and (b) night.

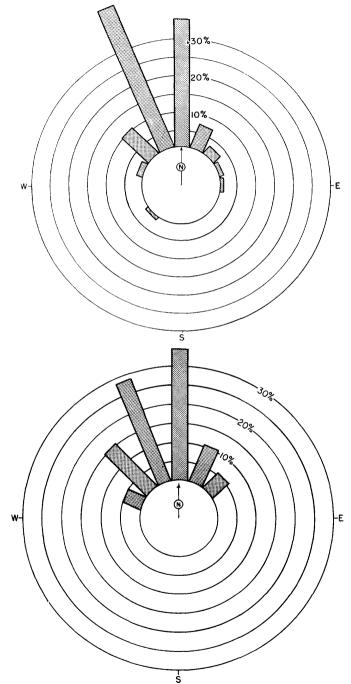


Fig. 6. The initial flight direction of all Mallards released under clear skies during (a) day and (b) night.

TABLE III

The effect of a temporarily obscured sun on the orientation of Mallards released in unfamiliar areas,
November 15, 19, and December 5, 1956.

	Sun V	isible	Sun Obscu	ıred
Direction of Flight	Number of Observations	Per Cent	Number of Observations	Per Cent
0	11	38.0	2	8.3
$22\frac{1}{2}$	4	13.8	4	16.6
45	6	20.7	5	20.8
$67\frac{1}{2}$			1	4.2
90			ī	4.2
$112\frac{1}{2}$			ĩ	4.2
135				
$157\frac{1}{2}$				
180			3	12.5
$202\frac{1}{2}$	2	6.9	1	4.2
225				
$247\frac{1}{2}$			1	4.2
270				
$292\frac{1}{2}$	1	3.4	1	4.2
315	2	6.9	2	8.3
$337\frac{1}{2}$	3	10.3	$\frac{2}{2}$	8.3
Totals	$\frac{\overset{\circ}{2}}{\overset{3}{29}}$	$\overline{100.0}$	$\overline{24}$	100.0

It was not always possible to trap Mallards for immediate release during desired weather conditions. For long periods during late fall and early winter, 1956-1957, there were few breaks in the overcast skies. Consequently, some ducks were held in captivity for several weeks awaiting clear skies.

Mallards which had been confined for several weeks were released on two clear days, December 26 and 27, 1956; the birds flew in diverse directions (Table IV). This loss of ability to orient was at first attributed to the prolonged period of captivity under cloudy con-It was assumed that wild Mallards also experienced the same prolonged overcast, but releases of month-long captive Mallards and recently-trapped ducks on January 10, 1957, showed marked differences in orientation between the two groups; the long-term captives flew in several directions, the short-term captives flew in northward direction. A release on February 12, a clear day, using Mallards trapped on January 8, again showed a disoriented response. The directional distribution of four releases of month-long captive Mallards showed (Table IV) a greater spread in choice of directions than that of short-term captives (Table I). Nevertheless, even under prolonged captivity, the northward sector of the compass was selected more frequently than the southward sector.

Upon release, almost every Mallard moved its head from side to side, as if trying to locate its whereabouts. For the first one-fourth to one-half mile most ducks usually flew low, about 50 feet, rising thereafter to a height of 500 to 700 feet by the time they were 1 mile away. In some instances, Mallards reached altitudes of 1,000 to 1,500 feet while still visible.

TABLE IV

The direction of flight taken by Mallards after prolonged captivity when released under clear skies, on December 26, 27, 1956,

January 10, and February 12, 1957.

Direction of Flight	Number of Observations	Per Cent
0	2	7.1
$22\frac{1}{2}$	1	3.6
45	2	7.1
$67\frac{1}{2}$	$rac{4}{2}$	14.3
90	2	7.1
$112\frac{1}{2}$		
135		
$157\frac{1}{2}$		
180	1	3.6
$202\frac{1}{2}$		
225	1	3.6
$247\frac{1}{2}$	2	7.1
270	2	7.1
$292\frac{1}{2}$	4	14.3
315	4	14.3
$337\frac{1}{2}$	3	10.7
Totals	$\overline{28}$	$\overline{100.0}$

On both cloudy and clear days, it was noticed that many ducks altered their line of flight to follow roads or fencerows for short distances. The many right-angled turns recorded on the individual flight charts (figure 2) are evidence of the temporary influence of such features.

Most ducks which took a northward direction on a clear day or night did so almost immediately upon release even when tossed into the air in a southward, eastward, or westward direction. Some flew south 100 yards, more or less, before doing an abrupt about-face and flying north almost directly over the observers.

It was quite evident that when a duck was confused, usually under cloudy conditions, it flew a zigzag or spiral-type search pattern similar to that outlined by Griffin (1955:175). For example, a duck might fly one direction for one-fourth to one-half mile, then change its course to another direction for a like distance before changing direction once again. Not infrequently, under cloudy conditions, a duck returned, flying in the opposite direction over the release point.

TABLE V

The observed distances flown by Mallards from a release point to the periphery of a circle with a 1-mile radius.

Light Period	Sky Condition	Number of Observations	Average Number of Miles
Diurnal	Clear	140	1.26
	Overcast	36	2.26
Nocturnal	Clear	38	1.17
	Overcast	26	1.60

Differences in flight patterns of Mallards under clear and cloudy skies have been compiled on the basis of the distance flown to reach a point 1 mile from the release point (Table V). The greater length of the zigzag or spiral pattern under cloudy conditions as compared to the more direct flight pattern under clear conditions is quite evident.

The average distance flown by Mallards released under overcast skies during the day was 1 mile farther than for ducks released under clear ones. At night, the distance flown averaged almost 0.5 mile

longer under overcast skies than under clear ones.

An experiment, conducted with wild-trapped Mallards on November 13, 1952, was the first indication of this species' propensity to orient northward under clear skies. These ducks were released in 7 groups of from 15 to 40 birds each at the University of Illinois airport, near Champaign, Illinois. They had been trapped a few days previously at the Chautauqua National Wildlife Refuge, near Havana, Illinois, about 95 miles west of the release point.

The 7 releases were composed of groups of adult drakes, juvenile drakes, and hens of unknown age. The experiment was undertaken to determine if small flocks of ducks could be followed on a radar scope. An effort was made to follow the birds on a radarscope and by observers on a tower and in an airplane for the purpose of comparing the effectiveness of the methods.

When the ducks took flight, they headed north as a flock. Each flock flew as a unit for 4 miles, the flocks then disbanding into smaller groups or singles as they approached within 0.25 mile of a radio transmitter.

Individuals from each release were observed in northward flight for several miles (figure 7). Ducks from two releases were followed north by plane for as far as 10 miles.

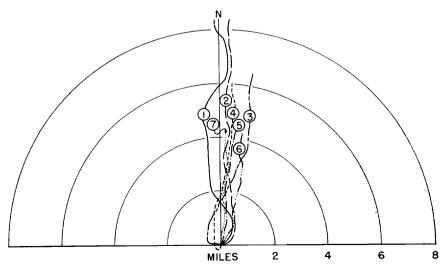


Fig. 7. The distance and direction flown by seven groups of Mallards followed by means of an airplane from the University of Illinois airport, November 13, 1952.

Several band recoveries were received from these ducks within the week following their release. One duck was shot 20 miles north of Champaign and several others were shot during the next few days at unspecified places in Champaign County. Only one bird was reported back in the Illinois River valley; it was killed 7 days after release, near Bluffs, Illinois, some 150 miles west-southwest of Champaign.

Other band recoveries from these Mallards indicated that they moved southward along customary flight lines to their wintering grounds in Arkansas and Louisiana.

DISCUSSION

When released in unfamiliar places, it was apparent that the Mallards used the sun during the day and the stars at night as a means of orienting northward. Clouds might cover up to 70 per cent of the sky, but if the sun were visible, Mallards were still able to orient themselves. When the sun became obscured even for only a few minutes, the Mallard's orientation ability began to deteriorate.

In similar field experiments in England, Matthews (1953a, b) found that Homing Pigeons (Columba livia) and Manx Shearwaters (Procellaris puffinus) used the sun for determining their initial flight headings. Griffin and Goldsmith (1955) reported that Common Terns (Sterna hirundo) also used the sun for flight orientation.

Many experiments performed under laboratory conditions by Krammer (1952) in Germany demonstrated that several species of passerine birds used the sun for determining direction. In the United States, von Saint-Paul (1956) conducted similar experiments with the Western Meadowlark (Sturnella neglecta) and concluded that it used the sun for finding directions.

At the time of our experiments with the nocturnal orientation of Mallards, we thought that this was the first demonstration of the possible use of stars by birds to determine direction at night. Subsequently I learned from Dr. J. J. Hickey that Sauer and Sauer (1955), in Switzerland, had reported evidence of celestial orientation in birds at night. They hand-reared several Garden Warblers (Sylvia borin) and Blackcaps (Sylvia atricapilla), and placed them in a circular cage. On starlit nights in the fall, these birds oriented toward their normal migration direction of SSW to SW. When clouds approached, the warblers' movements became uncertain, and, when the sky was completely overcast, they became disoriented. However, when the moon was visible, the birds gave up their normal flight direction and flew toward it.

After the manuscript for this paper had been completed, we learned of a further paper (Sauer, 1957; reviewed in *Bird-Banding*, **29**(1): 49-50, January, 1958) on celestial navigation in Old-World warblers. "Garden Warblers, Blackcaps and Lesser Whitethroats possess a mechanism of migration orientation which enables them, independently of local topography and of their individual experience, to determine, with the help of their ability to assess time, their specific course of migration while steering by the starlit sky. For the functioning of the mechanism, it is sufficient that the bird is able to see sections of the starry sky. Azimuth and the declination of the star pattern are im-

portant for the functioning of the migration orientation by astronaviga-

On clear nights with and without a moon, released Mallards flew northward. On nights with the stars obscured by a light overcast but with the moon visible, Mallards did not orient toward it, or to any particular direction. It, therefore, seems evident that Mallards used the stars to determine their direction of flight. At present it is conjectural as to the star, the constellation or constellations used by the Mallards. It seems logical to suppose that circumpolar constellations would be employed because they are the only ones continuously above the horizon, not only through the night, but every night of the year. Other constellations rise and set during the night, and appear and disappear as the seasons progress.

Because Mallards flew northward under clear skies, regardless of the direction of their release from the Illinois River valley, they may be considered to possess a one-direction type of orientation. However, the Homing Pigeon and Manx Shearwater according to Matthews (1953a, 1953b, and 1955) are able to use a biocoordinate system of orientation to determine a homeward direction regardless of the direction of release.

The Common Terns studied by Griffin and Goldsmith (1955:275) were like Mallards in exhibiting a one-direction orientation when the sun was visible, but the direction selected by the terns was southeasterly rather than northerly. These workers suggested that the southeasterly flight might serve to bring the birds back to the Coast "after any excursion inland from their normal range."

Such a hypothesis, of course, does not apply to the Mallard. At the time of the releases in November, Mallards were in southward migration; later releases, in December and January, took place when the Mallards were wintering and more or less non-migratory; and the releases in March occurred when Mallards were migrating northward. Irrespective of the stage of migration, released Mallards oriented northward in initial flight headings.

From observations and band recoveries of Mallards released in November 1952 in Champaign County, there was evidence that the birds flew northward until they reached a suitable body of water where they came to rest. Subsequently, as shown by band recoveries, they migrated southward in a normal manner.

Why Mallards orient northward initially is a moot question. Possibly there is an innate desire on the part of a Mallard under duress to head toward its basic home, namely, the area where it was reared.

Perhaps there is some relationship between the northward orientation of Mallards and that reported for Homing Pigeons. Kramer et al. (1956) found that Homing Pigeons homed better from the south than from any other direction. In these experiments Homing Pigeons were taken at varying distances from their home loft in Durham, North Carolina, and released simultaneously at the cardinal points of the compass around Durham. Those pigeons released to the south of Durham returned home faster and in greater numbers than those released to the north, east, or west.

SUMMARY

- 1. From November 1956 to March 1957, we tested the ability of wild-trapped Mallards to orient themselves under various sky conditions during the day and night. The birds were released over agricultural lands at distances of 11 to 33 miles from their haunts in the Illinois River valley.
- 2. The initial flight directions taken by individual Mallards were charted for 1 mile or more. At night the course of flight was followed by observing a pen-light attached to the duck.
- 3. Data were obtained on 240 flights of Mallards released on 20 occasions under 4 basic sky conditions: (1) diurnal with clear skies, (2) diurnal with overcast skies, (3) nocturnal with clear skies, and (4) nocturnal with overcast skies.
- 4. The initial flight headings of recently-trapped Mallards were to the north and northwest when the birds were released under clear skies, day or night.
- 5. The initial flight headings of recently-trapped Mallards were more or less at random when the birds were released under overcast skies, day or night.
- 6. Time of day, low to moderate wind velocities, wind direction, and season were factors which did not affect the northward orientation of Mallards under clear skies.
- 7. The presence or absence of a visible moon had no effect upon the directional orientation of ducks at night. On clear nights, with or without a moon, Mallards flew northward. On a night when the constellations were invisible but the moon was quite visible, the ducks flew in diverse directions.
- 8. Obscuring the sun, even temporarily by clouds, resulted in the disorientation of many released Mallards.
- 9. Mallards which had been held in captivity a month or more tended to lose their ability to orient northward even on clear days.
- 10. Upon release, Mallards usually flew about 50 feet above the ground for the first 0.25 mile, and rose to a height of 500 to 700 feet by the time they were 1 mile from the release point. In some instances, ducks reached a height of 1,000 to 1,500 feet while still visible.
- 11. Under overcast conditions, Mallards invariably flew a circuitous flight course, approaching either a zigzag or spiral search pattern. This resulted in birds flying about 1 mile farther on overcast days and one-half mile farther on overcast nights than on clear ones to reach a point 1 mile from the release site.
- 12. Seven groups of 15 to 40 wild-trapped Mallards which were released on November 13, 1952, at the University of Illinois airport, near Champaign, flew in a northward direction for 4 to 10 miles. Band recoveries indicated that some of these ducks landed on water areas in Champaign County, and later recoveries indicated a normal southward migration to Arkansas and Louisiana.
- 13. There is no known reason for the northward orientation of the Mallard, but it is speculated that it may relate to the area in which it was reared.

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LEG SIZES AND BAND SIZES: THIRD REPORT

By Charles H. Blake

Introductory

If some excuse is needed for a third report on this subject, it may be grounded on the large number of additional species (nearly the total of the first two reports), some data now presented on subspecies, a further consideration of the tentative conclusions of the second report, or on an apparent relation between maximum weight and tarsal cross-section.

Many of the birds in the present report are West Indian. Descriptions and common names may be found in Bond (1936 or 1947) and distribution of the particular subspecies mentioned will be found in Bond (1956a).

As before, I am indebted to others for help in accumulating data used here. Mr. and Mrs. Parker C. Reed and Mr. and Mrs. James R. Downs have given continued assistance. Principal John H. Parry of the University College, Ibadan, Nigeria, formerly at the University College of the West Indies, Jamaica, not only added to the Jamaican data but secured a number of measurements in California.

The table of data (Table I) differs from my earlier tables in omitting the range of the measurements. The observed ranges seldom exceed 2 σ each side of the mean. The 99 percent range can be readily calculated from the span given in Blake (1954, p. 12). The band sizes given are the majority band size and the next most frequent size. Proportions of other band sizes are calculable by those interested.

Scientific names have been used throughout as being less confusing than common names, especially for the West Indian species, and showing the relationships more clearly. The use of common names for