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Do migratory flight paths of raptors follow constant geographical or geomagnetic courses?

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We tested whether routes of raptors migrating over areas with homogeneous topography follow constant geomagnetic courses more or less closely than constant geographical courses. We analysed the routes taken over land of 45 individual raptors tracked by satellite-based radiotelemetry: 25 peregrine falcons, *Falco peregrinus*, on autumn migration between North and South America, and seven honey buzzards, *Pernis apivorus*, and 13 ospreys, *Pandion haliaetus*, on autumn migration between Europe and Africa. Overall, migration directions showed a better agreement with constant geographical than constant geomagnetic courses. Tracks deviated significantly from constant geomagnetic courses, but were not significantly different from geographical courses. After we removed movements directed far from the mean direction, which may not be migratory movements, migration directions still showed a better agreement with constant geographical than constant geomagnetic courses, but the directions of honey buzzards and ospreys were not significantly different from constant geomagnetic courses either. That migration routes of raptors followed by satellite telemetry are in closer accordance with constant geographical compass courses than with constant geomagnetic compass courses may indicate that geographical (e.g. based on celestial cues) rather than magnetic compass mechanisms are of dominating importance for the birds' long-distance orientation.

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Much effort has been put into elucidating the orientation system responsible for guiding birds migrating long distances, often several thousands of kilometres, to their appropriate destinations. In many species, juvenile birds on their first migration perform this task without guidance from experienced conspecifics, and it is clear that at least a crude spatiotemporal migratory orientation programme is inherited (Gwinner 1996; Berthold 2001). However, the underlying orientation mechanisms used by free-flying birds on actual migration remain somewhat unclear (Alerstam 1996). Caged migrants have been shown to be able to use the geomagnetic field for migratory orientation (e.g. Wiltschko & Wiltschko 1995 and references therein); however, other studies have shown that birds can orient in the appropriate migratory direction also in the absence of magnetic cues but with celestial (stellar) cues present (e.g. Mouritsen 1998). Many studies have investigated the hierarchy among different orientation cues such as stars, sunset and the geomagnetic field (reviewed in Wiltschko & Wiltschko 1995; Able & Able 1996), but the results are equivocal. A recent field experiment by Cochran et al. (2004) indicated that songbirds used a sunset compass to select the direction for each

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night's flight, while the magnetic compass was calibrated relative to this sunset compass and used to maintain the flight direction during the dark hours of the night.

A few studies have evaluated constant compass course migration routes (i.e. routes following from migrating in a constant compass direction) in relation to the geomagnetic field. Using routes extrapolated from observations at single sites, Alerstam & Gudmundsson (1999), Alerstam et al. (2001) and Muheim et al. (2003) found that migration routes of arctic birds could not be reconciled with orientation along either constant geographical or magnetic compass course routes.

We tested the effect of geomagnetic declination on the track directions of individual birds of three raptor species, which were recorded by satellite-based radiotracking throughout their autumn migration between Europe and Africa (honey buzzards, *Pernis apivorus*, and ospreys, *Pandion haliaetus*) and between North and South America (peregrine falcons, *Falco peregrinus*). We removed coastal movements from the data set to exclude the influence of major topographical features and also excluded sudden deviations from the general track that are probably external to migratory direction. Our objective was to investigate whether the tracks over relative homogeneous areas, where birds can be presumed to be guided predominantly by their compass, adhere most closely to constant geographical or constant geomagnetic compass courses. The first alternative would indicate a dominating influence of celestial compass mechanisms on the large-scale orientation of the birds, while the second alternative would indicate that the birds primarily use their magnetic compass mechanism for long-distance orientation.

There are important differences between geomagnetic and geographical directions, and the geomagnetic declination (the difference between the directions to the geomagnetic and the geographical North Pole) varies with global position. When following a constant geomagnetic compass course and moving towards increasing declination, geographical courses change clockwise, and the gradual course change is anticlockwise when moving towards decreasing declination. In North America this means that expected autumn routes for birds orienting along a fixed magnetic course curve anticlockwise (south to east) when migrating southeast in western North America and clockwise (south to west) when migrating southwest in the east. In Europe autumn routes towards the southwest are expected to curve anticlockwise.

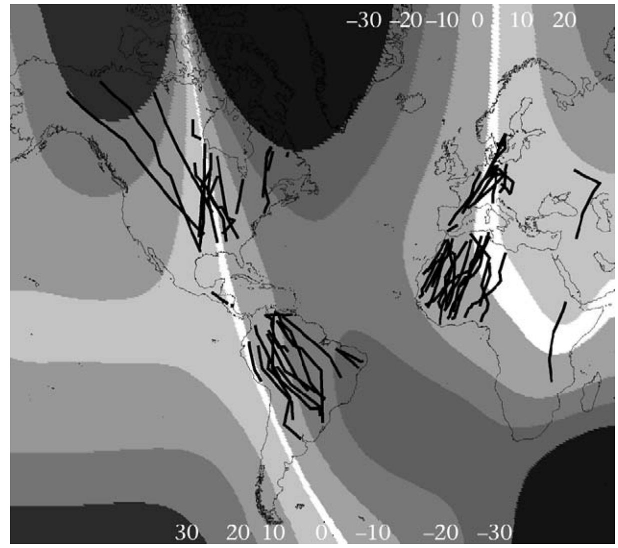

Figure 1. Map showing analysed tracks (lines) and isoclines of geomagnetic declination. Intensity of shading indicates declination strength; the 0 interval includes declinations from −1° to +1°. American birds are peregrine falcons. Palearctic—African birds are honey buzzards and ospreys combined. Black lines show migratory segments well away from the coast. Track data from Fuller et al. (1998), Hake et al. (2001, 2003) and Kjellén et al. (2001). (Mercator projection.)

METHODS

Satellite-tracking Data

We used data from raptors on autumn migration tracked with the satellite-based radiotelemetry of the Argos system (Fig. 1) previously published by Fuller et al. (1998), Hake et al. (2001, 2003) and Kjellén et al. (2001). The data set comprised trackings of European and North American birds. The European part consists of adult ($N = 11$) and juvenile (yearling, $N = 2$) ospreys and juvenile honey buzzards ($N = 7$). In addition to the results for three juvenile honey buzzards presented by Hake et al. (2003), we included data for four juvenile honey buzzards tracked by satellite-based radiotelemetry from Sweden to tropical West Africa in the autumns of 2004 and 2005. In both species the juveniles migrate independently from the adults, and ospreys especially normally travel solitarily (Hake et al. 2001). The American part of the data set consists of peregrine falcons ($N = 49$ adults). This species normally also travels solitarily and might be less dependent on soaring flight than ospreys and honey buzzards (but see Cochran 1985; Cochran & Applegate 1986), and thus less influenced by topographical features.

We used segments between positions separated by at least 1 day (a few adult ospreys), or for most individuals at least 3 days and 100 km (segment length was usually 300—800 km), resulting in a total of 252 European segments (272 position readings) and 478 American segments (544 position readings). Segments were separated by at least one stationary nocturnal resting period giving time for new orientation decisions. Hence, we have regarded these segments as independent observations in our statistical analyses, and individual autocorrelations between consecutive segments were not significant. The nominal accuracy of the positions was either within 1 km (31%; categories 3, 2 and 1 in the Argos system) or of unspecified accuracy (categories 0, A, B and Z in the Argos system; category Z less than 1%; http://www.cls.fr/manuel/).

Our analysis is restricted to segments where birds have presumably been guided by their compass. Thus, we excluded segments close to the coast. From the data set, we removed segments (straight lines between positions) close to the coast by using ESRI ARCVIEW 3.2 software (ESRI, Redlands, CA, U.S.A.). As bird tracks are not usually straight and uncertainty is associated with position estimates from the Argos system, we chose to remove segments that at any point were closer than 50 km to the coast. Furthermore, we did not include trackings of adult honey buzzards since they make a distinct detour when travelling to their winter sites, changing their direction abruptly along the migration route (Hake et al. 2003).

Argos satellite system transmitters (Platform Transmitter Terminals, PTTs) produce static and transient magnetic fields (P. W. Howey, personal communication), and these could disturb the sensing of the geomagnetic field. The static fields are caused by the magnetic components of the transmitter. Transient fields are caused by power production in the battery (a DC field) and actual transmission (an AC field), and both are strongest when actually transmitting, which is about 0.33 s every minute. The magnetic field produced by the PTT transmission is a high-frequency AC field, and it is doubtful whether a biological system can respond to such a system (P. W. Howey, personal communication). According to Mouritsen et al. (2003), only negligible magnetic disturbances to the geomagnetic field are produced by 30-g PTTs (Microwave Telemetry Inc., Columbia, Maryland, U.S.A.) similar to the ones used in this study. At 10 cm from the transmitter, the magnetic field produced by a transmitting or silent transmitter (<300 nT) is in the same order of magnitude as daily variations in the geomagnetic field and less than 1% of the natural geomagnetic field at the study site (table 1 in Mouritsen et al. 2003). For the raptors included in this study, the distance from the transmitter to the head of the bird was 10−15 cm.

Statistical Analysis

To calculate geographical loxodrome (constant geographical compass course) directions between the consecutive positions, we used the formulae in Imboden & Imboden (1972). For each segment (track between positions), we estimated geomagnetic declination at the mid-point of the segment from 0.1° latitude/longitude declination grids. We calculated declination grids for 15 September each year 1995−2005 with tracked birds according to the WMM-1995 and WMM-2000 models (Quinn 2000, http://www.interpex.com/magfield.htm).

The slope of the relation between geographical track direction and magnetic declination is expected to be 0 if the birds maintain constant geographical courses and +1 if they orient according to constant geomagnetic courses. Slopes deviating significantly from both 0 and 1 (e.g. <0 or >1) indicate curved routes where the birds change their track directions in relation to both geographical (celestial) and geomagnetic compass cues (Table 1). This could be the result of cues external to these compasses.

We fitted general linear models (GLM) to the data sets, using PROC GLM in SAS (SAS 1990). We included individual bird identification (ID) and geomagnetic declination as independent variables, and we entered geographical direction as the dependent variable. Individual ID accounted for differences in mean direction between individuals, and including geomagnetic declination gave estimates of the slope of the relation between direction and declination. In general, the interaction term ID*declination was not statistically significant when added to the GLM model, and hence the term could be omitted.

Many individual routes did not span a large interval of declinations compared to the variation in directions between consecutive segments. Thus, individual relations between geographical direction and declination were relatively variable. As no significant effect of ID on the relations with declination was found, it seems justified to use the combined data set. This resulted in a larger span of declinations and less variation in estimates. Thus, our analyses show results for overall migration routes, not for individual birds.

Because migration direction and declination are circular variables, the correlation and regression measures are not the same as those used for linear variables (Fisher 1995). However, both variables show large concentrations justifying the use of linear statistics on the circular data, and we obtained similar results with circular statistics. As linear statistics permit easy inspection and identification of the data, we give only these results throughout. To use circular statistics, we calculated sine-transformed linear variables from the circular variables as sine (migration direction − mean migration direction) and sine (declination), respectively.

The treatment used assumes that the observed variation in track direction is random variation from a mean migration direction. However, some apparent migration movements, especially in adults, might have been trips to known foraging areas or, alternatively, simply the result of erroneous position readings. To control for this we also ran the analysis on a data set from which we removed directions deviating the most from mean direction (we arbitrarily removed directions deviating more than 45°).

Table 1. Our interpretation of different values of the slope of geographical course as a function of declination

Slope	Geographical	Geomagnetic	Possible interpretation
<0	−	−	Curved route
≈0 and <1	+	−	Geographical compass
>0 and <1	−	−	Combination/curved route
>0 and ≈1	−	+	Geomagnetic compass
>1	−	−	Curved route

≈: Not significantly different from; < or >: significantly different; +: the respective constant compass course is accepted; −: the respective compass course is excluded.

RESULTS

The slopes between geographical courses and magnetic declination were, for all three species, closer to the expectation for constant geographical compass courses (i.e. closer to 0) than for constant geomagnetic compass courses, differing significantly from a constant geomagnetic course but not from a geographical one (Table 2, Fig. 2). In North American peregrine falcons, the slope of the relation between geographical courses and geomagnetic declination (−0.16; Table 2) was close to the expectation from a constant geographical compass. In European honey buzzards and ospreys, the slopes of the relation between geographical courses and declination in data sets were less than expected from a constant geographical compass (slopes of −2.89 and −2.22, respectively; Table 2).

After we removed directions deviating more than 45° from the mean direction, the slopes were also closer to the expectation for constant geographical compass courses than for constant geomagnetic compass courses. For North American peregrine falcons, the slope of the relation between geographical courses and geomagnetic declination (−0.35; Table 2) was close to the expectation from a constant geographical compass. In European honey buzzards and ospreys, the slopes of the relation between geographical courses and declination in data sets were close to the expectation from a constant geographical compass (slopes of +0.09 and −0.78, respectively; Table 2), but they were not significantly different from the expectation from a constant geomagnetic compass either.

DISCUSSION

Overall, the observed patterns are described best by constant geographical courses, and in no cases do the tracks indicate the use of constant geomagnetic courses. Geographical rather than geomagnetic courses were indicated for all subsets. Visual inspection of migration routes of North American ospreys obtained in a study by Martell et al. (2001), with similar breeding and winter areas to the peregrine falcons in our study, showed similar paths to those taken by the peregrine falcons in our study, as did adult peregrine falcons from Alaska tracked by Britten (1998).

The nonsignificant directional change observed along the migration route in honey buzzards and ospreys, with birds moving more south in Europe and more southwest in Africa, is in the opposite direction to the one expected according to changes in geomagnetic declination (assuming orientation along a constant geomagnetic course). Hake et al. (2001) also noted that there is no general tendency for a gradual leftward geographical course shift among the ospreys, as would be expected if they oriented along a constant magnetic compass course.

In Europe, constant geomagnetic compass course routes are slightly shorter than geographical compass course routes and vice versa in North America (Alerstam 2001). However, according to our results European birds did not seem to take advantage of the possibility of flying along the distance-saving constant magnetic compass course routes.

Mechanisms

Our results indicate that, if constant compass orientation occurs over longer distances on migration, celestial compass mechanisms guiding the raptors along constant geographical courses are of dominating importance, while the raptors seem not to follow constant geomagnetic courses over long distances. This does not necessarily mean that the geomagnetic compass is used to a small degree on migration; it may still be highly important and frequently used, for example after recalibration to celestial cues (cf. Cochran et al. 2004) and in temporary situations when celestial cues are lacking.

Several studies have demonstrated the importance of the magnetic field for orientation in cages (reviewed in Wiltschko & Wiltschko 1995). Reviewing the hierarchy among orientation cues, Wiltschko & Wiltschko (1999) concluded that birds during migration generally calibrate geographical (celestial) cues using directional information from the geomagnetic field as the external reference, at least after several exposures to a manipulated magnetic field. They found only one contradictory study, where, in Savannah sparrows, *Passerculus sandwichensis*, geomagnetic

Table 2. Effect of geomagnetic declination on direction using circular variables

Data	N_i	N	Slope (a)	P (a=0)	P (a=1)	Geographical	Geomagnetic
Full data set							
Osprey	13	92	−2.22	0.07	0.01	+	−
Honey buzzard	7	65	−2.89	0.08	0.02	+	−
Peregrine	25	106	−0.16	0.72	0.009	+	−
Data set excluding large angle deviations (>45°)							
Osprey	13	82	0.09	0.88	0.14	+	+
Honey buzzard	7	58	−0.78	0.48	0.11	+	+
Peregrine	24	93	−0.35	0.31	0.0002	+	−

Models for each species include declination, intercept and ID (ID accounts for differences in individual mean directions; estimated intercept and individual means not given). N_i: the number of individual birds; N: the number of segments used for analysis in a given model; Slope: the slope (a) of the relation between geographical course and declination; P ($a=0$): the probability that the slope is 0; P ($a=1$): the probability that the slope is 1; +: the respective constant compass courses are accepted; − : the respective compass courses can be excluded. Ospreys are adult and juvenile birds combined, honey buzzards are juveniles only and peregrine falcons are adults only.

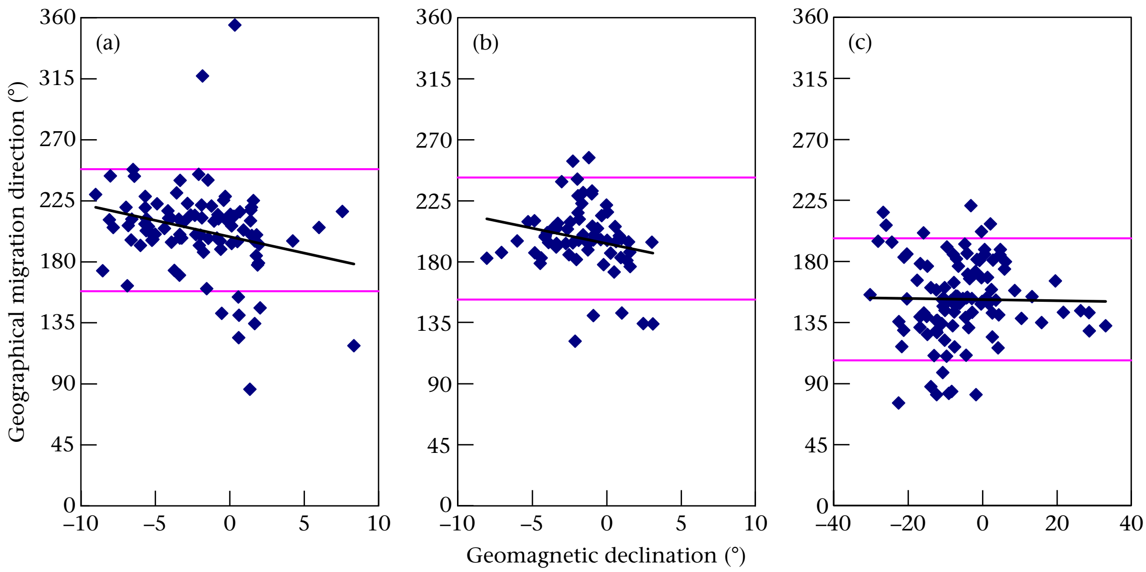

Figure 2. Relation between geographical migration direction and geomagnetic declination. (a) Adult and juvenile ospreys, (b) juvenile honey buzzards and (c) adult peregrine falcons. A slope of 0 is expected if birds migrate along constant geographical compass course routes and a slope of +1 if birds migrate along constant geomagnetic compass course routes. Thick lines are slopes and horizontal lines mark migration directions deviating more than 45° from the mean direction. In all cases, constant geographical directions fit better than geomagnetic directions (cf. Table 2). Note the different scales on the *X* axis for ospreys/honey buzzards and peregrine falcons.

cues seemed to be recalibrated by celestial cues (Able & Able 1996), and it is unclear whether the different responses found are due to species-specific differences or experimental conditions. However, it would be difficult to imitate in cage studies the complex conditions met over long ranges by free-flying birds, and our results indicate that over longer migration distances the birds were not primarily guided along constant geomagnetic compass courses.

Studying birds in free-flying conditions, Sandberg et al. (2000) found evidence that released birds followed for short distances had recalibrated their geographical compass according to a manipulated magnetic field. Contrary to this, Cochran et al. (2004) found evidence that the magnetic compass was recalibrated from twilight cues before migratory flights in birds that they followed by conventional radiotelemetry for full migratory flights. If birds recalibrate their magnetic compass daily from twilight cues, using the sunset azimuth as a fixed reference as suggested by Cochran et al. (2004), the birds' tracks should follow neither constant geomagnetic nor constant geographical course routes (since the sunset azimuth changes with season and latitude).

Homing by birds has been studied intensively (e.g. in pigeons, *Columba livia*). Vanishing bearings of homing birds indicate the use of a geomagnetic compass, but homing success (navigation) is not affected by magnets that disturb this compass (Wiltschko & Wiltschko 1995; Wallraff 1996). In studies on long-ranging birds where the magnetic field has been disturbed with attached magnets (Benhamou et al. 2003; Bonadonna et al. 2003, 2005; Mouritsen et al. 2003), no impairment of home-finding capability was found in spite of the disturbance of the magnetic compass, and similar results were obtained on migratory green turtles, *Chelonia mydas* (Papi et al. 2000). These results show that the animals are at least able to use means of orientation other than the geomagnetic field. Radiotransmitters used for satellite tracking produce a weak magnetic field, which is generally smaller than the daily variations in the geomagnetic field (Mouritsen et al. 2003). This field is unlikely to have prevented the use of the geomagnetic field as a cue. However, even if its use was prevented the results still show successful orientation to the wintering grounds in the absence of the geomagnetic field.

The geomagnetic compass may still be important for migrating birds, such as under cloud cover or when migrating long distances east or west, where resetting of the internal clock may be problematic. Furthermore, the patterns seen in raptors and seabirds need not be the same for all birds. These birds fly primarily by day and regularly use soaring flight (either thermal or wave soaring). Thus, the relative importance of the different compasses may be different in, for example, night-migrating passerines using sustained flapping flight.

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