

CELESTIAL ORIENTATION IN JUVENAL WATERFOWL

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Seasonal passage of waterfowl throughout the temperate regions of North America is well documented by field observations and banding studies. Cooch (1955) conclusively demonstrated that the main autumn flight of Blue Geese (*Chen caerulescens*) from James Bay to Louisiana, over 1700 miles, was accomplished in less than 60 hours, possibly without a stop. Observations of exceptionally heavy migrations during brief periods in the fall (Bellrose, 1957) demonstrate that other species of waterfowl traverse great distances in a single flight. These flights in all probability encompass a period of daylight and darkness indicating that orientation mechanisms must be operative both during the day and at night.

The cues guiding these flights of passing waterfowl have been the subject of considerable speculation and discussion in recent years. Hochbaum (1955) has clearly shown that the topographic configuration of the surface of the earth channels the flights of waterfowl, at least in certain areas. These observations in themselves do not, however, give evidence that features of the terrain establish the basic course of flight but only that passing birds respond to topography. The possibility that topographic configuration plays a secondary role was recognized long before we had any conclusive evidence that celestial orientation among birds was a reality. Lucanus (1922) stated this possibility, and Schenk (1924) suggested that some means of maintaining a fixed flight direction was "primary," whereas responses to visible terrestrial landmarks might be "secondary."

Recently Bellrose (1958b) reported that Mallards (*Anas platyrhynchos*) and other species of waterfowl (Bellrose, in press) captured along waterways of central Illinois and released in open fields nearby take a predictable course away from the point of release. For the Mallard the course is northerly. Using small lights attached to the legs of Mallards, Bellrose was able to establish that this response was directionally the same at night as during the day. The response persists unchanged in the period of normal spring and fall migration. This northerly trend is only manifest under clear skies, either during the day or at night. Under overcast skies, flights scattered. It seems implicit that celestial cues are involved in the orientation process.

These findings for waterfowl are in general agreement with a considerable body of experimental evidence for various other species of birds. Under experimental conditions that test spontaneous migratory orientation, and for birds in free flight returning to a familiar area, the correlation persists, that is, oriented behavior is observed under clear skies, whereas disoriented behavior occurs when skies are completely overcast. For spontaneous migratory activity during the day this correlation has been established for the Starling, *Sturnus vulgaris* (Kramer, 1952), and at night for three species of European garden warblers, *Sylvia atricapilla*, *S. borin*, *S. communis* (Sauer, 1957) the White-crowned Sparrow, *Zonotrichia leucophrys* (Mewaldt and Rose, 1960), and the Bobolink, *Dolichonyx oryzivorus* (personal observation). The Starling can respond differentially on the basis of the sun's position or to an area of sky of something under 45° on either side of it. Direct visibility of the sun itself is apparently not necessary (Kramer, *op. cit.*).

For birds in free flight, homeward orientation during the day under clear skies has been established for the homing pigeon, *Columba livia* (Kramer, 1952; Matthews, 1953a), and Manx Shearwater, *Procellaria puffinus* (Matthews, 1953b). Other species seem to respond in a manner similar to that reported by Bellrose (1958b), that is, they take a fixed course under clear skies. Under clear daytime skies this response is made

by the Common Tern, *Sterna hirundo* (Griffin and Goldsmith, 1955), but as yet there has been no report of effective night orientation by birds in free flight other than the observations made by Bellrose. To date there has been no demonstration of initial homeward orientation by any species at night.

Sauer (1957) and Sauer and Sauer (1959) demonstrated conclusively that Garden Warblers can use the stars to tell direction. Confirming evidence came from studies using the artificial stars of a planetarium. The experimental birds could use this artificial sky to tell direction in the absence of the moon and planets. In fact, when the moon was present in the natural sky, appropriate migratory orientation failed and the birds took up a position facing the moon or the side of the apparatus lighted by it. In Bellrose's experiments with free flying Mallards, orientation persisted on clear nights with or without the moon. With thin overcast obscuring the stars but permitting the moon to shine through, orientation failed. The body of this evidence, then, suggests that for a number of species of birds the stars are the orienting cues in the night sky.

This paper reports experiments designed to test the orientation of species of migratory ducks under various sky conditions and to establish what use ducks might be able to make of celestial cues in determining direction. Ducks are particularly suitable subjects for such experiments since they are easily held in captivity, they learn to respond to a reward rapidly, and they are active or can be induced to become active during the day and at night.

METHODS

The general plan of experimentation was to train birds to choose a reward in a particular compass direction. This method of studying orientation capacity has been used by Kramer (1952) with Starlings and von Saint-Paul (1956) with Western Meadowlarks (*Sturnella neglecta*). The birds were trained to find a food reward in a rubber cup. In these earlier studies training was confined to a certain time of day, whereas tests were made at other times. This method of rigorously timed training allowed Hoffmann (1954) to investigate the role of the internal clock and its part in the celestial orientation process. The goal of the present investigation was to determine orientation capacity throughout the day and night, taking advantage of the comparatively flexible feeding schedule of ducks. For this reason a rigid time training was not employed and the birds were permitted to feed and drink through the day. Tests were made by depriving the birds of water for some time in advance of the test time.

The birds used in experiments were Pintails (*Anas acuta*), Blue-winged Teal (*Anas discors*), and a single Green-winged Teal (*Anas crecca*). All were reared from eggs laid by wild birds within a few miles of the Delta Waterfowl Research Station at Delta, Manitoba, Canada. The eggs were hatched in incubators at the station. When the birds were approximately 24 hours old they were transferred to the test cage and held in this environment until the time of experimentation.

Description of the apparatus.—The experimental apparatus consisted of a circular cage with open top and a central floor 125 cm. in diameter. The surrounding vertical wall, 73 cm. high, had 12 evenly spaced doors. Preliminary tests indicated that a water reward would be more effective than a food reward. The water source was hidden from the birds by a vertical screen and to see this water the duck had to pass through a door and peer around the screen. An opaque circular screen was placed around the cage to block visibility of all landmarks and any other visual orienting features of the environment near the horizon. The top was left uncovered. From the eye level of a bird in the apparatus, a view subtending approximately 90° of the sky remained.

Standing directly against one wall of the apparatus a bird could see to within 15 degrees of the horizon. The general plan of the apparatus is shown in figure 1.

Training and testing methods.—Training of birds to respond to the test situation was continuous from the time they were originally placed in the test apparatus. The food dish was left in position in the center of the test arena. In initiating the training cycle a dish of water was placed at the edge of the arena in full view of the birds. Soon

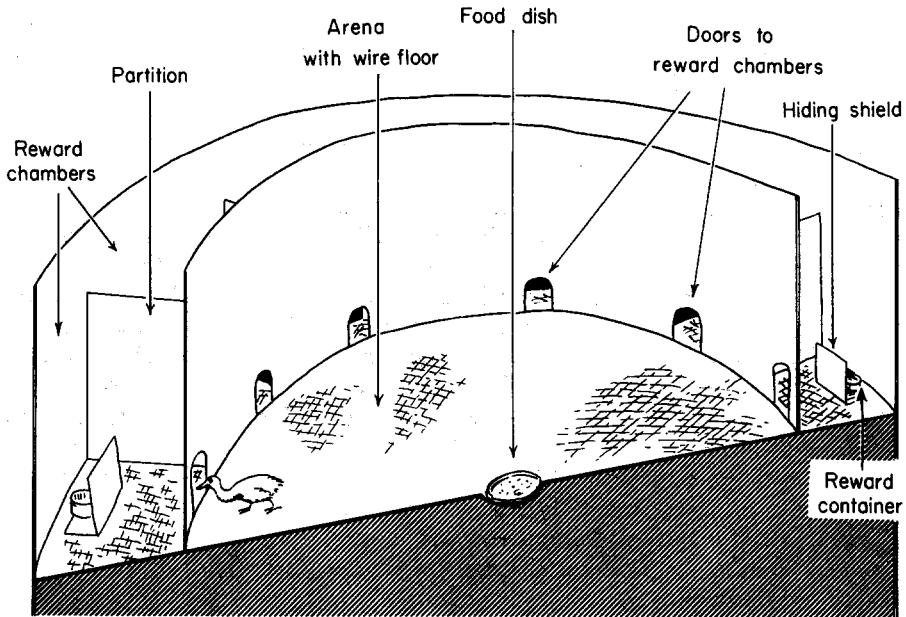


Fig. 1. Cross section of the experimental apparatus. See text for a complete description.

the birds were using both containers freely, feeding and then moving to the water dish to soften the dry food. As soon as the birds were well adjusted to this routine, the water dish was shifted to a compartment. From this stage on in the training cycle the compass direction of the water source was held constant.

Throughout the period of training and testing, the apparatus was rotated before the doors were opened. All parts of the apparatus visible to the experimental birds rotated, including the vertical walls, compartments, and the bottom of the apparatus. During the later stages of training, the doors were raised simultaneously by a draw-string arrangement from below. The observer watched through a small opening in the opaque bottom of the cage. The observer's compartment was darkened so that movement could not easily be detected by the birds above him (fig. 1).

When the birds were three weeks old, critical tests were initiated. Only one test period was possible per day. Prior to a test the doors were closed and the food supply left in place. Just before the test the birds were removed from the test arena and placed in a large holding crate.

The original plan called for the return of the birds to the test arena one by one as a test of their ability to locate the water source. But when a bird was placed in the arena alone, it stood in place, continuously uttering the "lost" call and usually refused to make any choice when the doors were opened. Occasionally a bird in this situation

would dash about blindly, pushing its head and neck into several compartments in rapid succession but quickly returning to the central arena. It seemed obvious that the bird was searching for another duck, not water. To remedy this situation birds were tested in pairs. Two birds were placed in the arena together and the choice of the first bird to pass its bill through any door was recorded. The usual behavior of the second bird was to follow closely behind the leader, entering whichever door the leader chose. No score was recorded for the second bird but it was allowed to remain and drink with the leader if the leader made a correct choice. Some individuals were quite consistent followers and were used more than once during a test session as "dummies," particularly with the strongest leaders.

When the birds were placed in the test situation, the experimenter retired to the observation site and waited 90 seconds before opening the doors. If the birds then made a correct choice they were allowed to remain until they had satisfied their thirst and returned to the arena. If the initial choice was incorrect, a second choice was allowed. If this choice, too, was incorrect, all doors were closed as soon as the birds returned to the arena. The birds were allowed to remain in the central arena 10 minutes and were then returned to a holding cage without water. These unsuccessful birds were repeatedly tested later in the test period until they made a correct choice. Occasionally it was necessary to provide a water reward in all compartments to avoid discouraging unsuccessful individuals from making any choice at all in subsequent tests.

The 10-minute waiting period following unsuccessful choices was used to avoid immediate disturbance following choices. The ducks used in these tests were all first generation birds from wild parents, and in spite of continued handling throughout the experiments they never became truly tame and fearless. The opening and closing of the doors caused considerable excitement, and when birds were removed from the apparatus immediately following unsuccessful choices, they soon became reluctant to make any choice in later tests.

The criterion for a choice was the movement of the bill through a door. The bird shown in figure 1 has arrived at this point in the experiment. Occasionally a bird would back out at this point, but it was necessary for the bird to move considerably farther into the compartment to determine presence or absence of water. Occasionally the two birds made simultaneous and different choices. The small number of such results have been eliminated from the data presented here.

Experimental birds.—Pilot experiments were conducted in the summer of 1956 with Pintails at the Delta Waterfowl Research Station. In subsequent research Blue-winged and Green-winged teals have been used. These latter species are better suited to this line of experimentation because of their small size. The Pintails outgrew the test apparatus soon after the initiation of critical tests. Pintails are particularly poor subjects because of their long necks. By standing fully erect and stretching they eventually could see out of the apparatus, thus defeating the purpose of the elaborate precautions taken to limit the visual experience of test birds.

In the summer of 1957 tests with Blue-winged Teal were initiated at the Delta Waterfowl Station with birds trained to an easterly direction. The same birds, reared in the test apparatus at Delta, were subsequently taken to Berkeley, California, and in 1958, they were retrained to find the reward in the west. Critical tests were continued through the spring and fall of 1958. An attempt to retrain the birds to the south in the spring of 1959 failed because of the wildness of the birds. The tests at Berkeley were made with the test apparatus situated on the top of the Life Science Building at the University of California.

Tests under clear skies were confined to those periods when the sun was directly visible to the birds and no large part of the sky was covered by clouds. Tests on overcast days were confined to those periods when the sky was completely shrouded and neither blue sky nor light spots in the sky were visible. The outline of the sun or its location was not discernible to the observer.

RESULTS

Preliminary tests with Blue-winged Teal indicated that if the deprivation period was held constant prior to all tests, sharp differences in performance resulted in the course of the day. The performance in the middle of the day showed exceptionally wide scatter, and often at that time some individuals were reluctant to make any choice at

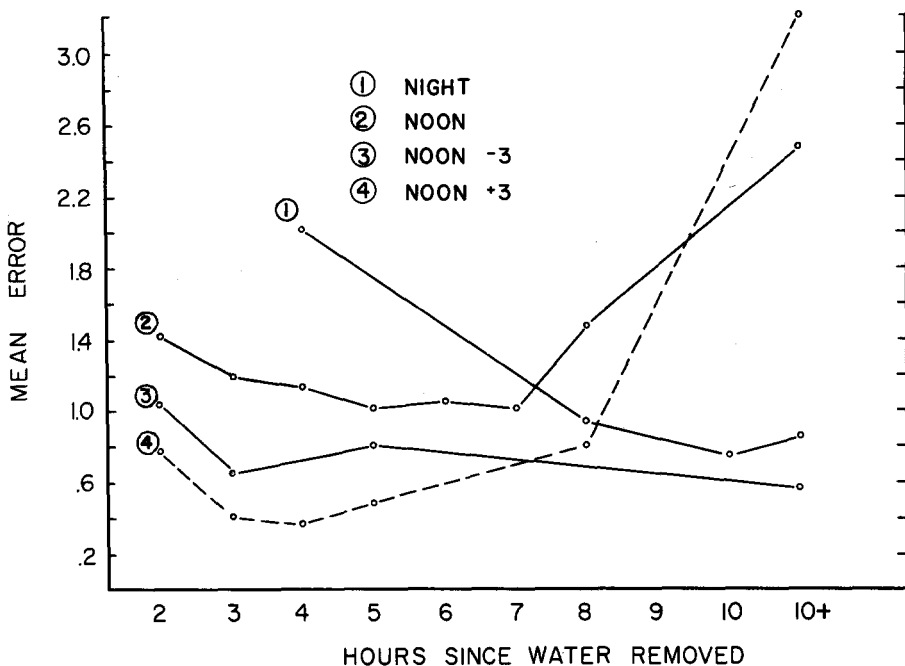


Fig. 2. Variation in orientation performances according to duration of deprivation. The numbered curves indicate results in relation to the times of various tests. A mean error of 3.0 indicates a chance performance; lower scores denote increasingly accurate choices.

all. It seems possible that the uniform period of deprivation might have a varying effect at different times of day. In order to determine whether such an interpretation would explain variation in performance, a series of tests was made to determine what might be the most effective period of deprivation. The results of these experiments are summarized in figure 2. The minimum period of deprivation tested was two hours. From the training schedule it was clear that periods shorter than two hours would not be effective in eliciting immediate responses. Each point on the graphs for daytime tests, presented in figure 2, represents the average of 10 tests made in August and September, 1957. Periods of deprivation including an overnight period are designated as 10+.

The earliest daytime tests possible with direct visibility of the sun were in the period from 3½ to 2½ hours before the culmination of the sun. Accuracy during this time improved as the preceding, early morning deprivation period was lengthened. If the period of deprivation was initiated in the late afternoon of the previous day (10 + hours in fig. 2), accuracy remained about the same as for maximum early morning deprivation. Midday tests were most effective when deprivation was initiated the previous evening or before the earliest morning activity. Deprivation initiated later showed an increased scatter of choices. This increase in scatter was correlated with an increasingly erratic behavior of the birds. As soon as the doors were opened, the birds would dash through one. This contrasted with the slow and apparently calculated choices resulting under other circumstances seemingly more favorable to accurate orientation.

For afternoon tests the same general result was obtained except that optimum performance resulted from lesser periods of deprivation. For all subsequent tests the period of deprivation giving the most accurate performance was adopted. For night tests this duration was about 10 hours. Early morning tests were set up about 3 hours in advance, midday tests 5 to 7 hours ahead of time, and afternoon tests 3 to 5 hours in advance. However, these optimal durations could only be approximated since testing took from two to four hours for completion.

When birds were in the apparatus, feeding and drinking usually ended about an hour after local sunset. The duration of deprivation before night tests (fig. 2) was taken from this time rather than from the actual time of tests. The 10 + hour category for night tests, therefore, refers to tests initiated more than 10 hours before the normal termination of activity in the evening. But in no instance was the duration of deprivation extended to the previous evening.

Periods of deprivation which had been sufficient to elicit a correctly oriented response during the day were ineffective at night, and it was necessary to initiate water deprivation early in the day to obtain results at night.

Orientation during the day.—During daylight hours preliminary tests were largely confined to the midday hours when incident sunlight enveloped a large part of the visual field of the experimental birds within the test chamber.

The results of the experiments with Pintails are summarized in figures 3A and 3B. These data are from a group of 12 Pintails trained in late June and July, 1956, and tested in late July and August of that year.

True north is positioned at the top of these and subsequent diagrams. If the data showed a consistent directional trend, a sector was determined, and this calculation is presented as an arrow at the margin of the circular diagrams. The number of choices recorded in each direction is indicated at the margin of each circular diagram. With the 12-door choice the maximum error possible is 6 doors away from the correct one and a bird choosing at random would make an average error of 3.00 doors. For the choices made by Pintails the average error was 0.66 doors (fig. 3A); this is considerably more accurate than expected if choices had been made by chance alone. Under overcast skies the average deviation was 3.48 doors (fig. 3B), not much different from random choice.

Under clear skies it is of interest to note the preponderance of errors to the left. The possible significance of this deviation is discussed later in connection with similar results with teal.

The pooled results for all Blue-winged Teal tested under clear and overcast skies are plotted in figures 3C to 3F. These data summarize the results of experiments conducted from August 1 through September 5, 1957, at Delta, Manitoba, with birds

trained to respond to an easterly reward (figs. 3C, 3D) and at Berkeley, California, for birds trained to a westerly reward (figs. 3E, 3F). For both of these localities and training directions there is a deviation to the north. The orientation of birds under clear skies is highly accurate, whereas that under overcast skies does not differ significantly from random orientation.

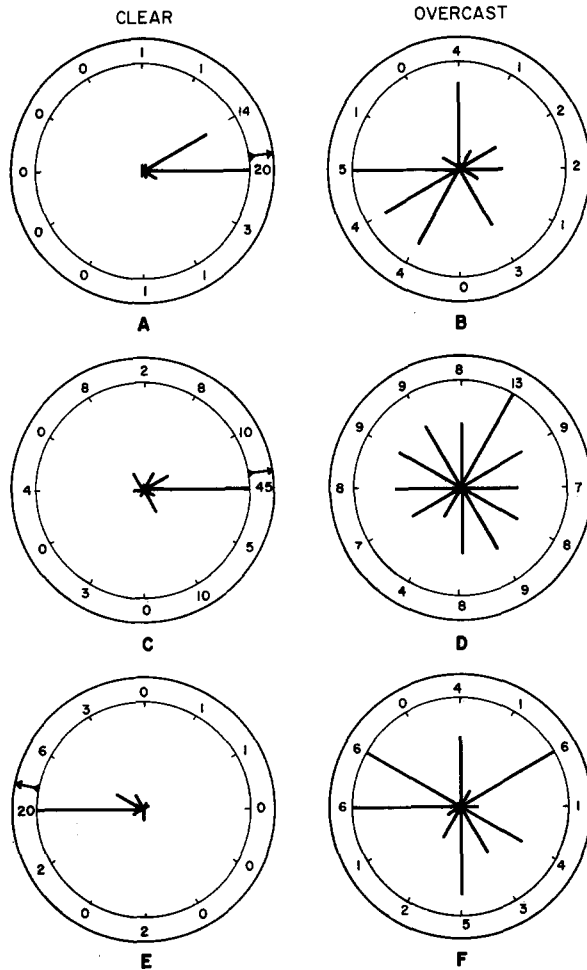


Fig. 3. Orientation of trained ducks under daytime conditions. Pintails trained to an easterly reward under clear, sunny skies (A) and under completely overcast skies (B). Blue-winged Teal trained to an easterly (C) and westerly (E) reward under sunny skies and overcast skies (D and F).

A single Green-winged Teal was inadvertently included with the group of Blue-winged Teal in the course of the training process. The performance of this individual for clear, sunny skies is indicated in figure 4A. This bird was exceptional in that only once did it follow the lead of another teal in making a choice. As a consequence a better record is available for this bird than for any other individual.

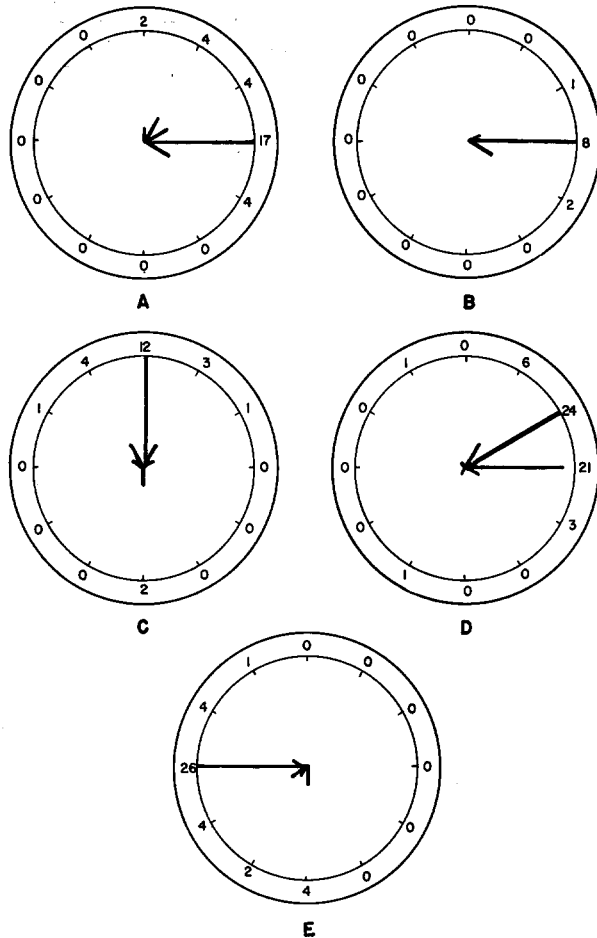


Fig. 4. Orientation under daytime (A) and night (B-E) conditions. A single Green-winged Teal trained to the east and tested during the day (A) and at night (B). Night tests with Blue-winged Teal with the moon in the sky, training direction east (C). The mode of response centers on the lighted north wall of the apparatus. This contrasts with the performance of the other individuals on the same nights and under the same conditions (D). Summary of orientation under clear moonless night skies with Blue-winged Teal trained to the west (E).

Night orientation.—Tests at night are not strictly comparable to daytime tests because of the difficulty in accurately assessing the motivation of the birds at night. Some individuals which regularly made choices during the day consistently froze in place when put in the test situation at night in spite of prolonged periods of water deprivation before darkness.

The grouped results of preliminary experiments at night under conditions of bright moonlight showed two peaks of oriented choices. One peak centered very slightly to

the left of the training direction while the other peak was three doors to the left. When this result was checked against individual performance it became apparent that certain birds accounted for the nearly appropriate orientation (fig. 4D), whereas another group of individuals had produced the mode well to the left (fig. 4C).

Following this result obtained from the initial night experiments, three individuals which had shown a tendency to nocturnal accuracy and a less pronounced tendency to move into the moonlit areas were selected for subsequent night tests. The results of these tests, conducted during the spring of 1958, at Berkeley, California, with birds trained to a westerly reward, are summarized in figure 4E. On moonless nights an accuracy of orientation comparable to that obtained from tests conducted with full visibility of the sun is indicated. The experiments summarized in figure 4E were made on clear nights without the moon in the sky, or if present, the moon was less than half and was low on the horizon so that it was not directly visible in the test apparatus. All the experiments were made in a period of from one hour before local midnight to three hours after midnight. These data confirm the suggestion that moonlight when present deflects the mode of choices.

The lone Green-winged Teal participating in these experiments maintained his effective search for water at night (fig. 4B). This bird was the only individual of 18 birds trained in 1957 which was apparently able completely to ignore the moon and the brightly lighted walls of the apparatus.

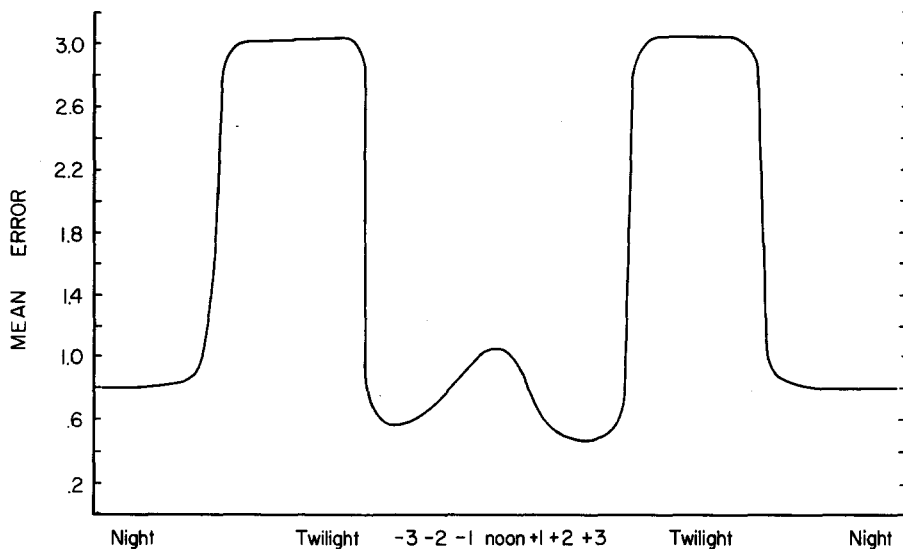


Fig. 5. Orientation performance throughout the day. A mean error of 3.0 indicates a chance performance. The duration of twilight is exaggerated by the design of the test apparatus.

Behavior of the orienting birds.—Figure 5 represents orientation performance throughout the day. Accuracy of orientation in daytime was demonstrated only for the $3\frac{1}{2}$ hours before and after the midday culmination of the sun. Earlier and later than these times, the opaque screen of the apparatus, used to prevent visibility of landmarks, cast a shadow of ever increasing dimension in the arena area. As the proportions

of the crescentic shadow continued to increase, the probability that the bird's head would be shaded, thereby preventing direct visibility of the sun, also increased. In this period the choice made was classified according to whether (1) the head was in the sun when the doors were opened 90 seconds after the bird was placed in the apparatus or (2) the head was in shadow at that moment. Of 43 such records the result is as follows: Under condition 1 the average score of 23 birds was 1.33 doors in error, whereas under condition 2 the score of 20 individual choices was 2.28 doors in error, a result approaching random performance. The sky above was fully clear under both conditions with the same amount of blue sky visible to the birds as was visible during the remainder of the daytime tests when accuracy was consistently high. The significance of this result is interpreted in the discussion.

During these parts of the day a particularly illuminating and surprising behavior pattern was often seen. Just prior to making a choice a bird would tilt its head, facing one side toward the sun and the other downward in much the manner of a Robin (*Turdus migratorius*) searching for worms. It seemed to the observer that the bird was actually scrutinizing the sun in its position just above the artificial horizon of the apparatus. The bird would maintain this position briefly, never for more than five seconds. It would then turn its head to a normal position and, usually, would proceed to make a choice.

In the period at twilight when a shadow no longer fell on the walls of the arena and there was no possibility of the birds seeing the sun directly, orientation failed. The results of experiments during this period in the early morning and in the evening are summarized as part of figure 5. At dawn 13 choices gave an average accuracy of 2.41, only slightly better than random performance, and in the evening the accuracy of 20 choices was 3.02, again no more accurate than anticipated by chance alone.

Under fully overcast conditions the behavior of the bird was often quite different from that observed under clear skies. Movements starting from near the center of the arena were no longer clearly directed from this point but rather were rapid movements, consisting of running to the walls and doors. Rather than enter a door a bird often circled the arena several times, perhaps looking in door after door as it passed. Without passing farther into the compartment the birds were unable to determine which chamber contained the water. Under these overcast conditions the birds often made no choice at all. Some of these birds reached the criterion of passing their bills through the door; hence their performance is scored with the record of more complete choices even though they never fully entered any compartment.

Diurnal variation in orientation performance.—The middle section of figure 5 indicates the degree of accuracy achieved by Blue-winged Teal through the period when the sun was directly visible. These tests, conducted with an easterly reward, show a decline of accuracy of orientation through the morning until noon when performance was poorest. Accuracy again improves from this time on until the sun is no longer visible to the birds.

DISCUSSION

The primary objective of the experiments described here was to determine the cues involved in celestial orientation and to relate motivation to the performance of the birds. The results might then be related to the migratory behavior of natural populations of waterfowl.

Experiments of Kramer, Hoffmann, and von Saint-Paul all utilized birds trained at one time of day and tested at another. Such experiments clearly demonstrate the capacity of the birds involved to allow for the passage of the sun and to make an

oriented choice. In the training system used here the test birds lived in the apparatus and during the training period could make a choice at intervals throughout the day. The basic question under investigation, the capacity of the species involved to determine direction under various sky conditions, is not complicated by the altered training system. Critical tests were performed only after the birds had been removed and the apparatus cleaned and rotated. These precautions are similar to the controls provided in timed-training studies so that the results of this study may be generally compared with other studies.

Two prominent differences should be mentioned, however. With constant availability of the reward through the training period, a bird can learn to compensate for the passage of the sun if it is used as an orienting cue. Hoffmann (1954) exposed his birds to the natural sky only during the brief period of training each day. There was no opportunity for the birds to learn where the sun might be when they were tested at a later time of day. The ability of these birds to compensate for the changed location of the sun suggests an innate timing mechanism. In the case of birds in continuous training one cannot say whether the capacity to orient throughout the day is innate or learned.

The other difference between timed training and continuous training is that, with continuous training, no potential pacing cue (Aschoff, 1958) is provided by the experimenter. Time-trained birds are rewarded day after day at a fixed time and this periodicity might itself provide a cue, especially since it is reinforced by feeding. In the case of continuous training the experimenter provides no timing cues. Life activities are pursued on an *ad lib.* schedule, and all visual timing information would seem to have to come from the celestial environment or some as yet unknown pacing cue.

The sun as an orienting cue.—The bulk of the evidence presented here seemingly suggests that the sun itself provides the critical orienting information during the day. When the sun was above the artificial horizon of the apparatus and thus visible directly to a bird in the test situation, orientation was generally accurate. With the sun in the same position under conditions of complete overcast, orientation failed. In the period after apparent sunset in the test apparatus, when the sun was above the true horizon and the sky was clear but featureless to the bird in the test apparatus, orientation failed. In a similar test situation spontaneous orientation persists for most invertebrates that have been examined (Birukov, 1957; Pardi and Papi, 1953). This apparent response to the polarized pattern of light in the sky has not been observed for any vertebrate in spite of the fact that a number of critical tests have been made. The experiments described here suggest that the Blue-winged Teal lacks such a capacity.

Failure of orientation in the twilight period provides additional circumstantial evidence concerning the orienting cues involved during the day. Correlated with the presence of clear skies are sharp shadows which fall on the walls of the test arena. These shadows could provide reliable orienting information, as complete and consistent as that provided by the sun itself. However, the failure of orientation at times when these shadows are visible and the sun is not suggests that the ducks do not use them as directional cues. Likewise, it has been suggested that stars might be visible to a bird during the day and serve as an orienting cue. This interpretation would fit the correlation of oriented response under clear skies and failure in orientation with overcast skies. But it does not fit with the failure of orientation in the periods of dusk. The stars, being obscured to our eyes by the diffraction of the sun's light in the atmosphere, become increasingly visible to both man and bird as the sun falls below the horizon. Yet in the test apparatus at this time of day the overhead sky provides the experimental

bird with no reliable directional information and it is lost until after dark when the stars become clearly visible to man.

Orienting cues at night.—From the foregoing discussion it seems clear that some features of the night sky provide critical orienting information. Planets probably play no great role in the orientation process, although the experiments described here do not rule out these bodies as orienting cues. Sauer (1957), however, found that he could obtain excellent orientation under the artificial sky of a planetarium without projecting the planets or the moon. Based on the evidence of the experiments reported in this paper and the circumstantial evidence from these other studies, it seems possible, therefore, that celestially directed migration of waterfowl at night is based on the stars.

In tests using spontaneous migration orientation, Sauer (1957) found that on moonlit nights Garden Warblers responded by facing either the moon or the wall of the apparatus lighted by it. Neither response was appropriate to the normal migratory direction. In the experiments reported here a majority of individuals, under conditions of bright moonlight, responded to the lighted wall of the choice apparatus by entering doors illuminated by the moon. These doors were not in the correct training direction. The apparent confusion of birds in moonlit apparatus is probably an artifact of the experimental situation since the moon and more especially the lighted wall of the apparatus become abnormally prominent features of the visual environment. The catastrophies which occur when migrating birds strike lighthouses, ceilometers, and lighted buildings and towers show a close parallel.

The fact that birds in the wild migrate freely and competently under a full moon is well known (Kramer, 1952), and Lowery and Newman (1955) have made extensive counts of birds migrating across the visible face of the moon. To a bird in free flight with clear visibility of the whole sky the moon would be a minor feature of the sky and would not contrast sharply with the remainder of the visual environment. The contrast is especially emphasized in the deep shadows of the test situation.

Directional errors and their significance.—A constant feature of the experimental results under clear night skies with the moon visible is the preponderance of errors to the north of the training direction. I interpret this as phototactic response to the lighted wall of the experimental apparatus. This is comparable to but of less intensity than the response noted under the moon. The evidence may be summarized as follows:

(1) With an easterly training direction during the day the error is in the direction of the sunlit area. Attraction to this area is suggested by an increased probability of deviation to the left, increasing to the time when the stimulus is greatest at noon.

(2) With a westerly reward during the day the preponderance of errors is also in the direction of the lighted area but to the right of the training direction rather than to the left.

(3) At night we know that incident moonlight attracts the ducks, so much so that under certain conditions and for certain individuals the response of trained birds is to the illuminated area rather than to the reward.

(4) At night even among those birds which respond well to the training direction there is a preponderance of errors in the direction of the lighted area suggesting that the two orienting stimuli may both play a part in determining the direction of the ultimate choice. This night response results only when the moon is in the sky. When incident moonlight is no longer present, and only the night glow, the stars, and the planets provide illumination, a normal distribution of errors results.

These data all point to the conclusion that directional errors result from the presence of illuminated areas within the apparatus which induce a positive phototactic response.

The experiments and the natural migration of waterfowl.—Since the experimental work reported here is primarily directed to an interpretation of cues used by waterfowl in migration, it seems appropriate to consider briefly the pertinence of the findings to the natural phenomenon we are indirectly investigating.

Studies by Bellrose (*op. cit.*) of delayed migration of Blue-winged Teal banded and released in central Illinois during the period of normal fall migration showed that recoveries come mostly from the southeast. Numbers of individuals were recaptured or shot in Cuba and along the northern coast of South America. When juvenal Blue-winged Teal were detained in Illinois beyond the time of departure of most adult teal from the area and then released, they showed a similar recovery pattern concentrated to the southeast, perhaps even more concentrated than were recoveries from the group moving with the natural migration. Bellrose (*op. cit.*) presents convincing evidence that these birds could not have determined a course by travelling with other species of waterfowl remaining in the Illinois area at the time these juveniles were released. The species remaining at that date have migratory routes leading due south to areas along the Gulf Coast where the birds winter. The only species which travel to the southeast from Illinois are the Ring-necked Duck (*Aythya collaris*) and the Pintail, and both of these species had deserted the area. Nor could Bellrose (*op. cit.*) find any evidence that prevailing winds might have directed the course of these birds.

Field observations clearly indicate that many species of ducks and geese use features of the terrain to guide their movements. This statement applies both to movement on the home range and to migration. Evidence for the latter comes from the observation that, like many other species of birds, banded ducks are much more likely to be recaptured in subsequent seasons at the same rather than at different migratory stations. Such evidence implies, at the very least, a recognition of familiar country once it is reached. Species normally migrating in flocks, such as those considered here, would be especially able to use an orientation mechanism based on the recollection of familiar terrain. But familiarity with the terrain cannot be the whole story. Such an explanation would not account for the oriented movement of juvenal birds not in the company of adults. And over the open water of the Caribbean out of sight of land no reliable surface cues persist. Here both juvenal and adult birds are confronted with an orientation problem that the most brilliant memory cannot resolve. These considerations suggest that these species might make use of celestial cues, equally usable over land and sea and unavailable only when the heavens are obscured by complete overcast.

Bellrose (1958a:37) concludes his discussion of orientation in Blue-winged Teal by stating that, "Although the use of the sun for orientation has not as yet been demonstrated for waterfowl, it seems reasonable to assume that juvenal Blue-winged Teal used the setting sun, or some celestial pattern at night, to be able to migrate southward over unfamiliar territory without guidance by adults."

It is that missing evidence which is presented in this paper. At least for the Blue-winged Teal and perhaps for all migratory waterfowl the sun during the day and the stars at night can provide sufficient information to allow appropriately oriented migration by inexperienced birds without the aid of terrestrial cues.

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SUMMARY

To test the ability of ducks to tell direction by the overhead sky, young birds were reared in an environment lacking directional landmarks. Only the overhead sky and the features of the apparatus remained as visual cues, and only the former provided consistent directional information since the apparatus was regularly rotated. The birds were allowed to obtain water in only one direction. By the time these birds were three weeks old their ability to locate the water source was well developed. In critical tests the experimental birds were removed from the orientation apparatus and deprived of water for a number of hours prior to testing. They were then returned, two by two, to the apparatus and required to choose one of 12 directions to obtain water. The periods of deprivation were such that under either clear or overcast conditions immediate choices could usually be expected.

In daytime tests, when the sun was obscured by cloud cover, random choices resulted. But with the sun directly visible to the birds, accurate choices were the rule. A view of clear blue sky was not sufficient for accurate orientation. In the twilight periods at dawn and dusk, with only blue sky overhead, orientation failed.

At night effective choices appear to be based on the stars. Under a clear moonless sky most individuals consistently made accurate choices although some could not be induced to respond at all. With the moon in the sky some birds diverted their direction of choice to the area within the apparatus lighted by incident moonlight. Other individuals ignored this false cue and maintained an effective search in the training direction.

The findings presented here are in general accord with what we know of the natural migration of waterfowl and experimental work based on the release of free-flying birds. These species migrate both during the day and at night. In experimental releases of Mallards in unfamiliar country, directional flight results under clear skies and disorientation is observed under overcast skies. Juvenal Blue-winged Teal, detained beyond the period of natural migration for the species, nevertheless make appropriate species-specific migrations of hundreds of miles over unfamiliar terrain and open water without the company of experienced birds. On the basis of findings reported here it seems likely that celestial cues provide the essential orienting cues for such flights.

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