ANIMAL BEHAVIOUR, 2006, **72**, 875–880
doi:10.1016/j.anbehav.2006.01.028

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

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(Received 27 June 2005; initial acceptance 10 August 2005; final acceptance 3 February 2006; published online 1 September 2006; MS. number: 8591R)

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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0003–3472/06/$30.00/0
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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.

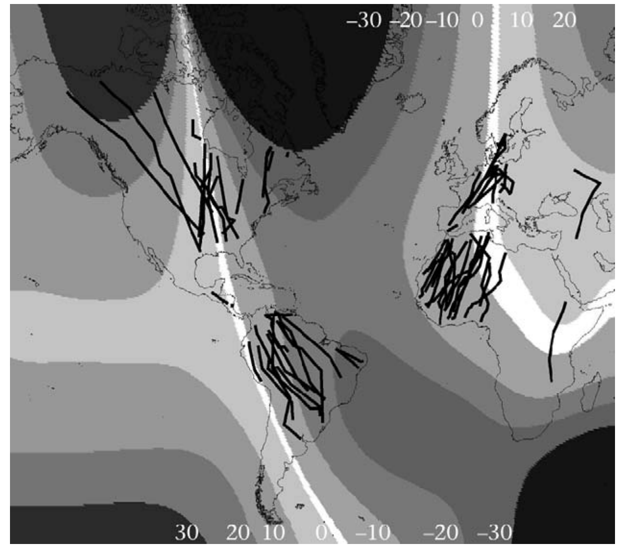

Figure 1. Map showing analysed tracks (lines) and isoclines of geomagnetic declination. Intensity of shading indicates declination strength; the 0 interval includes declinations from $-1°$ to $+1°$. American birds are peregrine falcons. Palearctic–African birds are honey buzzards and ospreys combined. 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