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Short communication

Naïve migrants and the use of magnetic cues: temporal fluctuations in the geomagnetic field differentially affect male and female Ruff *Philomachus pugnax* during their first migration

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In many species, naïve first-time migrants undertake migration without adults, supposedly on the basis of a 'simple' vector programme that combines an innate directional preference with a temporal programme that specifies distance. In strongly dimorphic species in which the sexes show distinct ecological requirements, the innate mechanisms of navigation may be expected to diverge between males and females with respect to their specific destinations. Based on captures of juvenile

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Ruff *Philomachus pugnax* at a migratory stopover over 21 years, a correlation was found between the year-specific sex ratio and the global magnetic field disturbance during the 2 weeks prior to the peak of captures in that year. This suggests that males and females respond differently to geomagnetic disturbance with changes in either the direction of migration or the level of migratory activity, and implies sex-specificity in the use of their geomagnetic navigational 'toolbox'.

On the basis of caged animals exposed to artificially altered magnetic fields, it has become well established that a wide range of vertebrates are capable of orientation by geomagnetic cues (Johnsen & Lohmann 2005). Numerous experiments have confirmed that geomagnetic orientation provides a fundamental source of knowledge on direction in diverse bird species (Wiltschko & Wiltschko 2005), but methodological limitations have kept the range of species studied small (Guilford *et al.* 2011). Most such studies have been carried out with adult birds, which are suggested to have a bi-coordinate map, derived at least in part from large-scale spatial gradients in the intensity and/or inclination of the magnetic field. (We adopt usage of 'map' from Lohmann *et al.* (2007): the term 'magnetic map' is a convenient shorthand that encompasses all uses of positional information derived from spatial variation 'in the Earth's field and makes no assumptions about the nature of the internal spatial representation (if any) that a particular animal has'.) However, few experiments have been done on inexperienced juvenile birds travelling without adults (Munro *et al.* 1997, Wiltschko & Wiltschko 2005) and only one has investigated navigation differences between adult and juvenile individuals (Deutschlander *et al.* 2012). The latter detected no evidence for a magnetic map in juveniles of the Australian Silvereye *Zosterops lateralis lateralis*, suggesting initial 'vector' navigation based on a magnetic compass alone, with the development of a bi-coordinate map during the first migration.

So far, no studies have been undertaken to investigate possible sex differences in the orientation and navigation of birds. Such differentiation may be expected in species in which males and females differ in their ecological requirements and which therefore use different migration routes to reach different wintering areas. In such species, an innate navigational programme for the first migration is likely to show sex differences. The independent evolution of such sex-specific traits could follow two scenarios: (i) evolution of the same navigational algorithms accompanied by a difference in how the

collected information is used between sexes, or (ii) independent use of two separate navigational systems.

The strongly sexually dimorphic Ruff *Philomachus pugnax* would seem an excellent species to study such sex-specific differences. Not only do Ruffs exhibit considerable sexual dimorphism in morphology and breeding behaviour (Hogan-Warburg 1966, van Rhijn 1991), the sexes also have distinct migration routes and wintering ranges (Girard 2009), with females mainly wintering south and southeast of the Sahara and males wintering either in Europe or in West Africa. Because juvenile Ruff migrate independently from the adults, they are likely to rely on innate navigational programmes during their first movements away from the breeding grounds.

Natural variation in the Earth's geomagnetic field caused by flows of charged particles released by solar flares (Gould 1984) provides a means by which to test the mechanisms of bird navigation. In situations in which geomagnetic orientation cues are important for navigation, one may expect negative correlations between the strength of geomagnetic field fluctuations and navigational performance (Schreiber & Rossi 1978, Alerstam 1990) and/or bird behaviour (Southern 1969). Previously, it has been shown that when natural spatial (local geomagnetic anomalies; Alerstam 1990) or temporal disturbances (geomagnetic field fluctuations; Keeton *et al.* 1974, Larkin & Keeton 1976, Richardson 1976, Moore 1977, Kowalski *et al.* 1988) occur, systematic variation in the bearings of migrating birds are observed. Here, we explore the effects of geomagnetic field disturbances on juvenile Ruff during their first migration by examining sex ratios in catches at Finnish migratory stopover sites.

METHODS

Between July and September in the years 1982–2006, a total of 1492 migrating first-year Ruff were captured in walk-in traps at ringing stations in southern Finland (Jaatinen *et al.* 2010), mostly at Raasio Wader Ringing Station (63°9′N, 27°43′E). The start and end dates of the capture sessions were set to cover the entire period of autumn migration, during which adult Ruff are only rarely caught or seen in southern Finland. First-year Ruff can be distinguished from adults by the rusty feather edges in their dorsal plumage (Cramp & Simmons 1983). Sexes were distinguished on the basis of wing lengths (maximum chord; Bairlein 1995), females having wings <170 mm (Jukema & Piersma 2004, 2006, Karlionova *et al.* 2007). Three years with fewer than 10 individuals captured (1983, 1984 and 1988) were removed from the analysis, and the final dataset contained 1478 individuals caught over 21 years. Sex ratios in captures were significantly biased towards females. Potential

reasons for this sex ratio bias have been discussed previously (Jaatinen *et al.* 2010), and we here focus instead on its year-to-year variation.

In view of our ignorance of the provenance of the young Ruff captured in Finland, which could come from as far away as easternmost Siberia (Girard 2009, Rakhimberdiev *et al.* 2011), we used the daily Average Planetary Magnetic Index (Ap) as a predictor. The Ap index indicates the average amplitude of the fluctuations of the K index (Lincoln 1967), widely used in earlier studies, and has been shown to be one of the best indices of the effect of magnetic fluctuations on homing behaviour of domesticated Rock Doves *Columba livia* (Schiffner & Wiltschko 2011). The indices are obtained from a network of geomagnetic observatories of the National Geophysical Data Center (www.ngdc.noaa.gov/stp/geomag/apstar.html) and are defined on the basis of variation in intensity of the horizontal component of Earth's magnetic field, which in turn is associated with fluctuations in total intensity, inclination and declination.

We tested for a linear relationship between yearly sex ratios in the juvenile Ruff and the intensity of geomagnetic disturbance during the migration period of the same year by logistic regression with the proportion of males (weighted by sample size) as the dependent variable (proportional data design in R; Crawley 2007, R Core Team 2013). For each year, we calculated weekly averages of daily Ap for 12 weeks preceding each year's peak of autumn captures. The 12 weekly average Ap values obtained for each of the intervals were used as explanatory variables in separate regression models. This 12-week period in advance of the migration peak covers all of the breeding and pre-breeding stages of the annual cycle in these waders, and these weeks were numbered from the peak of capture backwards to the pre-breeding period of the same calendar year. Thus, the first two (2 weeks before the peak of captures) coincided with active migration, weeks 6–10 coincided with breeding, and weeks 11–12 with the pre-breeding period. The best model was indicated by the lowest Akaike information criterion (AIC; Akaike 1974). As average Ap was highly correlated between the periods within each year (mean Pearson correlation coefficient = 0.39 ± 0.2 sd), traditional Bonferroni corrections for multiple comparisons were made with the per-test critical α level adjusted to 0.004.

To test for a relationship between sex ratio and Ap, we used the former as the dependent variable in a Poisson logistic regression. To assess whether geomagnetic disturbance delayed (or accelerated) arrival of one of the sexes at the research site, we calculated lags between peaks of arrival of males and females for each of the years and used these as response variables in linear models with the same for each of 12 weekly Ap averages as the explanatory variable.

RESULTS

The model with Ap averaged for the second week before the peak of captures (i.e. the period of most intensive migration) was the most parsimonious among the 12 models (AIC weight = 0.91; Burnham & Anderson 2002). The proportion of males was negatively correlated with average daily Ap for the second week preceding the peak of captures (Fig. 1), which explained 45% of the deviance (D^2, Guisan & Zimmermann 2000) in the proportion of males ($P < 0.0001$). This was significant after a Bonferroni correction. There was no evidence that the time-lag between peaks of arrival of the two sexes correlated with geomagnetic field disturbance in any of the periods. This means that after the period of disturbance, males or females arrived in different proportions, but not systematically earlier or later.

DISCUSSION

The strong negative correlation between the proportion of males in flocks of Ruff at migratory stopover sites in southern Finland and Ap during the time of migration towards these sites suggests that disturbance of the geomagnetic field affects the sexes differently during migration, but not during the breeding period (the AIC weight of 0.91 of the best model makes it over 10 times
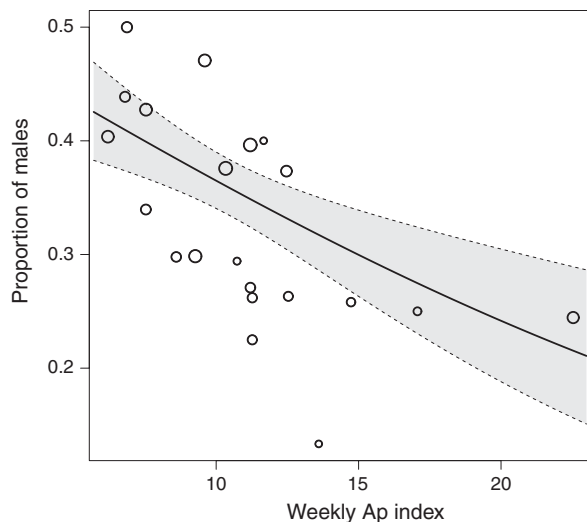

Figure 1. Year-specific sex ratios of juvenile Ruffs staging in southern Finland as a linear function of the average Ap for the week prior to the peak of captures in that year. Dots show original data with size proportional to log of number of birds per sample where the smallest symbol = 15 birds and the largest = 181 birds. The line gives the prediction from a Poisson logistic regression, with the shadow encompassing 95% confidence interval of the mean.

more likely than the others). Thus, we do not consider variation in sex-specific fledgling production or other effects during the breeding season to be potential causes of the observed effect.

The correlation explained 45% of the variance in sex ratios, a proportion that is normally considered quite substantial in ecological studies. However, as we are proposing the first evidence of magnetic-dependent sex ratio variation in a migrating wild bird, it may be worth considering the logical possibility that the observed effect is due to a spurious correlation with other factors (Fig. 2). There is a possibility (i) that both magnetic field and sex ratio depend on another unexplored factor or (ii) that magnetic field affects sex ratio indirectly by altering some other factors, e.g. weather. In most cases in which an ecologist evaluates the potential of a hidden factor controlling variation in two other variables and causing a correlation between them, there is usually a rich set of possible confounding factors (weather, changes in habitats, competitors, etc.) that could be at work. In this case, however, we are seeking a confounding factor that is external to the 'sun activity – Ruff population' system. We can only conceive of time as a potential factor that affects both. Given that neither magnetic activity nor Ruff sex ratios (Jaatinen *et al.* 2010) showed any discernible patterns with time, we conclude that Scheme 1 cannot explain the correlation between these two variables.

With respect to the second explanation (Scheme 2 in Fig. 2), i.e. that some other intermediate effect of variation in solar activity could be causing the variation in sex ratio, we feel that this is very unlikely. We know that the joint effect of A and B explains 45% of the variance in the data (A × B ≤ 0.45), so we should explore B (i.e. some factor that drives sex ratio and is affected by sun activity). We know that B would have to be ≤1, which would imply that A would be ≥0.45. To the best of our knowledge, the strongest effect of solar activity on any weather variable has been van Loon and Shea's (1999) finding that solar cycles may explain up to 44%
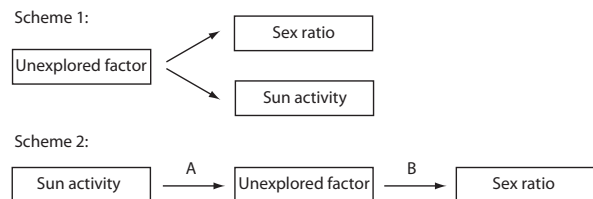

Figure 2. Potential alternative relationships that may cause correlation of sun activity and sex ratio. Scheme 1 suggests that sex ratios and geomagnetic field oscillations are both affected by some unmeasured factor, and Scheme 2 suggests that there is some additional relationship, but not the oscillation of the magnetic field, that causes the described relationship.

of the variance in the change in mean summer temperature of the troposphere. Because it would be unlikely for A to be so high (most other environmental correlations with solar activity are much weaker) and for B to be very close to 1, we conclude that sex ratio is directly linked to solar geomagnetic activity.

There are two main navigational mechanisms that might be affected by temporal variation in the magnetic field: (i) compass and (ii) bi-coordinate map. The changes of AP we describe here are too weak to affect magnetic compass orientation, i.e. a deviation in the direction of magnetic north of less than 1° (Mayaud 1980), but they could affect estimates of geographical position derived from a magnetic map. If, for example, during the first migration females use the inclination compass to orientate in a fixed direction (vector strategy), whereas males use an inherited bi-coordinate map (true navigation), variation in the magnetic field may cause males to change their routes and appear at the catching site in Finland less often, biasing the sex ratio towards the other sex (Fig. 3a). Evidence for inheritance of a magnetic map has been obtained in juvenile Loggerhead Turtles *Caretta caretta* (Lohmann *et al.* 2012) and very recently for the Pacific Salmon *Oncorhynchus tshawytscha* (Putman *et al.* 2014). However, the available evidence indicates that juvenile birds rely on a vector strategy that combines an innate compass preference with a temporal programme that specifies distance (Wiltschko & Wiltschko 2009). A subsequent test of the magnetic map hypothesis was negative with juvenile birds, although positive for adults (Deutschlander *et al.* 2012).

Even if there is no inherited bi-coordinate map in juveniles, birds that have completed one round-trip migration to and from the wintering grounds do appear to make use of a bi-coordinate map at least partially derived from the geomagnetic field (Munro *et al.* 1997, Fischer *et al.* 2003, Deutschlander *et al.* 2012). If this is the case, naïve birds on their first migration (even if guided by a 'vector strategy') should keep track of magnetic values so that they can use spatial variation in the magnetic field to help guide the return to their breeding grounds. For this spatial information to be as accurate as possible, it is conceivable that they have evolved a mechanism to avoid migrating when there are high levels of magnetic activity. Preliminary evidence that temporal variation in the magnetic field may suppress the expression of migratory orientation by young birds was obtained in an early study of Ring-billed Gull *Larus delawarensis* chicks and fledglings (Southern 1969, 1971). Under this scenario, if one of the sexes is less likely to initiate migration when there are high levels of temporal variation in the magnetic field, and remains at a stopover site until the magnetic field decreases, then it will accumulate more fat during the non-flying days and will be able to fly longer distances before having to land at another stopover site (Fig. 3b). Flying longer distances means less time 'on stage' and fewer captures at the
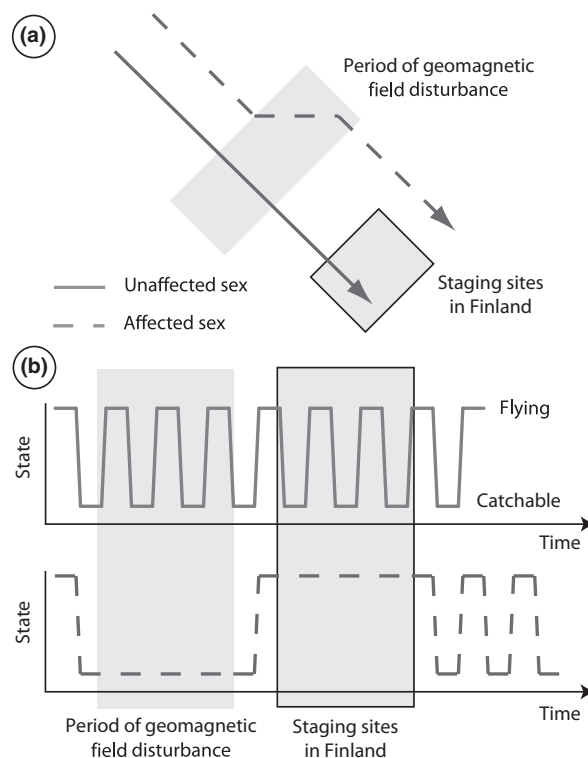

Figure 3. Graphical representation of the suggested relationships between geomagnetic disturbances *en route* and the sex ratio in juvenile Ruff at stopover sites in Finland.

staging areas. This is what we see in the data – fewer males after a magnetic storm 7–14 days before the peak of captures.

We hope that the possibility that magnetic disturbance affects the migratory behaviour of wild birds will attract more research in both the physiology and the ecology of avian migration. Although we do not know of any discussion of the acquisition of the navigational map by naïve birds during their first migration (when they are likely to be using a vector strategy), this certainly has to be going on, or they would not be able to show true navigation on their return migration. Future research could build on the current results and those on pigeons (Keeton *et al.* 1974, Larkin & Keeton 1976) and gulls (Southern 1969, 1971), perhaps incorporating new tracking technologies (Guilford *et al.* 2011, Schiffner & Wiltschko 2011), to better understand how migrating birds gather information and use it to guide their journeys.

In two ways this paper owes its existence to Prof. W.T. Keeton, Cornell University. First, it extends some work that he first did with homing pigeons. Also, the paper happened to be developed and first drafted in the house he built in Ithaca. We

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