Multi-author Review

Orientation in birds

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Orientation in birds: A foreword

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The following papers describe numerous impressive discoveries by talented and energetic investigators concerning the environmental cues used by birds to orient themselves during migratory and homing flights through unfamiliar territory. I can add only a few speculative comments and suggestions for future experiments. For example, Richardson reviews evidence that winds have an important influence on migrants, and perhaps provide directional information. But we need more detailed and critical data on the headings and tracks of migrants flying where wind speed and direction are measured. The telemetric studies of Cochran[6] have come closest to providing such data, but future investigations of this type would benefit from simultaneous radar data measuring wind velocity by tracking small balloons.

The most firmly established orientational ability is the use of the sun and stars to determine appropriate compass directions. This requires compensation for the earth's rotation, based on internal circadian 'clocks', as clearly demonstrated by the experiments conducted and reviewed by Schmidt-Koenig. Able points out that the azimuth direction of the setting sun, and the polarized patterns of sky light around the time of sunset, also have marked effects on the directional choices exhibited in orientation cages. Polarized skylight patterns could theoretically inform an animal of compass direction, latitude and even longitude, if it could observe with sufficient accuracy the rotation of polarization patterns at 15 degrees per hour around the pole point, as analyzed by Brines[3]. But experimental testing of this possibility is needed.

Papi reviews extensive evidence that pigeons make some use of olfactory information in determining the home direction, and Wallraff's chapter and another recent paper[14] support Papi's conclusions. But it remains unclear just what odors are available to provide useful orientational information. The Wiltschkos review numerous experiments indicating use of the earth's magnetic field as a source of directional information by small passerines exhibiting migration restlessness in orientation cages. Yet, as noted by Able and Bingman[1], these data are quite 'noisy', that is, the effects are small and require statistical analyses to demonstrate any significant effects of experimental manipulations such as shifting the horizontal component of the normal earth's field. Many experimental results that initially seemed excitingly significant have been difficult to replicate. For example, Keeton[7] reported that bar magnets attached to pigeons caused their homeward orientation to deteriorate, but only when the sun was not visible. But extensive replications of these experiments before his untimely death in 1980 failed to confirm these results, as recently analyzed by Moore[10]. And all attempts to elicit conditioned responses to magnetic stimuli similar to the earth's field have yielded negative results or proven resistant to replication[2,5,8,9,11]. This lack of improvement in the signal-to-noise ratio after many years of experimentation with magnetic orientation contrasts with electric orientation and communication in certain fishes and echolocation by bats and odontocaete cetaceans. The original evidence of orientation by means of the previously unsuspected cues was soon reinforced by physiological data demonstrating well developed sensory mechanisms and highly organized portions of the central nervous system devoted to the newly discovered mode of perception[4,12]. Such coherence of several relevant types of behavioral and physiological evidence has unfortunately not yet emerged from the study of magnetic orientation in birds. Perhaps the data reported in the chapter by Semm and Beason mark the beginning of such a rounded body of mutually reinforcing evidence that will at last constitute a fully convincing explanation of avian orientation. But the history of exciting preliminary results that have been difficult to replicate suggests cautious reservation of judgement, pending unambiguous identification of sensory and central mechanisms that would be required for accurate orientation based on the earth's magnetic field.

The methods that have so far been available to investigators of avian orientation may not be adequate to identify the relevant variables. For instance each release of a homing pigeon provides only its initial heading or vanishing bearing and the time required to reach home. It has not yet been possible to vary conditions experimentally during the first minute or two after release, when pigeons apparently select the homeward direction, because no one has succeeded in inducing pigeons to indicate the homeward direction before being released and actually flying away. An alternative approach would be to equip the pigeon with a radio-controlled instrument allowing the experimenter to manipulate stimuli postulated to be used in selecting the homeward direction. Walcott and Green[13] reported that artificial magnetic fields around a pigeon's head caused deterioration in homing under overcast skies. Replication of this experiment with remote control of the artificial field might open up an important new approach to the challenging problem of bird navigation.

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The sun compass

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Summary. The sun compass was discovered by G. Kramer in caged birds showing migratory restlessness. Subsequent experiments with caged birds employing directional training and clock shifts, carried out by Hoffmann and by Schmidt-Koenig, showed that sun azimuth is used and sun altitude ignored. McDonald found the accuracy to be $\pm 3° - \pm 5°$. According to Hoffmann and to Schmidt-Koenig, caged birds trained at medium northern latitudes were able to allow for the sun's apparent movement north of the arctic circle but not in equatorial and trans-equatorial latitudes.
In homing experiments, and employing clock shifts, Schmidt-Koenig demonstrated that the sun compass is used by homing pigeons during initial orientation. This finding supports the existence of a map and compass navigational system. Pigeons living in equatorial latitudes utilize the sun compass even under the extreme solar conditions of equinox (Ranvaud, Schmidt-Koenig, Ganzhorn et al.). The use of the sun compass during zenith passage of the sun is being investigated.
Key words. Sun azimuth compass; clock shift; initial orientation; directional training; homing pigeon.

Experiments with caged birds

Discovery of the sun compass

In the late forties, Gustav Kramer[8] discovered that migratory restlessness of caged migrants was directed rather than random. In a series of pioneering studies with starlings (*Sturnus vulgaris*) Kramer[9] was able to show that the sun is the directional cue used by the birds during daytime. Following Santschi's mirror experiment[18], mirrors attached to the testing cage shifted the bird's directionality as predicted (fig. 1). These initial investigations were dependent upon the bird's migratory restlessness, which is highly seasonal and restricted to certain hours of the day. In order to overcome these restrictions Kramer and St. Paul[11] and Kramer[9] succeeded in training starlings in a circular cage to look for food in a certain compass direction. This technique made experimenting independent of migratory season and time of day.
With only sky and sun visible to the birds in the training apparatus, the birds maintained their training direction in the course of the day. This result strongly supported the conclusion of the preceding mirror experiment: