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Waved albatrosses can navigate with strong magnets attached to their head

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Summary

The foraging excursions of waved albatrosses *Phoebastria irrorata* during incubation are ideally suited for navigational studies because they navigate between their Galápagos breeding site and one specific foraging site in the upwelling zone of Peru along highly predictable, straight-line routes. We used satellite telemetry to follow free-flying albatrosses after manipulating magnetic orientation cues by attaching magnets to strategic places on the birds' heads. All experimental, sham-manipulated and control birds, were able to navigate back and forth

from Galápagos to their normal foraging sites at the Peruvian coast over 1000 km away. Birds subjected to the three treatments did not differ in the routes flown or in the duration and speed of the trips. The interpretations and implications of this result depend on which of the current suggested magnetic sensory mechanisms is actually being used by the birds.

Key words: waved albatross, *Phoebastria irrorata*, navigation, magnetic orientation, satellite telemetry.

Introduction

Magnetic compass orientation is well established in night-migrating songbirds (for example reviews, see Wiltschko and Wiltschko, 1995a, 1996), but the sensory mechanism is unknown. Two different hypotheses have been proposed, and both are supported by some experimental evidence. Magnetic fields may be sensed *via* a quantum chemical, light-mediated, proton pumping or free radical mechanism in the eye of the bird (Leask, 1977; Ritz et al., 2000; Wiltschko et al., 2002) and/or magnetic fields may be sensed *via* single-domain magnetite crystals located in the nasal region (Walker et al., 1997; Walker, 1998; Williams and Wild, 2001; Kirschvink et al., 2001). Experimental evidence that night-migrating songbirds seem to orient magnetically only under light of specific wavelengths (Wiltschko and Wiltschko, 1995b) and only if the bird's right eye is functional (Wiltschko et al., 2002) support the mechanism involving the eye, whereas experimental evidence that a strong magnetic pulse seems to deter orientation for days (Wiltschko et al., 1994, 1998; Beason et al., 1995) supports the magnetite-mediated mechanism. Wiltschko et al. (1998) suggested that both mechanisms may be used by birds, with the light-mediated mechanism exclusively involved in magnetic compass orientation, and the magnetite-mediated mechanism exclusively used to sense small changes in intensity, inclination and/or other local deviations in the field as part of a 'map-sense'.

In contrast to the relatively large number of studies on magnetic compass orientation in night-migrating songbirds

(e.g. Wiltschko and Wiltschko, 1972, 1995a, 1996; Mouritsen, 1998), we do not presently know which compasses homing pelagic seabirds use. We do know that homing pigeons *Columba livia* use a sun compass (Schmidt-König, 1961; Schmidt-König et al., 1991; Chappel, 1997; Wallraff et al., 1999) and probably also a magnetic compass (e.g. Keeton, 1971; Walcott and Green, 1974; Visalberghi and Alleva, 1979; Wiltschko and Wiltschko, 1995a), even though magnetic compass orientation in homing pigeons has been difficult to replicate (e.g. Lamotte, 1974; Moore, 1988). It has also been suggested that magnetic cues may be used by homing pigeons as the basis for an extrapolated 'map-sense' (for reviews, see Walcott, 1991; Wiltschko and Wiltschko, 1995a). However, the cues used by homing pigeons during the map-step of the map and compass model (Kramer, 1953, 1957) are a source of constant controversy.

Many pelagic seabirds face the problem of finding a small island in the middle of a vast ocean that seems to provide no visual landmarks. Migration and homing over open ocean, therefore, seem to present seabirds with some of the most difficult orientation and navigation challenges faced by any type of bird.

Since the late 1980s, satellite transmitters communicating *via* the Argos satellite system have been commercially available to avian researchers (Jouventin and Weimerskirch, 1990), but since these transmitters and the associated satellite time are very expensive, they have, until now, been used

primarily for conservation purposes to elucidate where threatened or endangered populations forage, breed and winter (e.g. Robertson and Gales, 1998; Tickell, 2000). However, satellite telemetry also has great potential for studying the orientation responses of freely migrating birds, particularly for individuals whose access to hypothesized orientation cues has been manipulated. Unfortunately, the tendency of many seabirds to travel and forage in unpredictable directions away from their breeding colonies makes detecting effects of navigational cue manipulations difficult.

Waved albatrosses breed almost exclusively on Isla Española, Galápagos, Ecuador, and during the incubation period they typically make direct trips to the up-welling zone off the coast of Perú, ca. 1300 km from Galápagos (Anderson et al., 1998, 2003; Fernández et al., 2001; see also Figs 2–4). Throughout most of the 60-day incubation period, both male and female breeders alternate incubation stints with long foraging trips lasting about 20 days. Birds making these long trips fly along straight paths to and from the foraging area. This straight-line flight path pattern has so far been observed using satellite tracking in nine tracks of long-trip flights taken by seven different individual non-manipulated adult incubating waved albatrosses (combining data from Anderson et al., 1998, and two additional individuals from this study). In addition, 19 trips from seven different chick-rearing birds followed by satellite in 1996 showed a broadly similar pattern (Fernández et al., 2001; Anderson et al., 2003). The straight-line nature of their routes and high predictability of their destination during the incubation period make waved albatrosses an ideal species for seabird navigation studies, since deviations from their intended flight paths caused by manipulated orientation cues can be easily detected.

The aim of our study was to test whether access to the undisturbed geomagnetic field is crucial to the orientation and navigation capabilities of waved albatrosses. We used satellite

telemetry to compare flight paths of magnetically manipulated albatrosses with those of controls.

Materials and methods

Waved albatrosses *Phoebastria irrorata* Salvin 1883 are large, long-lived seabirds that nest almost exclusively on Isla Española, Galápagos, Ecuador (1°22'S, 89°39'W) (Harris, 1973; Anderson et al., in press). Females lay a single egg in minimal nest scrapes on the ground from mid-April to early June. Males and females share incubation and chick-rearing, alternating bouts of incubation or food provisioning from egg-laying until fledging 6–7 months later (Harris, 1973; K. P. Huyvaert and D. J. Anderson, unpublished data). The experiment was conducted in a subcolony of 80–100 breeding pairs at Punta Cevallos, the southeastern point of Española (for additional details of the study site, see Anderson and Ricklefs, 1987).

Satellite transmitters and location data

We tracked a total of 14 incubating albatrosses in 2000 and an additional seven incubating albatrosses in 2001. In both 2000 and 2001, incubating birds were temporarily removed from the nest and 30 g Platform Transmitter Terminals (PTTs; Microwave Telemetry Inc., Columbia MD USA) were sewn to Tesa tape (Tesa Tape, Inc., Charlotte, NC 28209, USA) feather 'sandwiches' constructed on their backs (see additional details in Fernández, 1999; www.wfu.edu/~djanders/PTTmount.jpg). These birds were then tracked using the satellites of the Argos System (Service Argos, Largo, MD, USA). The transmitters themselves produce only negligible magnetic disturbances (see Table 1). Since the distance between the transmitter and the head of the albatross was 30–33 cm when flying, the magnetic disturbances from the transmitter were about one order of magnitude smaller than the natural daily variations in the geomagnetic field (bold numbers in Table 1).

Table 1. Magnetic disturbances (in nT) produced by our PTTs (all distances relative to its centre of mass)

	Distance in front of PTT (cm)							
	10	15	20	25	30	35	40	45
Transmitting and silent transmitter								
<i>x</i>	–271	–190	–125	–85	–49	–35	–26	–18
<i>y</i>	17 207	17 225	17 229	17 230	17 239	17 239	17 239	17 242
<i>z</i>	44 466	44 479	44 473	44 465	44 458	44 450	44 447	44 443
Change in field strength								
<i>x</i>	–260	–179	–114	–74	–38	–24	–15	<10
<i>y</i>	–33	–15	–11	–10	<10	<10	<10	<10
<i>z</i>	26	39	33	25	18	10	<10	<10

PTT, platform transmitter terminal.

Magnetic disturbance was measured by a high-precision three-axial flux gate magnetometer (MEDA FVM-400).

Reference values (natural field, no transmitter): $x=-11$; $y=17,240$; $z=44,440$, where x defines the direction towards the bill, y defines the direction perpendicular to the bill (positive to the left of the bill, negative to the right of the bill) and z defines the vertical component (positive towards the earth, negative towards the sky).

nT, nano Tesla; PTT, platform transmitter terminal.

Bold values are the magnetic disturbances from our transmitter fixed 30–33 cm from the head of the birds when flying.

In 2000, two PTTs transmitted continuously, and five PTTs transmitted on an 8 h:24 h on:off duty cycle to conserve battery power. All PTTs used in 2001 operated on a continuous transmission cycle since the conservative 8 h:24 h on:off cycle was too limiting on the number of positions that we could collect. The girth of the Earth at the equator also limits the number of satellite views of the PTTs (Service Argos user manual, v.1 1988, Landover, MD, USA) so that the average number of contacts (including classes 3, 2, 1, 0, A and B) in this study was 0.22–0.73 locations per PTT per day (mean 0.54) for the conservative duty cycle and 1.42–3.73 locations per day (mean 2.52) for the continuous duty cycle. To maximize data collected, we used six of seven location quality classes provided by Argos (all but class Z), as in previous studies (Anderson et al., 1998; Fernández et al., 2001). Ground-truthing conducted at the site in 1995 showed that the lowest quality locations that we used, Class B, had a mean error of 17.8 km (9.6 nautical miles; Anderson et al., 1998).

Geomagnetic field manipulation equipment

Attaching a strong, permanent magnet to a bird is a commonly used way of depriving free-flying birds of information from the undisturbed geomagnetic field (for a review, see Wiltschko and Wiltschko, 1995a, p. 160). To examine the effects of magnetic field manipulation on waved albatrosses, we glued a 3.5 g neodymium–iron–boron magnet to the back of the head of ten incubating albatrosses. We also glued a 0.05 g neodymium–iron–boron magnet to each bird at the proximal end of the culmen's dorsal surface. Brass ('sham') pieces of similar mass and size (3.5 ± 0.5 g and 0.05 ± 0.01 g), which did not affect the magnetic field, were attached in the same manner to nine other incubating adults. The birds were assigned semi-randomly to treatment group, so that the first two birds included one magnet and one sham bird, the next two, one magnet and one sham bird, and so on. Within each set of two birds, the assigned treatment order was randomized taking into account the sex of the birds, so that the sexes were also evenly represented in each group. In addition, we tracked the flights of two untreated controls (no head attachments) to confirm that the albatrosses still used the same routes and foraging areas as in 1995 (Anderson et al., 1998). The seven tracks from incubating birds followed in 1995 provide seven additional control tracks from five different individuals.

The 3.5 g (ca. 4.5 g together with the epoxy embedding) magnet imposes a stationary magnetic field stronger than 100,000 nT (100 000 nT=1 Gauss) within 10 cm of the magnet. The direction of this field depends on the orientation of the magnet. We oriented the large magnets so that each added a horizontal magnetic component of at least 100 000 nT to the entire head of the albatross, including the proximal 1.7 cm of the beak. The horizontal magnetic field disturbance was still greater than 30 000 nT as far as 14 cm from the magnet, which includes the nares, located at most 12 cm away from the large magnet. Using our attachment method, the magnetic compass disturbance was maximized at the suggested

magnetic sensory locations including the eyes and the nasal region, since the resultant magnetic field vector (found by adding the Earth's field to the magnet's field) will always point in approximately the same horizontal direction relative to the head of the bird independent of the bird's bearing. Furthermore, it is important to realize that the geomagnetic field strength and direction stay constant in the geographical frame of reference, whereas the field produced by the stationary magnets glued to the bird follows the movement of the bird's head. Therefore, the strength of the resultant field sensed by the bird will constantly change up to 60 000 nT (\pm the strength of the geomagnetic field) when the bird moves its head.

The 0.05 g (ca. 0.08 g with the epoxy embedding) magnet imposes a stationary magnetic field stronger than 50 000 nT, 25 000 nT and 5000 nT to volumes larger than 2 cm, 3 cm and 5 cm in radius, respectively, around the magnet. We placed the small magnet at the dorso-proximal end of the bill to ensure that the proposed magnetite-mediated magnetoreceptor in the nasal region (Walker et al., 1997; Walker, 1998; Williams and Wild, 2001; Kirschvink et al., 2001) was blocked from obtaining meaningful magnetic information, even if the large magnet was lost.

Exposing migratory songbirds to a strong magnetic pulse designed to disturb the magnetization of single-domain magnetite crystals deflected their orientation, but did not, at least in some cases, seem to impair their ability to pick a consistent compass direction (Beason et al., 1995; Wiltschko et al., 1994, 1998; Wiltschko and Wiltschko, 1995b). Given these data, it has been suggested that the proposed magnetite-mediated magnetoreceptor in the nasal region is involved in sensing magnetic map cues rather than magnetic compass cues (Wiltschko et al., 1998). We therefore oriented the small magnets so that they changed the horizontal component of the magnetic field (and thereby the inclination) as much as possible. Around the magnetic equator, the total field strength is ca. 30 000 nT and the inclination is close to 0° . Magnetic inclination changes approximately 2° per 1 geographical degree moved on the north–south axis around the magnetic equator. Thus, a change of just 1000 nT in the vertical magnetic component is equivalent to a north–south displacement of one geographical degree [$\text{inv tan}(1000/30000)=2^\circ$ inclination=1 geographical degree] equal to 111 km. Consequently, even small changes of the vertical magnetic component imposed by our stationary magnets should lead to loss of homing ability in waved albatrosses if they use a magnetic map to navigate.

Magnet and sham attachment and nest monitoring

We monitored sets of 35 (2000) and 42 (2001) nests with daily visits, beginning at nest initiation in late April and early May of 2000 and 2001 and continuing until nests were assigned to a treatment category. We discontinued monitoring unassigned nests after all treatment categories were filled. Satellite transmitters and magnets or brass shams were attached after 9–20 days of incubation to 12 incubating albatrosses (six of each treatment) in 2000 and seven birds (four magnet and

three sham) in 2001. We attempted to deploy gear on birds at the end of a typical incubation stint to increase the chances that the bird left the colony shortly after attachment of equipment, thereby saving battery power. All birds left the colony between a few hours and 8 days post-deployment.

During attachment of satellite transmitters and magnets or shams, individuals were placed in a canvas bag and restrained gently in the investigator's lap. The bird's head was passed through an opening at the distal end of the bag to isolate the head during gear attachment and to decrease potential thermal or respiratory stress. All birds were released at their nests within 20–40 min of capture. To attach the rear treatment or sham, a small circle of skin on the back of each manipulated or sham bird's head was exposed by clipping away the feathers. Magnet or brass pieces embedded in hardened epoxy resin were glued to the exposed skin using a thin layer of Vetbond (3M, www.3m.com) for the initial group of six birds. Several small feathers were cut away from the area at the feather–culmen interface at the proximal end of the bill and the smaller magnets and shams were glued into the small pocket created by the clipped feathers.

Despite numerous successful laboratory tests with the initial Vetbond attachment method, the first three magnet birds and the first three sham birds returned from their trip without head attachments. In the second and subsequent rounds of attachment, the rear-mounted magnet and brass pieces were glued with epoxy resin to the non-adhesive side of strips of Tesa tape (4 cm long) 1–2 days prior to attachment. We sandwiched several head feathers between the Tesa tape-treatment piece and a second piece of Tesa tape, affixing this to the exposed skin using a layer of Vetbond directly on the skin as a protectant, and several drops of a cyanoacrylate glue (Duro Super Glue, Manco, Inc., Avon, OH, USA) over the Vetbond and adjacent feathers to adhere the treatment to the bird. Following this modification, three birds returned with both magnets still attached, and four additional birds returned with the front magnet only. After removing the equipment from birds returning with magnet or brass pieces still in place, we treated the exposed skin with Betadine as a precaution to avoid infection, although we detected no broken skin or sign of infection in any bird carrying a magnet or sham. All procedures were approved by animal care and use committees in Canada and the US and by the Charles Darwin Research Station in Galápagos.

To complement the satellite data collected to document routes, trip duration and ground speed of the traveling birds, we visited the nest of each bird twice daily, at 06:00 h and 18:00 h, recording the identity of the incubating bird and the disposition of the gear, if applicable. Additional notes were recorded whenever we passed through this part of the colony at other times of the day.

Incubating adults remain at their nest or in small areas adjacent to their nesting territories when on land (K. P. Huyvaert, unpublished data), so we can safely assume that our birds were still at sea if they were not found in the study subcolony. The satellite data strongly supported this assumption in all cases in which the satellite transmitters were



Fig. 1. Satellite picture showing the cloud cover between Galápagos and Perú on 23 June 2001 at 13:15 h local Galápagos time.

still attached and functioning properly on return. Therefore, both the satellite data and the twice-daily searches enabled us to collect accurate total trip length duration data.

Tracking data and meteorological correlates

For all birds fitted with continuous duty cycle transmitters, we calculated the resultant (straight line) traveling speed of the albatrosses seen over a period of approximately 24 h during their outward and homeward travel. In practice, this was done by calculating the fastest recorded straight-line speed between two satellite fixes, which were recorded at least 20 h apart. Data from birds fitted with conservative duty cycle transmitters proved too sparse to properly evaluate traveling speeds.

During the entire tracking period, we monitored the cloud cover at each bird's location by downloading weather satellite images (See example in Fig. 1; <http://goes-8-gems.cira.colostate.edu>) at 3 h intervals. The satellite images were calibrated by comparing the corresponding satellite image with careful local cloud cover observations made 5 times daily during the experiment at Española and during an airline flight between the Galápagos and mainland Ecuador on 24 July 2000. In 2000, the cloud cover was generally minimal during the entire period of testing, which is atypical for the season. In 2001, the weather was more typical for the season; cloudy conditions mixed with sunny periods dominated.

Results

All birds (magnet-, sham- and untreated control birds) left the colony and found the foraging area at the Peruvian coast, and all birds except one sham bird returned successfully to their nest. Magnet birds did not spend significantly more or less time in the colony between attachment of gear and departure from the colony than did non-magnet birds [magnet birds: 92 ± 65 h (mean \pm S.D.), range 5–189 h; non-magnet birds: 79 ± 68 h, range 8–200 h; *t*-test; $t=0.455$; d.f.=19; $P=0.654$]. The trips of males did not differ from females so we analyzed data from birds of both sexes together. Some birds lost one or both magnets/shams before they returned, as detailed in Table 2.

Table 2. Summary of raw data including trip length, cloudiness, attachment status and speed of each bird

Individual	Year	SA ^a	LA ^a	Total trip duration		Outward journey		Homeward journey		Time from attachment to departure (h)	Comments
				Days	Mean (days)	Clouds ^b	Speed (km h ⁻¹)	Clouds ^b	Speed (km h ⁻¹)		
Control											
Female 4	1995	-	-	31	20.4±6.0	-	-	-	-	-	8/24 duty cycle
Female 5	1995	-	-	22	20.4±6.0	-	-	-	-	-	8/24 duty cycle
Female 6	1995	-	-	21	20.4±6.0	-	-	-	-	-	8/24 duty cycle
Female 6	1995	-	-	15	20.4±6.0	-	-	-	-	-	8/24 duty cycle
Male 8	1995	-	-	20	20.4±6.0	-	-	-	-	-	8/24 duty cycle
Male 7	1995	-	-	11	20.4±6.0	-	-	-	-	-	8/24 duty cycle
Male 8	1995	-	-	27	20.4±6.0	-	-	-	-	-	8/24 duty cycle
10241 H	2000	-	-	19	20.4±6.0	0-1	-	-	-	40-48	8/24 duty cycle
06109 A	2000	-	-	17-18	20.4±6.0	No data	-	-	-	126-138	8/24 duty cycle
Sham											
05503 I	2000	No	No	19-20	21.4±5.8	0-1	-	-	-	2-14	8/24 duty cycle
05818 R	2000	No	No	21-22	21.4±5.8	1-0	-	No data	-	25-37	8/24 duty cycle
21291 U	2000	No	No	23-24	21.4±5.8	0-1	19	No data	-	194-206	8/24 duty cycle
10241 R2	2000	No	No	16-17	21.4±5.8	1-2	-	2-1	-	3-15	8/24 duty cycle
21292 U	2001	-	-	-	21.4±5.8	1-2	22	-	-	ca. 180	Didn't return
10228 FF	2001	Yes	No	34	21.4±5.8	0-1	28	2-3	31	ca. 60	
05818 Z	2001	Yes	No	22-23	21.4±5.8	2-1	23	2-3	25	ca. 108	
05503 G2	2000	Yes	Yes	15-16	21.4±5.8	1-2	-	No data	-	74-86	8/24 duty cycle
06109 1001	2000	Yes	Yes	18	21.4±5.8	1	-	No data	-	23	8/24 duty cycle
Magnet											
21292 F	2000	No	No	20	20.6±3.9	0-1	20	0-1	31	14-22	
10228 G	2000	No	No	20-21	20.6±3.9	1	-	1-2	-	110-114	8/24 duty cycle
09953 M	2000	No	No	20	20.6±3.9	1-2	-	No data	-	185-193	PTT failed
21292 A2	2000	Yes	No	20	20.6±3.9	1-0	20	2-0	33 ^c	14-24	
10241 F	2001	Yes	No	26	20.6±3.9	1-0	24	2-3	34	ca. 125	
06109 K	2001	Yes	No	19-20	20.6±3.9	1-2	24	3-2	21 ^d	ca. 180	
05503 MM	2001	Yes	No	24	20.6±3.9	0-1	22	3-2	32	0-10	
05818 Z7	2000	Yes	Yes	26	20.6±3.9	1-2	-	2-1	-	67	8/24 duty cycle
10228 M2	2000	Yes	Yes	14	20.6±3.9	No data	-	2-3	-	86-96	8/24 duty cycle
05818 OO	2001	Yes	Yes	16	20.6±3.9	1-3	28	No data	No data	ca. 120	PTT battery dead

PTT, platform transmitter terminal; 8/24 duty cycle, 8 h:24 h on:off cycle for PTT. Other PTTs operated on a continuous transmission cycle.

^aThese columns indicate whether the small attachment (SA) and large attachment (LA) were still present on return.

^b0=clear (<10% cloud cover), 1=clear with clouds (10-50% cloud cover), 2=cloudy with clear patches (50-99% cloud cover), 3=cloudy (apparent 100% cloud cover). If two numbers are given, the first number indicates the cloudiness during the majority of the trip whereas the second number indicates the cloudiness during a minor part of the trip.

^cIf speed is based on a 12 h period, a 56 km h⁻¹ travelling speed was recorded for this bird.

^dIf speed is based on a 10 h period, a 35 km h⁻¹ travelling speed was recorded for this bird.

The albatrosses in this study, regardless of treatment, tended to use a more southerly route on the home journey from the South American coast to Galápagos than they used during their outward journey from Galápagos to the South American coast (Figs 2–4). Furthermore, the return trips were made at higher straight-line ground speeds than were the outbound trips: for trips with enough reliable satellite fixes to calculate straight-line ground speeds during both journeys, outward and homeward speeds averaged 23 ± 3 km h⁻¹ and 30 ± 5 km h⁻¹, respectively (within subject comparison: paired *t*-test: $t=-2.941$, d.f.=6, $P=0.026$; considering only birds returning with at least one magnet/sham in place: outward speed, 23.5 ± 2.7 km h⁻¹, homeward speed, 29 ± 5 km h⁻¹; within subject comparison: paired *t*-test: $t=-2.337$, d.f.=5, $P=0.067$). Given this difference between outward and homeward ground speeds, we analyzed performance during the two journeys separately.

Treatment groups did not differ in several estimates of performance (Fig. 5). (1) Total trip length (all birds considered: one-way ANOVA: $P=0.92$ and pair-wise comparison between magnet and sham birds: *t*-test, $t=-0.337$, d.f.=16, $P=0.74$; considering only birds returning with at least one magnet/sham in place: one-way ANOVA: $P=0.84$ and pair-wise comparison between magnet and sham birds: *t*-test, $t=-0.447$, d.f.=9, $P=0.67$; considering only birds returning with the large magnet/sham in place: one-way ANOVA: $P=0.71$ and pair-wise comparison between magnet and sham birds: *t*-test, $t=0.393$, d.f.=3, $P=0.72$); (2) outward speed, all birds considered: mean outward speed= 23 km h⁻¹ for both magnet and sham birds (*t*-test, $t=0.0$, d.f.=8, $P=1.00$); considering only birds returning with at least one magnet/sham in place: mean outward speed= 24 km h⁻¹ for magnet birds and 26 km h⁻¹ for sham birds ($t=-0.735$, d.f.=5, $P=0.495$); (3) homeward speed, (all birds considered: mean homeward speed= 30 km h⁻¹ for magnet birds and 28 km h⁻¹ for sham birds (*t*-test, $t=0.518$, d.f.=5, $P=0.627$); considering only birds returning with at least one magnet/sham in place, mean homeward speed= 30 km h⁻¹ for magnet birds and 28 km h⁻¹ for sham birds ($t=-0.408$, d.f.=4, $P=0.704$); and (4) route (see Figs 2–4).

To further test if the birds' ability to locate Galápagos in a vast ocean was affected by the attached magnets, the straightness of the return paths was evaluated by comparing the orientation of each section (at least 100 km long) of the return journey relative to the true home direction (Fig. 6). In this analysis, we included only birds returning with at least one magnet/sham in place and for which we have at least five reliable (class B or better) satellite fixes. The expected mean direction from the Peruvian upwelling zone to Galápagos was 308° , and both magnet and sham birds were very well-oriented in the correct homeward direction (magnet birds: $N=26$ track sections, $\alpha=307^\circ$, $r=0.89$, $P<0.001$; sham birds: $N=14$ track sections, $\alpha=310^\circ$, $r=0.85$, $P<0.001$). The magnet birds in fact showed slightly less directional scatter during the homeward trips than did sham birds. Thus adult waved albatrosses, even with strong stationary magnets attached close to their proposed magnetic sensory locations, showed no signs of reduced navigational abilities. Figs 2–6 and Table 2 summarize the results.

Cloud cover varied during trips (Table 2). The cloud scores in Table 2 are conservative, because when the satellite images were compared with local observations at Espanola, birds homing under cloud score '3–2' probably encountered completely overcast conditions. However, a few holes in the cloud cover cannot be excluded for any trip. Thus, all we can safely say is that both magnet and sham birds were able to home during predominantly cloudy conditions.

Discussion

This study provides detailed orientation data from wild, free-flying birds performing non-forced natural navigational tasks with magnets attached to their head. The navigational task facing our albatrosses was a double homing process between two well-known locations. If the two homing processes are compared, then the outward trip navigational task (Galápagos to Perú) seems relatively easy. Any bird flying approximately east will hit the South American continental shelf. By contrast, the homeward navigational task (Perú to Galápagos) seems more challenging, since it involves finding a small archipelago in a vast ocean. One would therefore expect that birds with reduced access to navigational cues would be most challenged during the homeward trip. Nevertheless, our data show that the homeward speeds of the magnet birds (30 ± 5 km h⁻¹) were not slower than those of the sham birds (28 ± 4 km h⁻¹), and the straightness of the tracks of the magnet birds show no signs of impaired ability to locate Galápagos in the vast ocean (Fig. 6). In fact, both magnet and sham birds travelled home to Galápagos faster

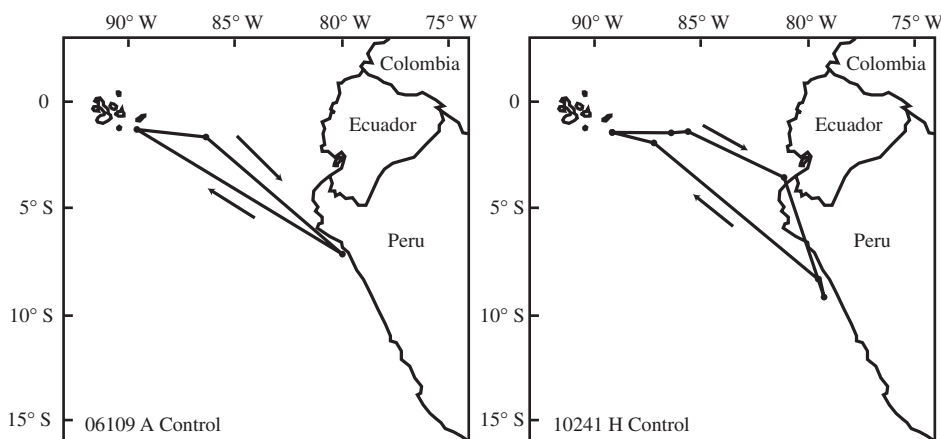


Fig. 2. Satellite tracks of two control birds tested in 2000.

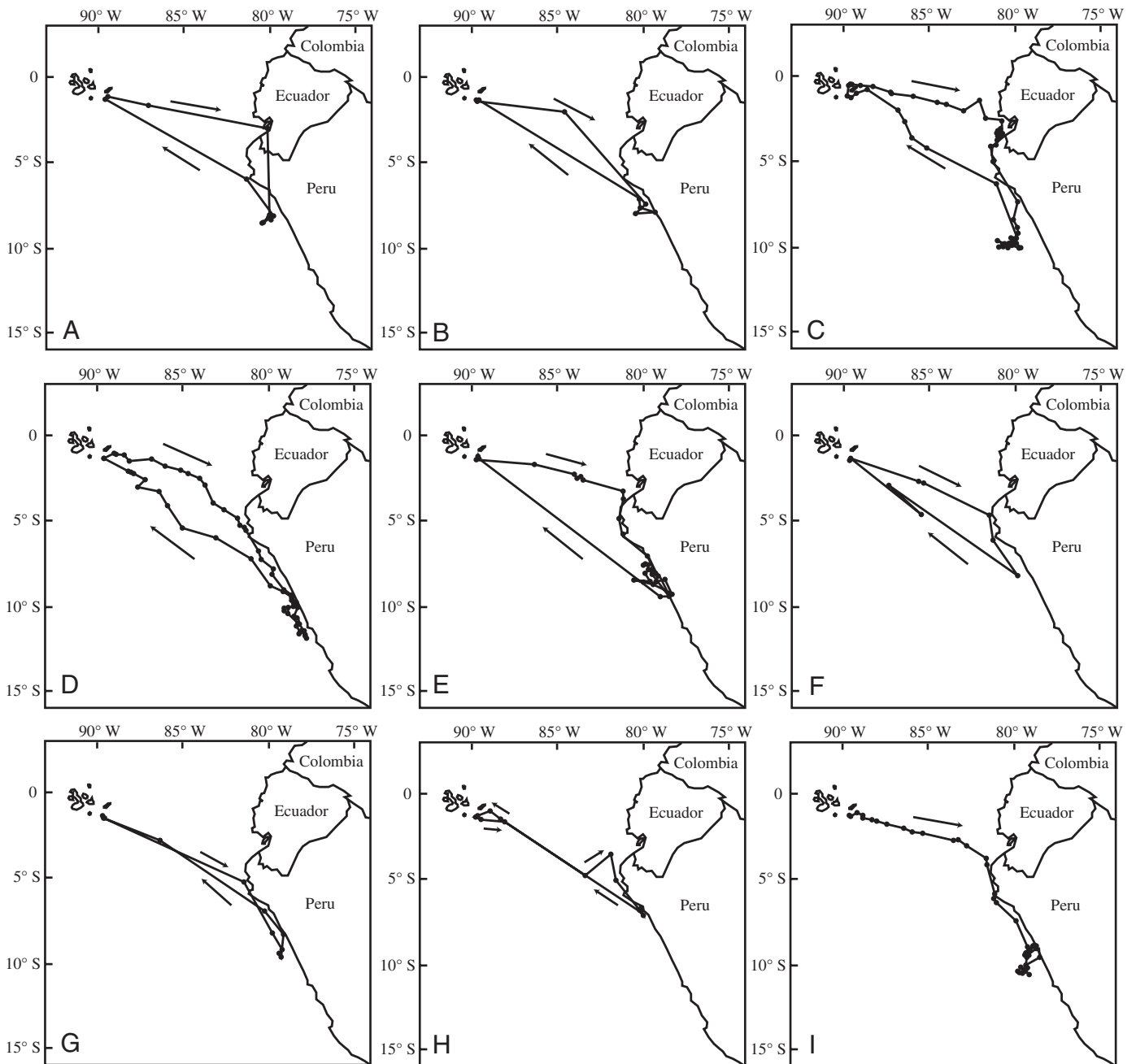


Fig. 3. Satellite tracks of sham birds tested in 2000–2001. (A,B) Birds returning with both shams still in place. (C,D) Tracks from birds returning with the nasal sham piece still in place. (E–I) Tracks of birds having lost both shams *en route*.

than they travelled during the outward journey. This difference could, however, be assisted by more favourable wind conditions (e.g. Anderson et al., 1998), the possibility of foraging on the outbound but not homebound legs, and/or a strong urge to return to the egg and relieve the incubating partner on the homebound leg. More favourable wind conditions may also explain the significantly more southerly homeward routes compared to the more northerly outward routes. However, the more southerly return routes could also be explained as a result of a deliberate strategy, where the albatrosses search the Peruvian upwelling zone for food from

north to south and then navigate back to Española along the most direct route.

Since we were conducting this study on a protected species with a limited distribution, we wanted to ensure that no animal would suffer from any long-term effects even if the magnets had a major effect on their orientation capabilities. To do this, we used a non-permanent attachment method designed to ensure that all magnets would fall off within 1–2 months, so that experimental animals would be able to regain their orientation and navigation capabilities in case the treatment had a dramatic effect on the birds' ability to find their way.

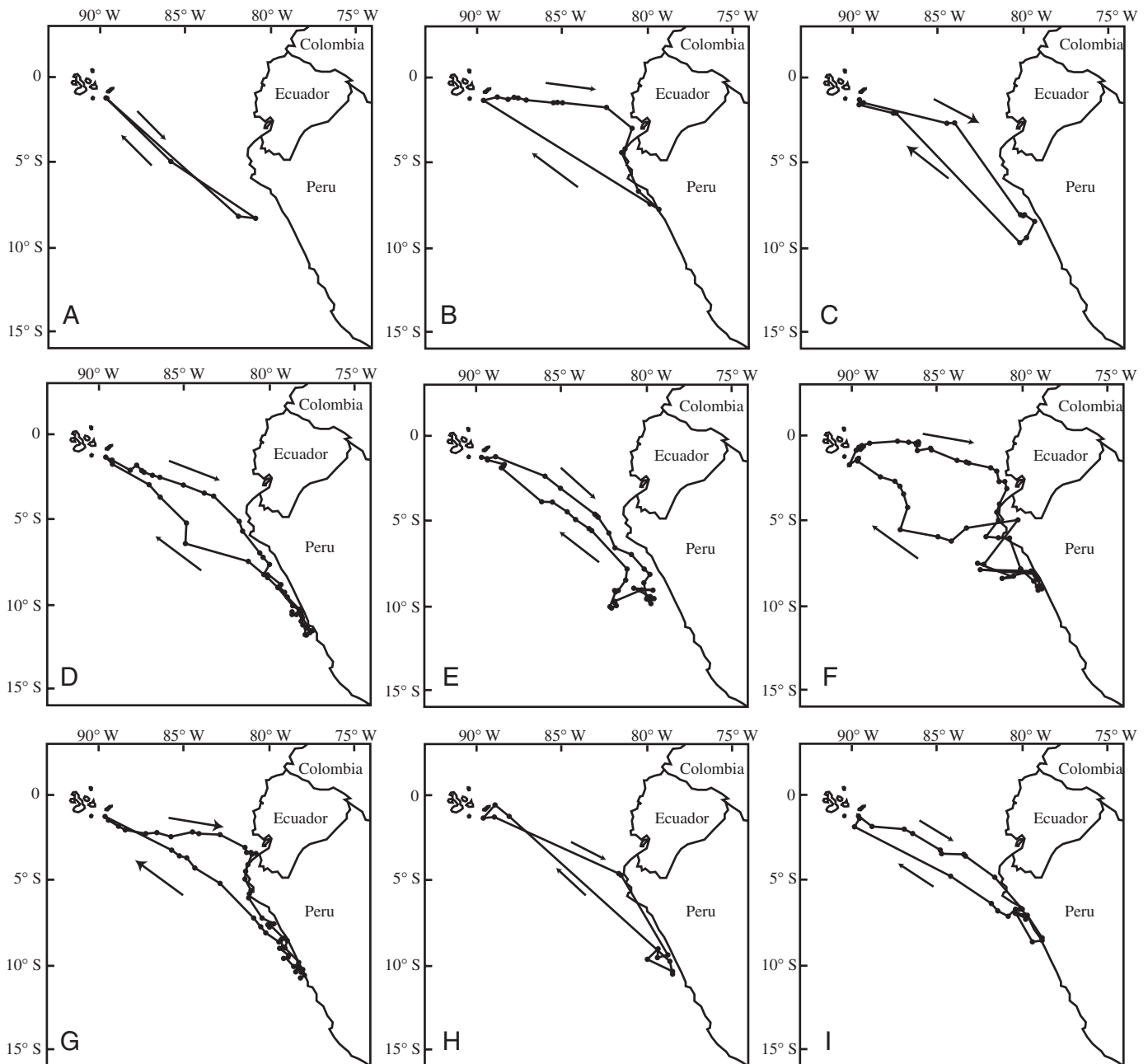


Fig. 4. Satellite tracks of magnet birds. (A–C) Birds returning with both magnets still in place. (D–G) Tracks from birds returning with the nasal magnet still in place. (H–I) Tracks of birds having lost both magnets *en route*.

Furthermore, we used attachment methods that did not impair the birds' feeding capabilities and could be easily removed without harming the birds when they returned with the attachments still in place. Subcutaneous placement of the magnets/shams was not a feasible option. Consequently, our attachment method was chosen as the best balance between the risks of losing the equipment prematurely and potential long-term effects on the subjects.

Of the 10 magnet birds, seven individuals returned with the small magnet still in position and three birds returned with the large magnet still in place (see Table 2). Of the nine sham

birds, four individuals returned with the small sham still in place and two birds returned with the large sham still in place. After fixing the magnets/shams, some birds stayed on their eggs for several days (up to 8) and they all retained their gear while in the colony. The birds that did lose the gear before returning probably did so when they had got to Perú and subjected the gear to saltwater and other foraging stresses. It is likely that most, if not all, birds carried both magnets/shams at least during the outward trip to the Peruvian coast. In any case, whether all birds were considered, or only those returning with the magnets still in place, no significant or suggestive

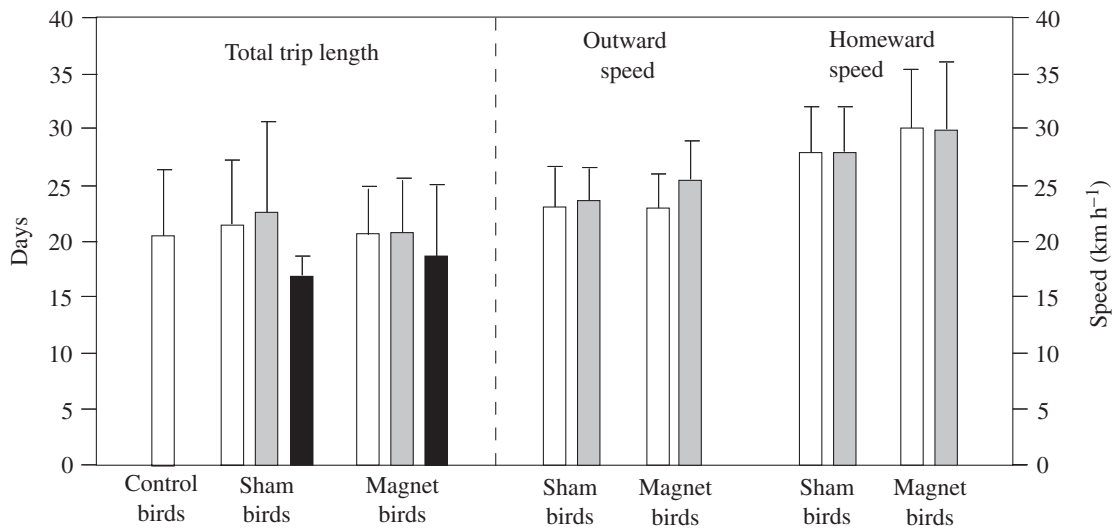


Fig. 5. Comparisons of total trip length, outward speed and homeward speed between treatment groups. No significant differences are observed. White bars, all birds; grey bars, birds with at least one magnet/sham in place upon return; black bars, birds with both magnets/shams in place upon return.

differences were observed with respect to delay before departure, total trip duration, outward straight-line flying speed, homeward straight-line flying speed, straightness of homeward journey, or large-scale route chosen.

Since four out of ten magnet birds returned with only the small magnet in place, it is relevant to discuss the disturbances in the Earth's magnetic field produced by the small magnet alone in relation to the proposed sensory mechanisms in the eyes and the nasal region. The head anatomy of the albatross means that the small front magnet will have imposed significant disturbances to the earth's magnetic field in the nasal and eye region, even if the large magnet was lost. The small magnet imposes an additional artificial field of strength 50 000 nT, 25 000 nT and 5000 nT at distances of 2, 3 and

5 cm, respectively, from the magnet. The distance (in cm) from the front magnet position (1) to the centre of the eyeball was 4.0 (males), 3.8 (females); (2) to the outer surface of iris, 3.3 (males), 2.9 (females); (3) to a point in mid-skull between the two irises, 2.7 (males), 2.6 (females); and (4) the diameter of eyeball, 2.0 (males), 1.9 (females). Even a change of 5000 nT in the vertical component would lead a bird using a magnetic map and relying at least partly on measuring inclination (the most reliable north–south magnetic parameter) to determine its position approximately 5 geographical degrees or ca. 555 km too far north or south of its actual position. Changes of 5000 nT or 25 000 nT in the horizontal component would make birds using a magnetic compass choose bearings that were off by up to 9.5° and 40°, respectively. Thus, even on their own, the small magnets would have produced significant disturbances in the magnetic field around the proposed magnetic sensory locations in the albatrosses' eyes and/or nasal region.

Can we be sure that magnetic field disturbances produced by stationary magnets completely inhibit birds' ability to obtain useful orientation information from the geomagnetic field? Below, we separately evaluate the theoretical influence of stationary magnets on magnetoreception for both the hypothesised magnetite-mediated and light-mediated sensory mechanisms.

Magnetite-mediated receptor, magnetic compass cues

When a stationary magnet positioned on the bird's head produces an additional horizontal magnetic field stronger than the Earth's field, the waved albatrosses cannot use any magnetite-mediated magnetic compass located in the head region, because a magnetite crystal will be affected by the total resultant field vector, and magnetic fields are vector fields. The resultant field vector is found by adding the magnetic field vectors from the attached magnets to the geomagnetic field

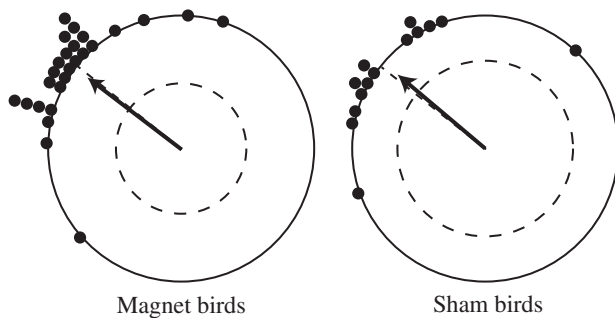


Fig. 6. Orientation of albatrosses returning from the Peruvian upwelling zone with magnets or shams still attached to their head. Each filled circle indicates the orientation of one section of the return journey, between two satellite fixes at least 100 km apart, for magnet and sham birds, respectively. The broken line indicates the correct homeward direction to Galápagos, and the broken circle indicates the length of the mean vector (solid arrow) required for significance at the 0.001 level according to the Rayleigh test.

vector. Consequently, if the horizontal disturbance from the stationary magnet is stronger than 30 000 nT (the approximate strength of the geomagnetic field around the Equator), the resultant magnetic vector stays in one half of the circle, for instance from west through north to east, so that no southern vector component ever exists, regardless of the geographical direction in which the albatross's head is pointing. Consequently, if birds use a magnetite-mediated magnetic compass, attaching a strong stationary magnet near the sensory location will prevent the bird from obtaining useful compass information from the Earth's magnetic field. For the same reasons, the possibility that waved albatrosses use magnetite-mediated magnetosensing to assemble outward journey information in a path integration strategy can also be excluded.

Light-mediated receptor, magnetic compass cues

As mentioned above, positioning a stationary magnet adding a field stronger than 30 000 nT to the head of a bird (for the large magnets, the artificial field at the eyes is much stronger than 100 000 nT) means that the resultant magnetic vector stays in one half of the circle (or even less) regardless of the geographical heading of the bird. At first glance, logic would lead one to conclude that such a compass would be dysfunctional no matter how the compass information is perceived. However, it could be argued that if birds use a radical-pair, light-mediated, magnetoreception mechanism (Ritz et al., 2000), they may be able to use the geomagnetic field as a compass even in the presence of a strong stationary magnet, since the ghost images hypothesised by Ritz et al. (2000) may still be modulated in a regular fashion. If that is the case, birds would, however, have to adapt to a completely new set of patterns. This would take some time and, more importantly, the birds would have to calibrate this novel pattern to another geographical frame of reference before it would be of use to them. We doubt that the albatrosses in this study had sufficient time to do this before they left the colony.

Light-mediated receptor, magnetic map cues

For theoretical reasons, birds using a light mediated, quantum-chemical mechanism are only able to sense the direction and gross strength of the total field, not the small modulations in intensity required for a magnetic map, and the currently suggested light-mediated mechanisms can therefore be excluded as magnetic map-senses.

Magnetite-mediated receptor, magnetic map cues

First of all, the evidence that birds can make use of minute gradients in the Earth's magnetic field strength and/or inclination to establish a magnetically based map is limited (Wiltschko and Wiltschko, 1995a). In fact, some researchers in the field challenge the validity of all evidence suggesting any involvement of a magnetic map-sense in pigeon and other bird navigation (e.g. Wallraff, 1999, 2001). For birds to derive positional information that is precise enough to locate a small island in a vast ocean, from a magnetic map-sense, they would need to sense their position relative to gravity with high

precision whilst also, in flight, detecting minute changes in the geomagnetic field's intensity (see e.g. Wallraff, 1999). If birds do have a magnetic map-sense, it must either rely on inherited magnetic parameters (which would then have to be based on fixed absolute values) or must be acquired by experience.

If a magnetic map-sense is based on measuring absolute values of magnetic parameters, a stationary magnet placed close to the sensory organ will obviously make it dysfunctional. If a magnetic map were instead acquired by experience, it could be plastic and/or based on relative values, and it could be argued that a stationary magnet might not interrupt the correct sensing of relative values, but remember that the magnetic field strength continuously varies up to 60 000 nT depending on the albatross's head orientation. Even if birds are able to deal with this highly unnatural situation, positional feedback from other cues facilitating a complete recalibration of the birds' map would be a prerequisite. Does a bird at the Peruvian upwelling zone have positional feedback available that would enable it to recalibrate all its magnetic map-values for use on its first journey after attachment of stationary magnets? That would require the birds to know/guess that the new 'magnetic anomaly' observed prior to leaving the colony is consistent all over the range covered by their magnetic map. We find that hard to believe.

Furthermore, any magnet glued to skin will be moving relative to any sensory location(s) inside the head of the bird, since the skin of waved albatrosses (and other birds) is not rigidly fixed to the skull. Consequently, even the most subtle movements of the stationary magnets relative to the sensory organ will be likely to produce magnetic disturbances too large to enable the bird to reliably sense the minute differences in the magnetic parameters needed to use the geomagnetic field as a map-cue.

Preliminary data (Haugh et al., 2001) from conditioning experiments with homing pigeons, *Columba livia*, suggest that pigeons can be trained to discriminate (rather poorly; 60–70% success rate) between two opposite directions based on a magnetic anomaly after a stationary magnet had been attached to their head. Are such results from conditioning experiments relevant to the interpretation of our albatross data? Birds in a conditioning experiment get direct feedback (in the form of a food reward) on how they should interpret the occurrence of a completely new magnetic field after application of a strong stationary magnet to their head. Therefore, adding a magnet to a bird's head in a conditioning experiment is merely a separate type of conditioning experiment. By contrast, no direct feedback is available to a wild free-flying bird trying to navigate over open ocean. Therefore, this type of conditioning experiment seems inadequate to answer the question of whether strong stationary magnets prevent free-flying navigating birds from obtaining useful information from the geomagnetic field.

Regardless of how birds may perceive magnetic fields, if our waved albatrosses needed to recalibrate a magnetic compass or a magnetic map, one would expect the magnet birds to stay in

the colony longer than the sham birds prior to departure. This is not the case. In fact, one magnet bird left the colony within just 5 h, and no significant differences in time to departure between magnet and sham birds were observed ($P=0.65$, see Results). Alternatively, if important navigational information had been disturbed, we expected that birds would not leave the colony or that they would feed in close proximity to the colony. Such behaviour by the magnet birds was not observed.

The ability of birds to home, orient and/or navigate with strong stationary magnets glued to their head has previously been found in homing pigeons and a few other species under mostly sunny conditions (for a review, see table 6.2 in Wiltschko and Wiltschko, 1995a). Our results agree with these findings. The only previous data from seabirds showed that Cory's shearwaters *Calonectris diomedea* could home over short distances (<400 km) with stationary magnets attached to their head, neck and wings (Massa et al., 1991) and that the trip lengths of black-browed albatrosses *Diomedea melanophris* were unaffected by the attachment of strong magnets (Bonadonna et al., 2003).

Given that the albatrosses in our study seem to have successfully navigated with strongly disturbed magnetic orientation cues, what other cue(s) could they have used to guide their open ocean navigation? The obvious compass candidate is the sun compass (Kramer, 1953; Schmidt-Koenig, 1961; Schmidt-Koenig et al., 1991). We did not observe reduced homing speed or increased trip length during cloudy conditions (see Table 2), yet it is difficult to be absolutely sure whether sun compass cues were available from holes in the clouds when, according to the satellite images, conditions appeared to be completely overcast. Therefore, we cannot exclude the possibility that the tracked birds had a sun compass available, at least irregularly, during all journeys reported here.

The waved albatrosses in our study may also have been aided partly by olfactory cues (Wallraff, 2001), particularly since the olfactory bulbs of procellariiforms (petrels, shearwaters and albatrosses) tend to show strong hypertrophy. The olfactory bulbs occupy up to 37% of the total brain volume in pelagic seabirds compared to ca. 3% in most other birds (Bang, 1966, 1971). Olfactory cues could provide map-like cues enabling seabirds to determine their position relative to home (Wallraff and Andreae, 2000) or they may provide a beacon-cue attracting birds to their destination.

In conclusion, our study shows that waved albatrosses are able to navigate between two well-known locations 1300 km apart along straight and predictable routes with strong magnets attached to their heads. Even though we find it unlikely that our albatrosses had access to any useful magnetic information, if their sensory organ is located in the head region, the definitive interpretation of these results depends on the magnetic sensing mechanism used by birds, and this is currently not known. So, while we cannot rule out that magnetic cues play a role in albatross navigation under natural conditions, our study does provide new, hard-to-obtain data from wild, free-flying birds performing non-forced natural navigational tasks in specifically manipulated magnetic fields,

against which future empirical and theoretical findings related to the magnetic sensory mechanism of birds can be evaluated.

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