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# Evidence for a Magnetite-Based Navigational “Map” in Birds

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Birds may use the magnetic field in two ways: as a compass for locating directions and as a component of the navigational “map” for determining position. Due to the different types of magnetic information involved, two different systems of magnetoreception have been proposed, and it has been speculated that one of these receptors is based on biogenic magnetite. Treatments with a brief, high-intensity magnetic pulse designed to alter the magnetization of magnetite particles found in the birds’ heads indeed affected orientation behavior. This supports the hypothesis that a magnetite-based receptor provides orientational information. However, since all birds tested previously had homing and/or migratory experience, it could not be decided whether the pulse has affected their “map” or their compass. Here we present data obtained on inexperienced juvenile birds which strongly suggest that the “map” rather than the compass is based on magnetite.

Ever since magnetite crystals of biogenic origin have been found in organisms [1, 2], it has been speculated that these particles are involved in magnetoreception [3]. Many birds show accumulations of magnetite in the ethmoid region [4, 5], which is consistent with the possibility of a magnetite-based sensor. Behavioral studies support this hypothesis. Subjecting birds to a brief high-intensity magnetic pulse, a treatment specifically designed to alter the magnetization of single-domain magnetite crystals, had a conspicuous effect on orientation behavior. It influenced the homeward orientation of displaced birds [6, 7] and caused a shift of up to 90° from the seasonally appropriate migratory direction in three migrants [8–10].

However, the precise role of magnetite-mediated information in the birds’ orientation system has yet not been defined. Birds use magnetic information in two ways [11, 12]: They have an innate compass sense that enables them to use the magnetic field to distinguish between directions, and they may include magnetic information in their “map”, which is a mental representation of the spatial distribution of navigation factors established by experience. The “map” is used to determine position and to derive appropriate courses to distant goals.

All previous pulse remagnetization experiments suffer from the fact that experienced birds with homing and/or migratory experience have been tested. It can be assumed that these birds have a well-established “map” as well as a magnetic compass. Consequently it is impossible to specify which orientation mechanism was affected by pulse remagnetization. However, if the effect of pulsing was due to an interference with “map” information, it follows that young, inexperienced birds that have yet not established a “map” [13] should not respond to the pulse treatment. Thus we monitored the effect of pulse remagnetization on the orientation of inexperienced, juvenile migrants.

The experimental birds were Australian silvereyes of the Tasmanian subspecies, *Zosterops l. lateralis*, which migrate regularly between Tasmania and the Australian mainland [14]. The birds were mistnetted in Hobart, Tasmania (42.54°S, 147.18°E), in February 1994 shortly after fledging, well ahead of the start of migration. They thus had little time to establish a “map” of their home region and no chance at all to establish a “map” of their migration route or their wintering area. On March 1 they were transferred to the testing site in Armidale, NSW (30.5°S, 151.7°E), on the Australian mainland, where testing began in early April. All orientation tests were performed indoors in the local geomagnetic field (56000 nT, –62° incl.) in the absence of visual cues.

The directional tendencies of the birds were recorded in funnel-shaped cages lined with typewriter correction paper [15]. In its attempt to escape the bird left scratch marks on the correction paper. The scratch marks were counted, and a heading was calculated from their distribution by vector addition [8, 16].

The experimental series began with a number of control tests to establish the directional preferences of each individual bird. After these tests the birds were treated with a very short, high-intensity magnetic pulse. This pulse was identical to those applied in previous studies with migrants and displaced birds [6–10]. Each bird was subjected to the pulse once in the evening immediately before the first test of the second part of the experiments.

The juvenile silvereyes preferred a mean direction of 20° (Fig. 1a), which coincides well with their autumn migratory direction [8, 14, 16]. The subsequent pulse treatment failed to affect the behavior of our young silvereyes. The birds continued to head into their seasonally appropriate migratory direction, and their orientation did not differ from that observed prior to treatment [17]. Figure 1b presents the means of their bearings recorded during the first two tests after treatment; Table 1 gives the mean vectors of these two and later observations.

The behavior of our birds is remarkable when considering a previous study on

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Table 1. Orientation of juvenile silvereyes before and after pulse magnetization

| Day(s) | N | Mean vector | | Difference from control |
|---|---|---|---|---|
| | | $a_N$ | $r_N$ | |
| Control (before treatment) | 19 | 20° | 0.90*** | |
| 1 (day of treatment) | 14 | 49° | 0.65** | +29° (ns) |
| 2 | 15 | 22° | 0.50* | +2° (ns) |
| 3 and 4 | 16 | 30° | 0.65*** | +10° (ns) |
| 5 and 6 | 12 | 1° | 0.67** | –19° (ns) |
| 8 and 9 | 18 | 33° | 0.83*** | +13° (ns) |
| 20 and later | 14 | 11° | 0.79*** | –9° (ns) |

N, Number of active birds; $a_N$, $r_N$, direction and length of the mean vector. Asterisks at $r_N$ indicate a significant directional preference by the Rayleigh test [17]: * = $p<0.05$, ** = $p<0.01$, *** = $p<0.001$. Control: second-order mean vector based on the mean heading of each bird calculated from 4–7 single recordings obtained in tests prior to the treatment. Test conditions: first-order mean vector based on one individual recording of each bird. The last column shows differences from controls (ns = not significant)

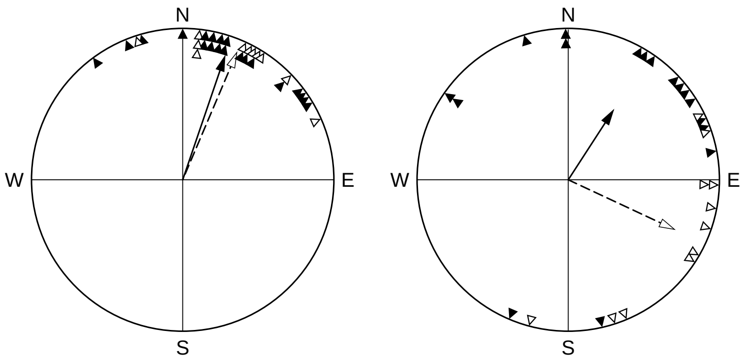

Fig. 1 a, b. Orientation behavior of silvereyes tested in the natural geomagnetic field in the absence of visual cues. *Triangles*, directional choices of individual birds; *arrows*, mean vectors calculated from these data (see [17]) in proportion to the radius of the circle; *solid symbols*, juvenile silvereyes tested here; *open symbols*, adult silvereyes tested previously under identical conditions [8]. a) Behavior before treatment; each data point represents the mean of 4–7 single nightly bearings. There is no difference between juvenile and adult birds ($p>0.05$). b) Behavior during the first two tests after pulse magnetization; juvenile birds differed from adult birds ($p<0.001$)

Tasmanian silvereyes which were caught as wintering adults at the test site in Armidale and later tested during autumn migration. They responded to the magnetic pulse by a conspicuous clockwise deviation of approximately 90° from their normal migratory course (Fig. 1b; [8]). The behavior of these adult birds tested under identical conditions is significantly different from that of our juveniles. Thus a treatment which alters the magnetic orientation of adult, experienced migrants neither shifts nor impairs magnetic orientation in naive juvenile birds of the same species. This absence of an effect in juveniles indicates that the change in behavior observed in adult birds was not due to an unspecific side effect of the treatment but to a specific interference with a component of the navigational system that differs between adults and juveniles.

A fundamental difference exists in the control of migration between juveniles on their first migration and adults. Juvenile migrants heading towards still unfamiliar winter quarters rely exclusively on an innate migration program that provides the compass course of their migration [18]. In contrast, adult birds which have already spent considerable time in their overwintering area incorporate information which they have learned during previous migrations into their orientation system. This leads to the development of a navigational "map" [19] which enables the birds to determine the compass course towards their goal by mechanisms of true navigation [13]. The deflection induced by pulse remagnetization in experienced migrants, but not in juveniles, may thus be attributed to an interference with magnetic components of the navigational "map."

Our present results, together with previous studies on pulse magnetization in birds [6–10], suggest that a magnetite-based receptor system provides at least one coordinate of the "map." Apparently, experienced birds can derive information on their geographic position from magnetic gradients such as total intensity and/or inclination. The deflections observed in adult migrants after pulse treatment thus appear to reflect "false" map information, which leads to a change in course.

The ability of our juvenile birds to maintain their normal magnetic orientation after pulse magnetization, on the other hand, indicates that the pulse does not impair the magnetic compass. This is consistent with evidence that the magnetic compass of birds involves a separate, light-dependent magnetoreception mechanism [10, 16] (see also [20, 21]).

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# Spontaneous Daily Torpor in Malagasy Mouse Lemurs

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Hibernation and daily torpor are powerful tools for saving energy in small mammals inhabiting moderate or subarctic climates [1–6], but tropical small mammals, in particular primates, may not require such states of torpidity. However, during our studies in the Malagasy dry forest we regularly observed daily torpor in two species of mouse lemurs, *Microcebus murinus* and *M. myoxinus*, which were kept in outdoor cages close to the trapping site. Torpor is characterized by a metabolic depression of almost 90% and a decrease in body temperature ($T_b$) close to ambient temperature. The lowest $T_b$ recorded was 15.4°C. Endogenous rewarming from torpor requires additional energy. However, in lemurs, these energy costs were minimal because they used the regular daily increase in ambient temperature and rewarmed passively at the end of each torpor episode.

In primates, hibernation or daily torpor was observed only occasionally in animals kept in captivity and incidentally in the field [7–9], but it remained obscure whether these were exceptional observations or if lemurs use daily torpor regularly in their natural environment. We investigated two mouse lemur species captured in a deciduous dry forest in the Morondava area of West Madagascar. Mouse lemurs are quoted as being the smallest primates on earth with 50 to 100 g body mass in the gray mouse lemur, *Microcebus murinus* [10], and only 25 to 35 g in the recently rediscovered pygmy mouse lemur, *Microcebus myoxinus* [11]. The gray mouse lemur inhabits the fine branche niche of the dry forest and feeds mainly on fruits, leaves, and insects [10, 12]. Fruit availability decreases after April and is low from July to October in Morondava due to the absence of rain [13, 14]. Mouse lemurs store energy as body fat prior to the dry season and exhibit a seasonal rhythm in tail volume [12]. Nevertheless, these body reserves are limited, and survival during the dry season may be improved by an additional reduction of energy requirements. Daily torpor is characterized by hypometabolic and hypothermic periods during the animals' resting phase [6, 15] and a return to normothermia during the activity phase. This allows maintenance of activity at high body temperature, e.g., feeding, territorial or social behavior, but saves energy during circadian periods of inactivity.

To analyze frequency, intensity, and energetic consequences of spontaneous daily torpor, nine *M. murinus* (five female, 54–95 g body weight; four male, 51–62 g) and two *M. myoxinus* (two male, 29 and 30 g) were trapped in the Forêt de Kirindy near Morondava using Sherman traps baited with banana. Three *M. murinus* and both *M. myoxinus* were used for continuous records of $T_b$, locomotor activity, and metabolic rate (MR) from May to June 1994 in outdoor cages near Morondava. These five lemurs were therefore implanted with temperature-sensitive transmitters and housed individually in 1 $m^3$ outdoor cages provided with a wooden nest box, twigs, and leaves. They were exposed to natural variations in temperature and humidity and fed once a day with banana pieces and occasionally with crickets, in order to maintain a constant body weight. $T_b$ was re-