COMPASS DIRECTIONAL TRAINING OF WESTERN MEADOWLARKS (*Sturnella neglecta*)

BY URSULA VON SAINT-PAUL

EXPERIMENTS at Wilhelmshaven, Germany, have demonstrated that a number of bird species are able to orient themselves by means of the sun's azimuth. The first step in these experiments was the observation that caged Starlings (*Sturnus vulgaris*) exposed to a clear sky at migration time strove to go in the general direction of migration. The sun was clearly indicated as the orienting factor in those easily observed migrational motions (Kramer, 1950a). At the same time, it was clear that the bird was able to correct for the sun's movement during the day.

As the migration activity drives the bird to choose a given visible direction for only a short period, it was considered desirable to devise experiments which were not dependent upon the migratory urge. Therefore a method with food as reward was used for directional training.

An ability to estimate the time of day must be an essential part of the complete mechanism of sun azimuth orientation. The "internal clock" on which the bird relies can be experimentally set back or ahead (Hoffmann, 1954). As a consequence, the direction chosen by the bird is changed by an amount which corresponds quantitatively to the length of time by which the daily rhythm of the bird was shifted.

There are three possibilities for testing whether or not the birds are orienting themselves by the sun: a) One tests when the sky is entirely overcast. The bird should show confusion. b) One fools the bird, changing the apparent position of the sun by mirrors. The direction of choice should change correspondingly. c) One can set up an "artificial sun" to substitute for the real sun.

By using these methods the following bird species have shown the ability to orient by means of the sun's azimuth regardless of time of day: European Starling (Kramer and v. St.-Paul, 1950); Red-backed Shrike, *Lanius collurio* (v. St.-Paul, 1953); Barred Warbler, *Sylvia nisoria* (v. St.-Paul, 1953), and Homing Pigeon (Kramer and Riese, 1952).

It seemed desirable to experiment with an other species in order to see how general sun orientation ability may be among birds. An opportunity presented itself in Wisconsin in summer of 1954.

Material and Methods.—The Western Meadowlark, an icterid and bird of the American grassland, was chosen for this experiment. Because this bird is quite similar in its manner of feeding to the

European Starling, it was possible to use the same apparatus which had been used for that species. In particular, meadowlarks pry into cracks by opening their bills to look inside as Starlings do. The rubber-covered feeder doors (devised by Kramer, 1950b.) with a slit in the rubber through which the birds poked their bills were well suited to the purpose.

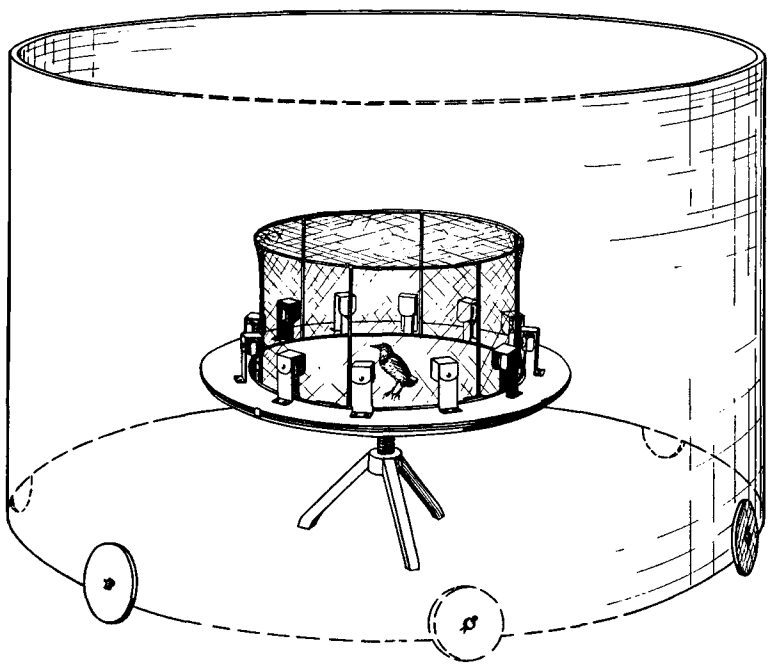

FIGURE 1. Training-cage showing 12 feeders arranged on a lower ring and 12 covers arranged on an upper movable ring. All feeders are covered in the position shown. The circular masonite wall, which excludes landmarks from the bird's view, can be rotated.

The basic procedure consists in conditioning the bird to expect food from one of the feeders which is distinguished by its compass bearing. Directional specificity is built up during the training period and will be obvious by the bird's growing success in hitting the correct feeder. To furnish the final proof, "critical choices" are arranged; these resemble the training choices except for being unrewarded. For obvious reasons the first rewarded choice in each training period is a critical one.

Figure 1 shows the apparatus used. Landmarks were excluded by the circular masonite wall 4 feet high and 7 feet in diameter, which could be rotated on six wheels. The experimental cage was placed in

the center of this cylinder with the multiple choice apparatus on a turntable. The apparatus consisted essentially of twelve feeders which were placed at equal distances on a ring around the cage. On a second ring which was movable there were twelve covers which hid the feeders. To elicit a choice, the bird was given free admission to all feeders by removing the covers simultaneously.

The birds spent most of their time in an aviary and were brought one at a time to the apparatus only for training or testing.

It is essential to have the birds both healthy and tame for training. Therefore eleven nestling meadowlarks, 9 to 11 days old, were taken from two nests and hand-reared. Five of these, two from one nest and three from the other, were subsequently trained. The birds were well fed at all times, except for a short time before each training or testing period when they were kept without food to give them appetite.

The experiments.—The experiments were planned in such a way as to show whether or not time of day was taken in account. An awareness of time can be demonstrated by keeping the training time always within the same brief period each day, then deliberately setting the test periods for another time of day.

Training of the first birds began on July 15, when the meadowlarks were six weeks old. At the start, the birds were trained for half-hour periods. Later, when they had learned to seek food in approximately the right direction, the training periods were shortened to 10 to 15 minutes. After about three weeks, the birds chose the training direction with such certainty that even though the correct feeder and every second feeder contained food, the influence of training was undisturbed. This also establishes that it was impossible for the bird to notice the reward in advance. In this stage of the training—from August 11 on—one or two and sometimes up to four choices without reward were offered before the bird received a reward. Simultaneously tests at other times of day were started. In these, the birds were *never* rewarded.

Of course it was impossible to protract tests without reward unless reinforcement was given during the training period at frequent enough intervals to keep the bird from "unlearning." The birds quickly learned that they could expect no reward except during training periods; sometimes during the tests they entirely refused to choose. So it appeared desirable not to offer more than three tests without reward. However, as the time for this study was limited, up to six choices without reward were sometimes offered, and this may have increased the width of the choice scatter. At least one reinforcement period was interspersed between every two test periods.

Figures 2A and 2B show the critical choices of the training period

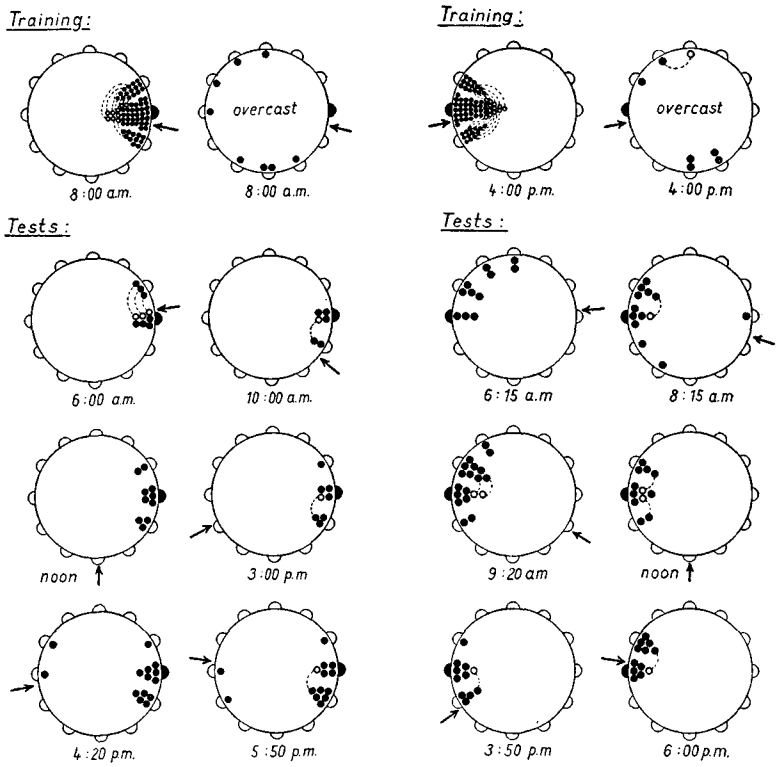

FIGURE 2. Choice diagrams of Meadowlarks 1 (*left*) and 2 (*right*). The arrow indicates the position of the sun. Each semicircle on the circumference represents the location of a feeder. The solid semicircles show the proper feeder of the training direction. Each solid dot indicates a critical choice. If a correction was allowed, these second choices are represented by open dots and connected by broken lines with the incorrect choice.

as well as choices at various test periods for Meadowlarks 1 and 2. Meadowlark 1 was trained to seek food from the east feeder between 7:50 and 8:00 A.M. The training period for Meadowlark 2 was between 3:50 and 4:10 P.M. The diagrams show that both birds held to the compass direction, even when tests were given at different times of day. Only when the azimuth had altered by approximately 180° or more were individual, major mistakes noticeable. Choices were elicited from both birds during periods of overcast occluding the view of the sun during training period. Those choices, shown separately in Figures 2A and 2B, are randomly distributed.

The results with Meadowlark 3 were similar to those with birds 1 and 2. However with this bird, the original training time (8:30 to

8:45 A.M.) could not be strictly adhered to, so that the data obtained from this bird are less valuable. Overcast conditions caused disoriented choices in this bird too.

Meadowlark 4 was trained toward the south at noon, and training was not started until August 17. Training was handicapped by the midday heat and as a result took longer than it did for the other birds. Owing to shortage of time, this bird could only be tested a few times

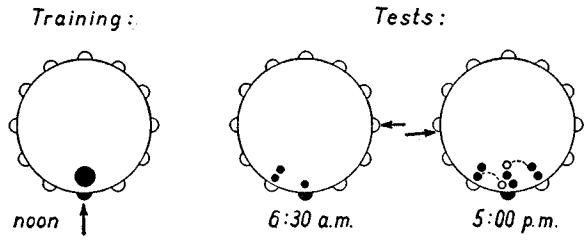

FIGURE 3. Choice diagram of Meadowlark 3. The total of critical choices during the training period is represented by one large dot.

after successful training. These few tests, however, show that this bird too, which was always rewarded in the direction of the sun, maintained its compass direction at times other than noon (Figure 3).

Meadowlark 5, a sib of Meadowlark 2, was trained toward the west between 8:45 and 9:00 A.M. As in the case of the others, the training period from August 11, on, was considered sufficient. The first data are presented in the top row of Figure 4. At 6:50 in the morning the sun's position is not far enough from the position at training time to determine whether the bird was holding to the compass direction or

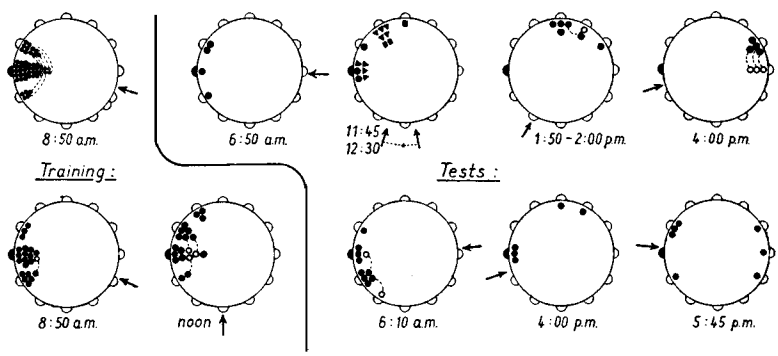

FIGURE 4. Choice diagram of Meadowlark 5. Between 11:45 A. M. and 12:30 P. M., choices during different testing periods are represented by different symbols. At 11:45 A. M. the choices are represented by circles, at 12:00 NOON by triangles, at 12:30 P. M. by squares. For further explanation see the text.

to the sun's actual position. With more drastic changes [illegible]uth it becomes clear, that this meadowlark held rather to a [illegible]ed sun angle than to a given compass direction. However the six choices straight toward the west cause one to suspect that this bird too had the potentiality for compensating by means of time sense but for some reason did not show it in most of the cases. The number of tests at various times of day is unfortunately small, and this is correlated with this particular individual's marked reluctance to make choices outside the training or reinforcement periods. During the last days of the experiment (August 28 to September 4) it was offered food rewards in the same compass direction at two different times of day; namely at the old training time and between 11:50 A.M. and 12:00 noon. The results from this day forth are designated in the lower row in Figure 4. The inclination to adopt the compass direction has now become more pronounced. Either ability, that of holding to a constant angle with the sun or of orienting in relation to the compass direction, could have governed this bird's choice.

Only a few choices could be obtained with overcast conditions from Meadowlark 5. Their distribution was random (not shown in Figure 4).

Discussion.—Among the birds which were examined for their ability to orient by the sun (see page 203), only two individuals, the shrike and one of the pigeons, reacted like Meadowlark 5, orienting themselves sometimes in relation to the actual sun azimuth and sometimes in relation to the compass direction.

Kramer (1952) tried to train a Starling to react to the actual sun direction rather than to the compass direction, and after many weeks, he had some, but only partial success.

Starlings, native in North America, showed a unique behavior, regularly choosing a direction between the fixed sun angle position and the compass direction (Rawson, 1954).

In general one may conclude so far that several species have an ability to compensate for changes in the sun's position. There is no doubt that all species so far examined could be trained to a constant angle between the feeder and some visual clue other than the sun. It remains a mystery why in most of the instances the sun is treated in a peculiar manner which is the product of an elaborate evolutionary process, while in a few cases it seems to play only the rôle of a visual landmark.

Acknowledgments.—This work was supported by financial aid from the Frank M. Chapman Memorial Fund, and I wish to express my thanks to the administrative committee for this fund. Housing and

working facilities were kindly offered by Dr. and Mrs. F. N. Hamerstrom, Plainfield, Wisconsin. I am grateful to Mr. O. Mattson for his help in technical preparations and to Miss E. Hamerstrom for efficient assistance in taking care of the experimental birds. The problem was suggested by Dr. G. Kramer, Wilhelmshaven. Parts of the technical equipment belonged to the Max Planck-Institut für Meeresbiologie, Abt. Kramer. I take special pleasure in acknowledging my indebtedness to Mrs. F. N. Hamerstrom in translating the German manuscript. I am grateful to Dr. and Mrs. F. N. Hamerstrom and to Dr. G. Kramer for critical reading of the manuscript. Many thanks are due to Mrs. L. Dinnendahl, who prepared the drawings reproduced here.

Summary.—Hand-reared Western Meadowlarks were trained by the method used by Kramer to seek food in a given compass direction. The training periods, which never lasted more than 30 minutes, were always at the same time each day. After 20 days of training, critical choices established that the birds had become capable of selecting the compass direction toward which they had been trained. The method used eliminated the possibility that the birds might be using visible landmarks other than the sun. On overcast days the birds were disoriented.

Tests conducted at times when the sun's position was different from that in the training period were to show whether the bird would choose on the basis of a constant angle with the sun's actual position or correct for the time of day and choose the compass direction. In Figures 2A and 2B, are shown the choices made by two individuals which selected the compass direction independently of the time of day. One out of five meadowlarks (Figure 4) usually chose on the basis of the sun's actual position, not allowing for its daily movement.

The results of this study give further support to the supposition that the ability of true azimuth orientation, where the sun's azimuth position and time of day are the necessary requirements, is general among birds.

LITERATURE CITED

HOFFMANN, K. 1954. Versuche zu der im Richtungsfinden der Vögel enthaltenen Zeitschätzung. Z. Tierpsychol., **11**: 453–475.

KRAMER, G. 1950a. Orientierte Zugaktivität gekäfigter Singvögel. Naturwiss., **37**: 188.

KRAMER, G. 1950b. Weiter Analyse der Faktoren, welche die Zugaktivität des gekäfigten Vogels orientieren. Naturwiss., **16**: 377–378.

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

KRAMER, G., and E. Riese. 1952. Die Dressur von Brieftauben auf Kompassrichtung im Wahlkäfig. Z. Tierpsychol., **9**: 245–251.

KRAMER, G., and U. v. SAINT-PAUL. 1950. Stare (*Sturnus vulgaris* L.) lassen sich auf Himmelsrichtungen dressieren. Naturwiss., **22**: 526–527.

RAWSON, K. S. 1954. Sun Compass Orientation and Endogenous Activity Rhythms of the Starling (*Sturnus vulgaris* L.) Z. Tierpsychol., **11**: 446–452.

v. SAINT-PAUL, U. 1953. Nachweis der Sonnenorientierung bei nächtlich ziehenden Vögeln. Behaviour, **6**: 1–7.

Max Planck-Institut für Meeresbiologie, Wilhelmshaven, Germany, May, 1955.