

NATURAL AND INDUCED MAGNETIZATION IN THE  
BOBOLINK, *DOLICHONYX ORYZIVORUS*  
(AVES: ICTERIDAE)

By ROBERT C. BEASON

*Biology Department, State University of New York, Geneseo, New York 14454,  
USA*

AND WILLIAM J. BRENNAN

*Department of Geological Sciences, State University of New York, Geneseo,  
New York 14454, USA*

*Accepted 4 April 1986*

SUMMARY

The magnetic characteristics of the heads from 28 bobolinks [Icteridae: *Dolichonyx oryzivorus* (L.)] were analysed using remanence magnetometers. The natural remanent magnetization of 12 freshly preserved heads averaged  $3.20 \times 10^{-7}$  electromagnetic units (e.m.u.) ( $1 \text{ e.m.u.} = 10^3 \text{ A m}^{-1}$ ) and was oriented horizontally from side to side. An electromagnet was used to induce magnetization with external field strengths of up to 0.7 Tesla (T). The average saturation isothermal remanent magnetization (sIRM) for 23 bobolink heads was  $2.49 \times 10^{-5}$  e.m.u. Because the IRM was attained partially below 0.1 T and totally below 0.3 T, we believe that the magnetic material in the bobolink is at least partially single domain magnetite. The relationship between the IRM acquisition and alternating field (a.f.) demagnetization curves indicates that the single or pseudo-single domain grains of magnetite interact. Similar results were obtained on one savannah sparrow (Emberizidae: *Passerculus sandwichensis*) head and one indigo bunting (Emberizidae: *Passerine cyanea*) head.

When some bobolink heads were subdivided, most or all of the magnetization was concentrated in the area from the nasal cavity to the orbit. Light microscopy and histochemical tests confirm the localization of inorganic iron in this region.

INTRODUCTION

Many species exhibit behavioural orientation responses in natural and artificial magnetic fields. These species range from bacteria (Blakemore, 1975, 1982; Kirschvink, 1980; Blakemore & Frankel, 1981) and insects (Lindauer & Martin, 1968; Martin & Lindauer, 1977; Gould, Kirschvink, Deffeyes & Brines, 1980) to fish (shark: Kalmijin, 1978; Walker, Dizon & Kirschvink, 1982; salmon: Quinn, Merrill & Brannon, 1981), amphibians (Phillips & Adler, 1978), reptiles

Key words: magnetic, orientation, migration, magnetite, bobolink, Aves.

(Rodda, 1984) and mammals (Mather & Baker, 1981). Research has been directed especially towards analysing the behavioural responses of birds to magnetic field information. The homeward orientation of the homing pigeon (Columbidae: *Columba livia*) can be altered by natural variations in the geomagnetic field (Keeton, Larkin & Windsor, 1974; Walcott, 1978, 1980; Kiepenheuer, 1982), magnetic storms (Larkin & Keeton, 1976; Carr, Switzer & Hollander, 1982), magnetic coils (Walcott & Green, 1974) or bar magnets (Keeton, 1971, 1972; Larkin & Keeton, 1976). Investigations on several European (Wiltschko & Wiltschko, 1975; Beck & Wiltschko, 1982) and a few North American (Emlen *et al.* 1976; Bingman, 1981, 1983; Beason & Nichols, 1984; R. C. Beason, in preparation) species of migratory birds have demonstrated that they too are sensitive to earth-strength magnetic fields. Modification of the ambient magnetic field produces predictable changes in orientation headings (Wiltschko & Wiltschko, 1975; Bingman, 1983).

Although several terrestrial vertebrate species have shown orientation responses to the geomagnetic field, nothing is known about the receptor and transducer mechanisms involved. The presence of a ferrimagnetic material, probably magnetite (Kirschvink, 1983), has been reported in several species, some of which have shown a sensitivity to geomagnetic information (Gould, Kirschvink & Deffeyes, 1978; Zoeger, Dunn & Fuller, 1981; Kuterbach, Walcott, Reeder & Frankel, 1982; Jones & MacFadden, 1982; Lohmann, 1984). Because of the manner in which single domain (SD) and pseudo-single domain (PSD) magnetite particles attempt to align themselves with the ambient magnetic field, it seems plausible that magnetite particles are involved in the perception of magnetic field information.

The bobolink (Icteridae: *Dolichonyx oryzivorus*) has the longest migratory pathway of any New World landbird. Its breeding range stretches across North America through the northern United States and southern Canada (AOU, 1983). The non-breeding season (austral summer) is spent from southern Brazil to northern Argentina (deSchauensee, 1966). Because of this long migratory path, the bobolink is unable to visualize the circumpolar stars of either hemisphere during its entire journey, and cannot use stellar cues for migratory orientation in the same manner as the indigo bunting (Emberizidae: *Passerine cyanea*) (Emlen, 1969, 1970). Instead, stellar cues appear to be used as part of an integrated navigation system which also involves the earth's magnetic field (R. C. Beason, in preparation).

#### MATERIALS AND METHODS

The magnetic properties of the heads of 28 adult bobolinks, one adult indigo bunting and one adult savannah sparrow (Emberizidae: *Passerculus sandwichensis*) were examined. Nine bobolinks were taken from the nest and hand-reared under laboratory conditions, and the other 19 were captured as adults.

Preliminary measurements of saturation isothermal remanent magnetization (sIRM) of 15 bobolink heads (including all nine hand-reared birds) were made on a

PAR SM-2 spinner magnetometer in the Department of Geological Sciences, SUNY at Geneseo. All 15 heads were skinned and fixed shortly after death in  $0.1 \text{ mol l}^{-1}$  phosphate-buffered glutaraldehyde (electron microscope grade). After fixing, seven heads were individually embedded in JB-4 methacrylate plastic using an organic catalyst. Since previous histological examination of tissues from various areas of the bobolink heads revealed concentrations of inorganic iron around the olfactory nerve and bulb, and in bristles which projected into the nasal cavity (Beason & Nichols, 1984), we used glass and brass knives to remove the portion of each head between the anterior nasal cavity and the middle of the orbit from the remaining eight birds. These sections were combined into a composite sample and tested in the same manner as the intact heads. Care was taken to align all sections parallel to one another.

The natural remanent magnetization (NRM) and sIRM of an additional 12 bobolink heads, one indigo bunting and one savannah sparrow were measured on a SQUID (Goree & Fuller, 1976) magnetometer manufactured by Superconducting Technologies, Inc. (SCT) at the Department of Geology and Planetary Science, University of Pittsburgh. The heads were prepared by anaesthetizing each bird and perfusing it with avian saline (0.75%) followed by  $0.1 \text{ mol l}^{-1}$  phosphate-buffered 2.5% glutaraldehyde (e.m. grade). Each head was then removed and the skin (including the nostril areas) completely removed by hand, and kept in the buffered glutaraldehyde until tested. Only glass-double-distilled water was used in preparing the specimens. At the time of measurement, each head was placed in the same polycarbonate plastic cylinder which was not subjected to any artificial magnetic field. At no time was the remanent magnetic moment of the cylinder above  $10^{-9}$  e.m.u. ( $1 \text{ e.m.u.} = 10^3 \text{ A m}^{-1}$ ). The sIRM of the original seven plastic-embedded heads and a plastic blank, which had been subjected to the same treatment as the heads, were remeasured on the SQUID. The sIRM of the blank ( $2.8 \times 10^{-6}$  e.m.u.) was subtracted from that of each embedded head. All measurements reported here for individual heads were made on the SQUID magnetometer.

Several heads, including the composite sample and plastic blank, were subjected to strong d.c. magnetic fields (up to 0.7 T for the PAR measurements and up to 0.5 T for the SQUID measurements) to impart an IRM or sIRM. In each test, the sample was placed between the poles of an electromagnet with no current flowing. The current was then increased to a pre-established level to produce the magnetic field desired. The current was reduced to zero before the sample was removed. The samples were maintained in a consistent orientation so that the resulting IRM was acquired in a direction perpendicular to the NRM (which averaged 5% of the sIRM). The IRM was thus acquired along a sample direction for which the NRM was zero.

Progressive a.f. demagnetization of the IRM was conducted on five bobolink and one indigo bunting heads. One additional bobolink head was cooled in liquid nitrogen and an sIRM imparted while the head was at 77 K. The sample was then allowed to warm to room temperature in the SQUID while the remanent magnetization was monitored to test for the presence of superparamagnetic magnetite.

## RESULTS

The average NRM of 12 unembedded bobolink heads was  $3.20 (\pm 1.70) \times 10^{-7}$  e.m.u. The orientation of the NRM was similar for all but one of the birds (Fig. 1). In general, the magnetization is directed horizontally through the skull, from right to left, and points somewhat towards the anterior. The one exception showed nearly the reverse orientation of the other heads. Because of the consistent orientation of the NRM in the fixed but unembedded heads, it is unlikely to have been caused by contamination of the nasal passages by air-borne material, nor could it have been the result of alignment with the ambient magnetic field following fixation because the orientation of the stored heads was random.

The average saturation magnetization for 23 bobolink heads (seven embedded individually in plastic, eight in a composite sample and eight unembedded) was  $2.49 (\pm 2.17) \times 10^{-5}$  e.m.u. There was no difference between embedded and unembedded heads ( $F = 3.69$ ,  $P = 1.00$ ). The greatest gain in IRM occurred in the 0–0.1 T range, although most samples gained additional IRM in the 0.1–0.3 T range (Fig. 2). No sample gained IRM in magnetic fields stronger than 0.3 T. The failure of any sample to gain IRM in fields stronger than 0.3 T is a good indication that there was no contamination during sample preparation. Most other non-magnetite contaminants continue to gain remanence above 0.3 T.

The AF demagnetization curve of the sIRM intersects the sIRM acquisition curve at about 20% of the sIRM, and indicates a remanent coercive force of 35–40 mT. An intersection at the 50% level and remanent coercive force of approximately 100 mT or higher indicates the presence of single domain grains with each grain uninfluenced by the others. An intersection at lower values, such as we found, indicates either an

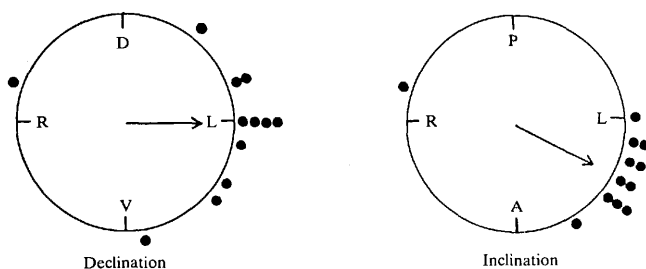


Fig. 1. The orientation of the natural remanent magnetization (NRM) in 12 bobolink heads and the mean vectors for two planes. A declination of  $0^\circ$  indicates that the NRM is directed towards the dorsal surface, a declination of  $90^\circ$  is directed towards the bird's right side,  $180^\circ$  is directed towards the ventral surface, and  $270^\circ$  is directed towards the bird's left side. Inclination is measured as deviation from a vertical plane through the head, with positive values anterior to the plane and negative values posterior. The mean orientation is shown by the arrows [declination =  $262^\circ$ , inclination =  $+29^\circ$ ,  $k = 6.8$ ,  $\alpha_{95} = 18.0$ : Fisher test, which measures dispersion on a sphere (Fisher, 1953)]. A = anterior, P = posterior, D = dorsal, V = ventral, L = left, R = right.

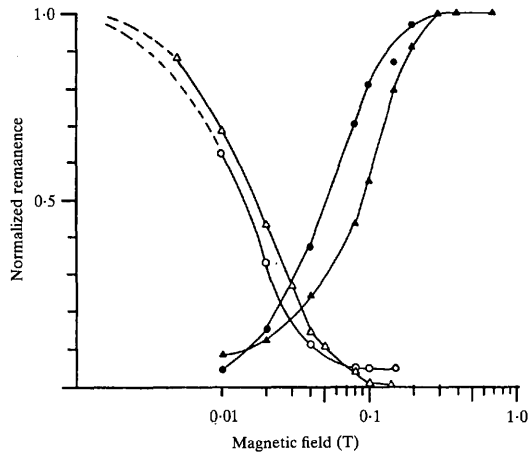


Fig. 2. Normalized acquisition (solid symbols) and a.f. demagnetization (open symbols) of saturation isothermal remanent magnetization for bobolink (triangles) and indigo bunting (circles) heads for applied magnetic fields. In both cases, the values were normalized relative to the sIRM of each head. Sample sizes: bobolink, five heads; indigo bunting, one head.

interaction between grains because of their close proximity to one another (Cisowski, 1981) or the presence of some multidomain material.

There was no loss of remanent moment as one head (which had been given an sIRM at 77 K) warmed from 77 K through the isotropic point of magnetite (130 K) to room temperature. Thus, none of the magnetic material in the bobolink appears to contain superparamagnetic magnetite.

The results from the indigo bunting ( $\text{NRM} = 3.20 \times 10^{-7}$  e.m.u.,  $\text{sIRM} = 7.48 \times 10^{-6}$  e.m.u.) and savannah sparrow ( $\text{NRM} = 1.70 \times 10^{-7}$  e.m.u.,  $\text{sIRM} = 1.23 \times 10^{-5}$  e.m.u.) were similar to those from the bobolinks. The orientation of the NRM in both species was similar to that of the majority of the bobolink heads (indigo bunting, inclination =  $16^\circ$ , declination =  $292^\circ$ ; savannah sparrow, inclination =  $43^\circ$ , declination =  $272^\circ$ ). The indigo bunting head was also subjected to a.f. demagnetization with results similar to those from the bobolink heads (Fig. 2).

#### DISCUSSION

Because all our samples attained sIRM in magnetic fields of 0.3 T or less, we believe that the magnetic material in the bobolink is magnetite. The theoretical maximum coercivity for magnetite is 0.3 T, whereas other ferromagnetic materials continue to gain remanent magnetization in stronger fields (McElhinny, 1973). Although the IRM data and the colour (black) of the material do not prove that the magnetization is due to the presence of magnetite, they are compatible with such an

explanation. Regardless of the magnetic material involved, the magnetization we observed is sufficient to allow a sensitivity to even slight changes in the geomagnetic field (Yorke, 1979, 1981).

Since multiple domain magnetite has a maximum coercivity of 90 mT (Evans & McElhinny, 1969), any IRM gain in fields of between 0.1 and 0.3 T must be due to single domain magnetite (Evans, McElhinny & Gifford, 1968). Because the specimens gained appreciable IRM below 0.1 T and the remainder between 0.1 and 0.3 T, the magnetic material in the bobolink heads appears to be interacting single domain magnetite or possibly pseudo-single domain magnetite grains.

Because magnetite is the only known ferrimagnetic material of biogenic origin (Kirschvink, 1983) and our data support such an explanation, we believe that most, if not all, of the remanent magnetization in the bobolink is carried by single domain and possibly some pseudo-single domain magnetite. Magnetite has also been reported at the same locations in the homing pigeon (Walcott, Gould & Kirschvink, 1979) as in the bobolink (Beason & Nichols, 1984), and proposed for some other species of migratory birds (Presti & Pettigrew, 1980). On the other hand, Ueda *et al.* (1982) concluded that no magnetite was present in the species of migratory and non-migratory birds they tested. Because they applied an external field of only 0.1 T, their samples probably did not reach saturation IRM. The values they report for NRM and IRM in a 0.1 T field are very similar to our results. Had they continued to apply stronger magnetic fields, it is plausible the heads would have continued to gain remanence.

Because magnetite has been reported or proposed (based on remanent magnetization) in many species using the geomagnetic field for orientation (see references in the Introduction), it may be a common feature across phyletic lines for magneto-reception (Walcott & Walcott, 1982). The mechanism by which magnetite may be used to transduce magnetic field information to the nervous system has not been established for any species. Although magnetic perception, apparently without the use of magnetite, has been reported in the homing pigeon (Semm, Schneider, Vollrath & Wiltschko, 1982; Semm, Nohr, Demaine & Wiltschko, 1984), such findings do not preclude the role of magnetite in magnetic sensory perception.

We thank V. Schmidt for graciously allowing use of the SQUID magnetometer at the Paleomagnetism Laboratory of the University of Pittsburgh. R. Selfridge provided assistance with the equipment.

#### REFERENCES

- AMERICAN ORNITHOLOGIST'S UNION (1983). *Check-list of North American Birds*, 6th edn. Lawrence, KS: Allen.
- BEASON, R. C. & NICHOLS, J. E. (1984). Magnetic orientation and magnetically sensitive material in a transequatorial migratory bird. *Nature, Lond.* **309**, 151–153.
- BECK, W. & WILTSCHKO, W. (1982). The magnetic field as a reference system for genetically encoded migratory direction in Pied Flycatchers (*Ficedula hypoleuca* Pallas). *Z. Tierpsychol.* **60**, 41–46.
- BINGMAN, V. P. (1981). Savannah sparrows have a magnetic compass. *Anim. Behav.* **29**, 962–963.

- BINGMAN, V. P. (1983). Magnetic field orientation of migratory Savannah sparrows with different first summer experience. *Behaviour* **87**, 43–53.
- BLAKEMORE, R. P. (1975). Magnetotactic bacteria. *Science* **190**, 377–379.
- BLAKEMORE, R. P. (1982). Magnetotactic bacteria. *A. Rev. Microbiol.* **36**, 217–238.
- BLAKEMORE, R. P. & FRANKEL, R. B. (1981). Magnetic navigation in bacteria. *Scient. Am.* **245**, 58–65.
- CARR, P. H., SWITZER, W. P. & HOLLANDER, W. F. (1982). Evidence for interference with navigation of homing pigeons by a magnetic storm. *Iowa State J. Res.* **56**, 327–340.
- CISOWSKI, S. (1981). Interacting vs. non-interacting single domain behavior in natural and synthetic samples. *Phys. Earth Planet. Int.* **26**, 56–62.
- DESCHAUENSEE, R. M. (1966). *The Species of Birds of South America and Their Distribution*. Narberth, Penn.: Livingston.
- EMLÉN, S. T. (1969). The development of migratory orientation in young indigo buntings. *Living Bird* **8**, 113–126.
- EMLÉN, S. T. (1970). Celestial rotation: Its importance in the development of migratory orientation. *Science* **170**, 1198–1201.
- EMLÉN, S. T., WILTSCHKO, W., DEMONG, N., WILTSCHKO, R. & BERGMAN, S. (1976). Magnetic direction finding: evidence for its use in migratory indigo buntings. *Science* **193**, 505–508.
- EVANS, M. E. & MCELHINNY, M. W. (1969). An investigation of the origin of stable remanence in magnetite-bearing igneous rock. *J. Geomag. Geoelect.* **21**, 757–773.
- EVANS, M. E., MCELHINNY, M. W. & GIFFORD, A. C. (1968). Single domain magnetite and high coercivities in gabbroic intrusion. *Earth Planet. Sci. Letts* **4**, 142–146.
- FISHER, R. A. (1953). Dispersion on a sphere. *Proc. R. Soc. A* **217**, 295–305.
- GOREE, W. S. & FULLER, M. (1976). Magnetometers using RF-driven SQUIDS and their application in rock magnetism and palaeomagnetism. *Rev. Geophys. Space Phys.* **14**, 591–608.
- GOULD, J. L., KIRSCHVINK, J. L. & DEFFEYES, K. S. (1978). Bees have magnetic remanence. *Science* **201**, 1026–1028.
- GOULD, J. L., KIRSCHVINK, J. L., DEFFEYES, K. S. & BRINES, M. L. (1980). Orientation of demagnetized bees. *J. exp. Biol.* **86**, 1–8.
- JONES, D. S. & MACFADDEN, B. J. (1982). Induced magnetization in the monarch butterfly, *Danaus plexippus* (Insecta, Lepidoptera). *J. exp. Biol.* **96**, 1–9.
- KALMIJIN, A. J. (1978). Experimental evidence of geomagnetic orientation in elasmobranch fishes. In *Animal Migration, Navigation, and Homing* (ed. K. Schmidt-Koenig & W. T. Keeton), pp. 348–354. Berlin: Springer-Verlag.
- KEETON, W. T. (1971). Magnets interfere with pigeon homing. *Proc. natn. Acad. Sci. U.S.A.* **68**, 102–106.
- KEETON, W. T. (1972). Effects of magnets on pigeon homing. In *Animal Orientation and Navigation* (ed. S. R. Galler, K. Schmidt-Koenig, G. J. Jacobs & R. E. Belleuille), pp. 579–594. Washington: NASA.
- KEETON, W. T., LARKIN, T. S. & WINDSOR, D. M. (1974). Normal fluctuations in the earth's magnetic field influence pigeon orientation. *J. comp. Physiol.* **95**, 95–103.
- KIEPENHEUER, J. (1982). The effect of magnetic anomalies on the homing behavior of pigeons. In *Avian Navigation* (ed. F. Papi & H. G. Wallraff), pp. 120–128. Berlin: Springer-Verlag.
- KIRSCHVINK, J. L. (1980). South-seeking magnetic bacteria. *J. exp. Biol.* **86**, 345–347.
- KIRSCHVINK, J. L. (1983). Biogenic ferrimagnetism: a new biomagnetism. In *Biomagnetism* (ed. S. J. Williamson, G.-L. Romani, L. Kaufman & I. Modena), pp. 501–531. New York: Plenum Press.
- KÜTERBACH, D. A., WALCOIT, B., REEDER, R. J. & FRANKEL, R. B. (1982). Iron-containing cells in the honey bee (*Apis mellifera*). *Science* **218**, 695–697.
- LARKIN, T. S. & KEETON, W. T. (1976). Bar magnets mask the effect of normal magnetic disturbances on pigeon orientation. *J. comp. Physiol.* **110**, 227–231.
- LINDAUER, M. & MARTIN, H. (1968). Die Schwereorientierung der Bienen unter dem Einfluss der Erdmagnetfelds. *Z. vergl. Physiol.* **60**, 219–243.
- LOHMANN, K. J. (1984). Magnetic remanence in the western Atlantic spiny lobster, *Panulirus argus*. *J. exp. Biol.* **113**, 29–41.
- MCELHINNY, M. W. (1973). *Palaeomagnetism and Plate Tectonics*. London: Cambridge University Press.

- MARTIN, H. & LINDAUER, M. (1977). Der Einfluss der Erdmagnetfelds und die Schwereorientierung der Honigbiene. *J. comp. Physiol.* **122**, 145–187.
- MATHER, J. G. & BAKER, R. R. (1981). Magnetic sense of direction in woodmice for route-based navigation. *Nature, Lond.* **219**, 152–155.
- PHILLIPS, J. B. & ADLER, K. (1978). Directional and discriminatory response of salamanders to weak magnetic fields. In *Animal Migration, Navigation, and Homing* (ed. K. Schmidt-Koenig & W. T. Keeton), pp. 325–333. Berlin: Springer-Verlag.
- PRESTI, D. & PETTIGREW, J. D. (1980). Ferromagnetic coupling to muscle receptors as a basis for geomagnetic field sensitivity in animals. *Nature, Lond.* **285**, 99–100.
- QUINN, T. P., MERRILL, R. T. & BRANNON, E. L. (1981). Magnetic field detection in sockeye salmon. *J. exp. Zool.* **217**, 137–142.
- RODDA, G. H. (1984). The orientation of juvenile alligators: evidence of magnetic sensitivity. *J. comp. Physiol.* **154**, 649–658.
- SEMM, P., NOHR, D., DEMAINE, C. & WILTSCHKO, W. (1984). Neural basis of the magnetic compass: interactions of visual, magnetic and vestibular inputs in the pigeon's brain. *J. comp. Physiol.* **155**, 283–288.
- SEMM, P., SCHNEIDER, T., VOLLRATH, L. & WILTSCHKO, W. (1982). Magnetic sensitive pineal cells in pigeons. In *Avian Navigation* (ed. F. Papi & H. G. Wallraff), pp. 329–337. Berlin: Springer-Verlag.
- UEDA, K., KUSUNOKI, M., KATO, M., KAKIZAWA, R., NAKAMURA, T., YASKAWA, K., KOYAMA, M. & MAEDA, Y. (1982). Magnetic remanences in migratory birds. *J. Yamashina Inst. Ornithol.* **14**, 166–170.
- WALCOTT, B. & WALCOTT, C. (1982). A search for magnetic field receptors in animals. In *Avian Navigation* (ed. F. Papi & H. G. Wallraff), pp. 338–343. Berlin: Springer-Verlag.
- WALCOTT, C. (1978). Anomalies in the earth's magnetic field increase the scatter of pigeon's vanishing bearings. In *Animal Migration, Navigation, and Homing* (ed. K. Schmidt-Koenig & W. T. Keeton), pp. 143–151. Berlin: Springer-Verlag.
- WALCOTT, C. (1980). Homing-pigeon vanishing bearings at magnetic anomalies are not altered by bar magnets. *J. exp. Biol.* **86**, 349–352.
- WALCOTT, C., GOULD, J. L. & KIRSCHVINK, J. L. (1979). Pigeons have magnets. *Science* **205**, 1027–1029.
- WALCOTT, C. & GREEN, R. P. (1974). Orientation of homing pigeons altered by a change in the direction of an applied magnetic field. *Science* **184**, 180–182.
- WALKER, M. M., DIZON, A. E. & KIRSCHVINK, J. L. (1982). Geomagnetic field detection by yellowfin tuna. In *Oceans '82 Conf. Rec.* pp. 755–758. New York: IEEE.
- WILTSCHKO, W. & WILTSCHKO, R. (1975). The interaction of stars and magnetic field in the orientation system of night migrating birds. *Z. Tierpsychol.* **37**, 337–355; **39**, 265–282.
- YORKE, E. D. (1979). A possible magnetic transducer in birds. *J. theor. Biol.* **77**, 101–105.
- YORKE, E. D. (1981). Sensitivity of pigeons to small magnetic field variations. *J. theor. Biol.* **89**, 533–537.
- ZOGER, J., DUNN, J. R. & FULLER, M. (1981). Magnetic material in the head of the common Pacific dolphin. *Science* **213**, 892–894.