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Authors: Pleskač, Lukáš, Hart, Vlastimil, Nováková, Petra, and Painter, Michael S.

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Spatial orientation of foraging corvids consistent with spontaneous magnetic alignment responses observed in a variety of free-roaming vertebrates

Lukáš PLESKAČ[1], Vlastimil HART[1], Petra NOVÁKOVÁ[1] and Michael S. PAINTER[1]*

[1] *Department of Game Management and Wildlife Biology, Faculty of Forestry and Wood Sciences, Czech University of Life Sciences, Kamýcká 129, 165 21 Praha 6, Czech Republic; e-mail: Pleskynol@seznam.cz, hart@fld.czu.cz, novakovap@fld.czu.cz, painter@fld.czu.cz*

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Abstract. Spontaneous magnetic alignment, in which an animal or group of animals, aligns its body axis in a fixed orientation relative to the geomagnetic field has been observed across a variety of vertebrates. Although a seemingly ubiquitous spatial behaviour, the adaptive significance and sensory mechanisms underlying spontaneous magnetic alignment remain unclear. Here we report another example of spontaneous alignment during feeding behaviour from five corvid species, a well-known and geographically widespread avian taxon. Consistent with previous observational studies of magnetic alignment in free-roaming vertebrates, first- and second-order analyses show that corvids exhibit robust axial alignment corresponding with the north-south magnetic axis. In contrast, when the data is pooled relative to the sun's azimuth, the first-order analysis is indistinguishable from random and the second-order statistics, although statistically significant, are a much weaker predictor of axial orientation compared to the distribution pooled relative to the magnetic field. The magnetic alignment behaviour exhibited by foraging crows reported here is compatible with previous hypotheses proposing that spontaneous magnetic alignment may help to coordinate and structure spatial behaviours in free-living organisms. Clearly, an experimental approach in future studies is needed to help shed light on the functional significance and biophysical mechanisms mediating spontaneous magnetic alignment. These data provide support for spontaneous magnetic alignment in free-roaming corvids, a widespread taxon with exceptional cognitive abilities that may offer unique advantages for future laboratory and field-based studies of magnetoreception.

Key words: compass, navigation, crows

Introduction

While the functional significance and sensory pathways underlying many forms of spatial behaviour, including long-distance navigation, migration, and local-scale orientation, have been identified, the biophysical mechanisms and adaptive relevance of spontaneous alignment are not well understood (Begall et al. 2013). Spontaneous magnetic alignment (SMA), in which an animal or group of animals aligns their body axis along the magnetic ~north-south axis, has been documented in observational studies of several classes of vertebrates (Begall et al. 2013, Malkemper et al. 2016, Obleser et al. 2016, Červený et al. 2017). Although experiments confirming the direct involvement of magnetic cues underlying SMA have been difficult to implement in field studies, magnetic alignment, compared to orientation relative to other available environmental cues, e.g. sun position, slope, wind direction, etc., show overwhelming consistency across disparate taxa, providing support for the involvement of magnetic cues underlying SMA responses, but see Hetem et al. (2011). Nest building assays involving rodents (Burda et al. 1990, Oliveriusová et al. 2014, Malkemper et al. 2015) and laboratory studies of invertebrates (Roonwal 1958, Wehner & Labhart 1970, Martin & Lindauer 1977, Vácha et al. 2010, Painter et al. 2013), have confirmed the involvement of magnetic cues mediating SMA by manipulating properties of the magnetic field. However, the behaviours and types of magnetic orientation exhibited in laboratory studies differ from those shown in observational studies of spontaneous magnetic alignment. For example, SMA in epigeic rodents, although oriented bimodially along the north-south axis like that shown in the majority of observational studies of free-roaming vertebrates, has only been shown for nest building behaviours (Oliveriusová et al. 2014, Malkemper et al. 2015). In

* *Corresponding Author*

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contrast, while invertebrates have been shown to align the body axis (or in some cases locomote) relative to magnetic cues, similar to the passive alignment behaviour in free-roaming vertebrates, several classes of dipterans (e.g. adult and larval *Drosophila* larvae (*D. melanogaster*), blowflies (*Calliphora erythrocephala*), and houseflies (*Musca domestica*)) as well as American cockroaches (*Periplaneta americana*) and honeybees (*Apis mellifera*)) exhibit an axially symmetrical quadramodal pattern of response (e.g. magnetic north, east, south, and west), rather than the north-south response shown in vertebrates (Becker 1963, Becker & Speck 1964, Wehner & Labhart 1970, Martin & Lindauer 1977, Vácha et al. 2010).

Although the adaptive significance of SMA remains enigmatic, previous studies have suggested that magnetic alignment may play a fundamental role in structuring and organizing individual spatial behaviour, and in social animals may also help to coordinate movements of a flock or herd. For example, evidence from honeybees that approach novel environments from a fixed magnetic direction suggests that magnetic cues may help to organize spatial behaviour, possibly by standardizing the vantage point for retinotopic maps in unfamiliar habitats (Collett & Baron 1994). Evidence for coordinated magnetic spatial behaviours have also been shown in flocks of waterfowl during complex water landings (Hart et al. 2013) and in the coordinated escape responses of wild roe deer (Obleser et al. 2016). Additionally, passive behaviours, such as grazing (cattle), resting or sleeping (red deer, roe deer, wild boar), and stationary behaviours of flamingos all exhibit SMA along the ~north-south magnetic axis and are consistent with previous forms of SMA shown in other wild vertebrates (see Begall et al. 2013 for review, Nováková et al. 2017).

Future studies designed to identify the functional significance and biophysical mechanisms mediating SMA in free-roaming vertebrates are clearly needed, however, several logistical and methodological challenges need to be overcome before significant progress can be made. One possibility is to identify SMA in a species that is well-suited for both laboratory and field studies of magnetic alignment, such as corvids, a geographically widespread and intelligent avian taxon. Corvids are considered a cosmopolitan genus, distributed globally, and therefore, are easily accessible for scientific pursuits. Furthermore, corvids' cognitive abilities also make them an attractive choice for laboratory studies of magnetoreception (Emery & Clayton 2004). For example, corvids may be exceptionally well-suited for learned magnetic compass assays, similar to those used for zebra finches (Pinzon-Rodriguez & Muheim 2017), which can investigate the biophysical mechanisms underlying magnetoreception. Therefore, we measured the orientation of five free-roaming corvid species observed in 14 localities across three countries to determine if they exhibit alignment behaviours consistent with those reported in previous SMA studies of free-roaming vertebrates. Indeed, these data show highly clustered axial alignment along the ~north-south magnetic axis. Although additional observational studies of SMA may only add to a growing list of species shown to exhibit SMA, we hope that these data also offer new opportunities for future research to help elucidate the remaining questions surrounding this seemingly widespread, yet surprisingly mysterious behavioural phenomenon.

Material and Methods

Digital photographs of free-living corvids were taken by four trained observers in 14 separate locations across three countries (Czech Republic, Italy, and Canada) from April 2011 to September 2015. A total of 2349 individual corvids from five species (*Corvus frugilegus*, *C. monedula*, *C. corone*, *C. cornix*, and *C. caurinus*), were observed and measured while feeding, defined as an individual with its head pointed downwards and the beak touching the ground. See Table S1 for details about sample sizes and sampling localities. Photographs were taken at different times of year, different times of day, in different geographic alignments relative to the bird and/or flock, and in different semi-urbanized habitat types (e.g. maintained lawns, agricultural fields, recreational areas), during daylight hours, typically under calm and overcast skies without precipitation. The alignment of each photograph, and therefore, the position of the observer relative to the flock, was recorded with respect to magnetic north using a handheld navigator's compass. The time, location, flock size, weather conditions, magnetic direction of the photograph, and habitat type were recorded for each measurement.

All digital photographs were then uploaded to Microsoft PowerPoint to derive the magnetic alignment of individual birds. Digital lines were overlaid on the long-axis of each individual, representing the axial alignment of each bird. The photograph was then removed and replaced with a digital "compass rosette" designed to compensate for angular distortions of each photograph (i.e. compass rosette was adapted for each photograph). The compass rosette was divided

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radially into 36 ten degree bins, and used to obtain axial bearings from each digital line at 10° resolution. All measurements of feeding alignment were treated as axial data. See Novákova et al. (2017) for similar sampling and analysis methods.

Measurements of individuals within the same flock, including mixes-species flocks, were considered dependent, and therefore, axial means for each flock, (or the axial bearing for an individual in the few cases when a photograph captured only one bird) were calculated relative to geomagnetic north and relative to the sun azimuth position. Sun azimuth directions corresponding to the time of measurement and location were obtained from the NOAA website https://www.esrl.noaa.gov/gmd/grad/solcalc/. Photographs taken on separate days or at different locations were considered independent. When photographs were taken on the same day and at the same locality, they were considered independent only if the flock size changed by > 10 individuals from the previous photograph, or at least 10 min had elapsed since the last photograph was taken.

Statistical analysis

All data were analyzed using the circular statistics program Oriana 4.02 (Kovach Computing) and Microsoft Excel. First-order statistics were calculated from independent measurements and pooled relative to magnetic north and relative to the sun's azimuth. Second-order statistics which assigns a "weight" to each mean bearing (ranging from 0-1.0) by taking into account the degree of clustering around the group mean were also calculated (Batschelet 1981). However, two separate second-order analyses were performed; one analysis includes all mean bearings, regardless of flock size, and a second analysis was performed excluding mean bearings containing less than five individuals to prevent small flock sizes, typically characterized by artificially large r-values, from biasing or "over-representing" the overall distribution (e.g. mean bearings derived from a sample size of one individual must have an r-value equal to 1.0).

Independent means were partitioned by species and a separate distribution for mixed-species groups. The overall data set was combined and analyzed using first- and second-order statistics, and the null hypotheses were accepted or rejected based on the Z and F test statistics (one sample Rayleigh test and one sample Hotelling's, respectively).

Mean bearings were also plotted as a function of flock size relative to magnetic north and as a function of time of day relative to sun azimuth position. Axial bearings for each scatter plot were transformed into the absolute deviation from the north-south axis or absolute deviation from the sun azimuth axis, resulting

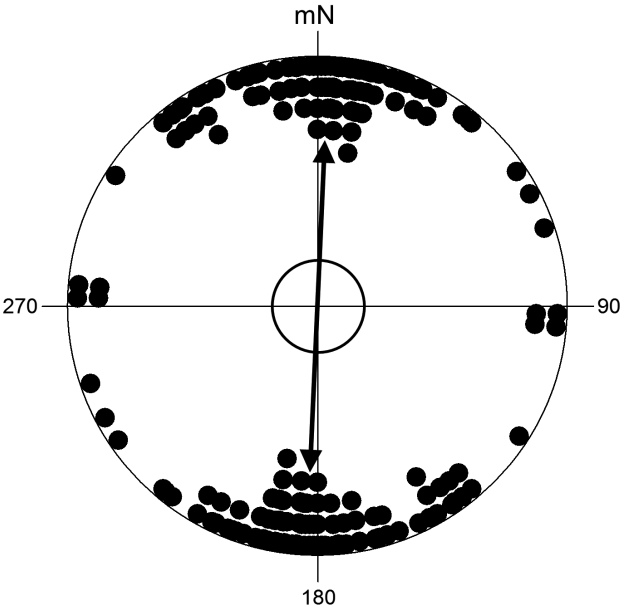


Fig. 1. Axial orientation from five corvid species exhibiting feeding behaviour pooled relative to magnetic North ("mN"). Each set of bearings represent an independent axial measurement. Black double-headed arrow represents the mean axial alignment of the distribution and the arrow length represents the strength of clustering around the distribution mean. The inner black circle represents the $p = 0.05$ significance level for the first-order Rayleigh test of uniformity.

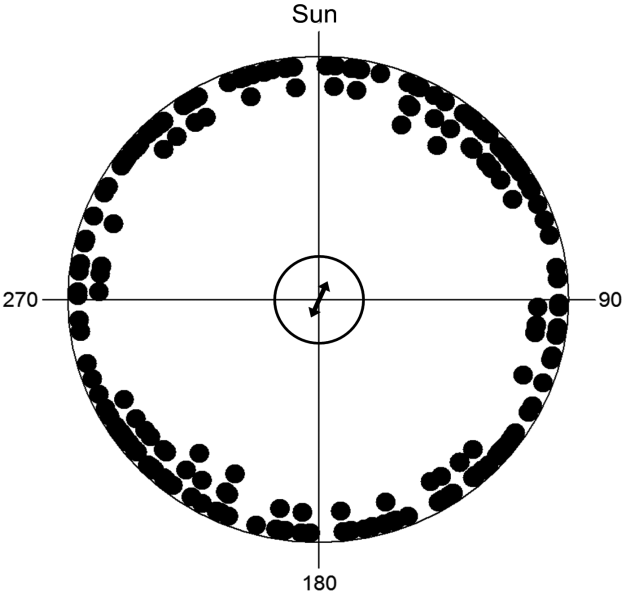


Fig. 2. Axial orientation from five corvid species exhibiting feeding behaviour pooled relative to sun position ("Sun"). Each set of bearings represent an independent axial measurement. Black double-headed arrow represents the mean axial alignment of the distribution and the arrow length represents the strength of clustering around the distribution mean. The inner black circle represents the $p = 0.05$ significance level for the first-order Rayleigh test of uniformity.

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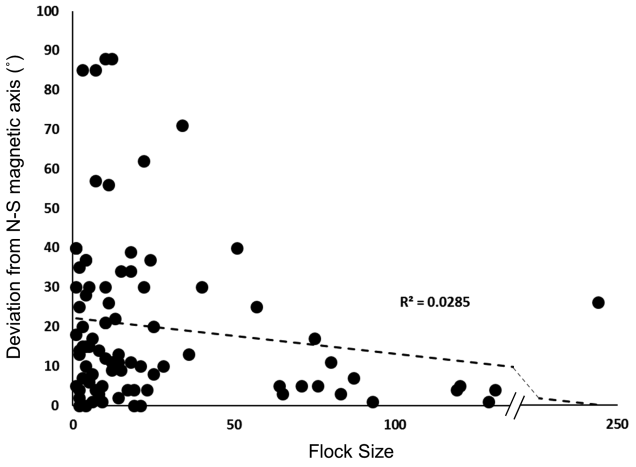


Fig. 3. Scatter plot showing the deviation of mean magnetic alignment as a function of flock size. Axial data was transformed to show only the absolute deviation from the north-south magnetic axis (0°). Therefore, only one bearing per measurement is graphed. All bearings represent the mean deviation from independent measurements. Linear regression is also shown (dotted black line), indicating no significant relationship between flock size and magnetic alignment.

in distributions that range from 0°-90°, reflecting the minimum and maximum deviation from each axis. Linear regressions were calculated for each scatter plot.

The magnetic direction of each photograph was used to determine the observer's magnetic position relative to each flock and was analyzed using the Rayleigh test to test for any effect of the observer on flock orientation (i.e. observer bias).

Results

As described in the methods, data from individual birds are not considered independent when photographs were taken at the same time and in the same location, and therefore mean bearings from each flock were calculated, resulting in a total of 89 independent measurements. The mean flock size for all independent measurements is 26.4 individuals (SD 39.1). First-order analysis shows three of the five corvid species, and flocks comprised of mixed species, exhibited highly significant axial alignment corresponding to the north-south magnetic axis (Table 1). *Corvus corone* also exhibited a north-south axial magnetic alignment, but failed to reach statistical significance, whereas *C. cornix* showed no magnetic alignment preference. The combined axial alignment of all corvid groups shows robust orientation along the north-south magnetic axis ($\mu = 2°$, $r = 0.67$, $p < 1 \times 10^{-12}$) (Fig. 1, Table 1). To determine if magnetic orientation was influenced by the number of birds within a flock, independent bearings were analyzed as a function of flock size. As shown in Fig. 3, the linear regression ($r^2 = 0.029$) suggests that there is no relationship between magnetic orientation and flock size.

In contrast to magnetic alignment, the combined orientation of corvids when pooled relative to sun's azimuth was indistinguishable from random ($\mu = 24°$, $r = 0.1$, $p = 0.45$) (Fig. 2, Table 1), and only two species and mixed species flocks exhibited significant orientation when analyzed separately (Table 1). However, it's possible that the pooled alignment relative to the sun over the course of the day could mask a more specific temporal pattern of sun alignment (e.g. corvids align relative to the sun during the morning and/or evening hours, but not mid-day). Therefore, axial alignment relative to the sun was analyzed as a function of time of day. As

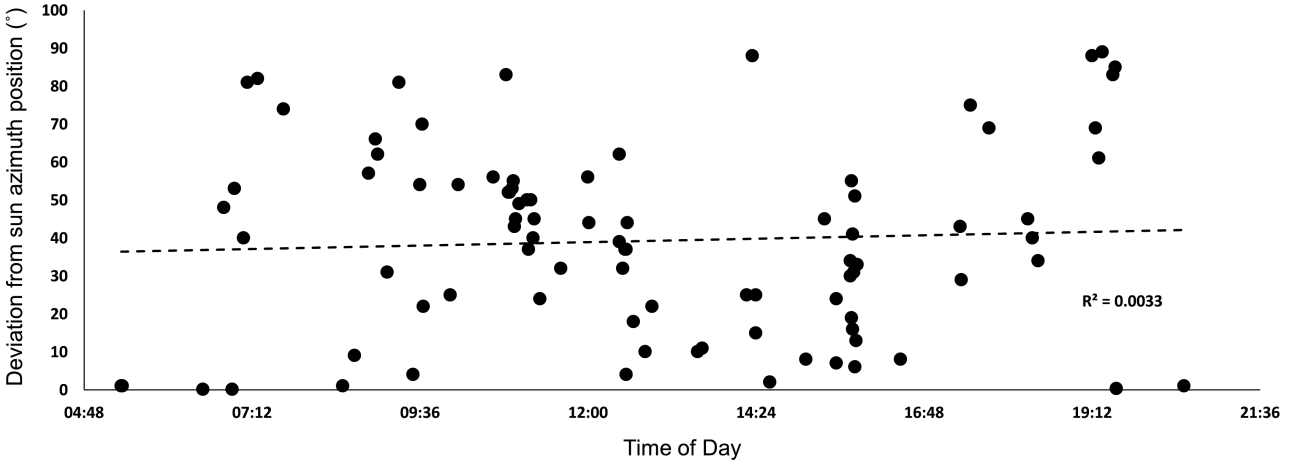


Fig. 4. Scatter plot showing the deviation of alignment relative to the sun as a function of time of day. Axial data was transformed to show only the absolute deviation from the sun's azimuth (0°), and therefore, only one bearing per axial measurement is plotted. All bearings represent the mean deviation from independent measurements. Linear regression is also shown (dotted black line), indicating no significant relationship between the time of day and alignment relative to the sun.

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Table 1. First order statistics for five species of free-roaming corvids during observations of feeding. Statistics are pooled relative to geomagnetic north and relative to the sun azimuth position. All data are treated as axial orientation, and statistics are calculated using independent measurements and partitioned into six subgroups (by species in cases of single-species flocks, and mixed-species flocks). A Rayleigh test was performed to determine if the data are distinguishable from random at the $p = 0.05$ significance level. Combined statistics for all five species are provided on the bottom row.

			Axial alignment relative to mN			Axial alignment relative to sun azimuth		
Species	Mean bearings (n)	Individuals (n)	Mean alignment	r-value	Rayleigh *p*-value	Mean alignment	r-value	Rayleigh *p*-value
C. frugilegus	23	1259	1°	0.71	< 0.0001	20°	0.53	< 0.001
C. monedula	32	331	0°	0.51	< 0.0005	119°	0.21	0.25
C. corone	7	15	14°	0.54	0.13	131°	0.46	0.23
C. cornix	2	46	103°	0.16	0.96	22°	0.04	0.99
C. caurinus	7	483	178°	0.90	< 0.001	125°	0.77	0.01
Mixed	18	215	4°	0.96	< 0.0001	40°	0.70	< 0.0001
Combined	89	2349	2°	0.67	$< 1 \times 10^{-12}$	24°	0.10	0.45

Table 2. Second order statistics for five species of free-roaming corvids during observations of feeding. Statistics are pooled relative to geomagnetic north and relative to the sun azimuth position. All data are treated as axial orientation. Analyses were performed using independent measurements, and mean bearings containing less than five individual birds (n = 22) were excluded from second order analysis to prevent biasing the weighted means from small flock sizes. Data are partitioned identical to those in Table 1. A Hotelling's one sample test was performed to determine if the ellipse derived from the weighed mean vectors overlaps with the circle's center at the $p = 0.05$ significance level. Combined statistics for all five species are provided on the bottom row.

		Axial alignment relative to mN			Axial alignment relative to sun		
Species	Mean bearings (n)	Mean alignment	r-value	Hotelling's *p*-value	Mean alignment	r-value	Hotelling's *p*-value
C. frugilegus	20	4°	0.31	0.002	24°	0.31	< 0.0005
C. monedula	24	0°	0.26	0.004	99°	0.05	0.85
C. corone	0	-	-	-	-	-	-
C. cornix	2	81°	0.12	n/a	163°	0.09	n/a
C. caurinus	7	176°	0.32	0.02	123°	0.25	< 0.0005
Mixed	14	8°	0.82	< 0.0001	44°	0.79	< 0.0001
Combined	67	4°	0.38	$< 1 \times 10^{-10}$	39°	0.21	0.001

shown in Fig. 4, no relationship between time of day and alignment relative to sun was found ($r^2 < 0.003$), nor does there appear to be an alignment preference at specific time periods throughout the day (e.g. sun rise, sun set, noon).

Second-order statistics were also calculated relative to magnetic north and relative to the sun's azimuth from independent group mean bearings (Table 2, Table S2). As discussed above, two separate second-order analyses were performed; one analysis includes all data regardless of flock size (Table S2), and a separate analysis excludes bearings derived from flocks comprised of fewer than five individuals (n = 22) (Table 2). Second-order analyses including all mean bearings, shows robust magnetic orientation ($\mu = 2°$, $r = 0.42$, $p < 1 \times 10^{-12}$), whereas when the data is pooled relative to the sun, the distribution is indistinguishable from random ($\mu = 31°$, $r = 0.21$, $p = 0.25$) (Table S2). However, we treat this data cautiously for the reasons outlined above. Excluding small flock sizes resulted in a total of 67 independent mean bearings from four corvid species and mixed species flocks (all photographs from *C. corone* were taken of single-species flocks with less than five individuals, and therefore are not represented in this analysis). Consistent with the first-order analysis, the combined distribution relative to magnetic North shows tighter clustering around the distribution mean ($\mu = 4°$, $r = 0.38$, $p < 1 \times 10^{-10}$), and was a stronger predictor of alignment compared to alignment relative to sun azimuth position ($\mu = 39°$, $r = 0.21$, $p = 0.001$) (Table 2).

The magnetic position of the observer relative to the direction of each flock was also evaluated (Fig. S1), showing a significant clustering of observer positions in the south-south-east magnetic direction ($\mu = 210°$, $r = 0.23$, $p = 0.01$). While the observations are distributed in all magnetic directions, there was a

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tendency for the observer to be positioned along the east-west magnetic axis.

Discussion

Here, we report robust axial alignment preferences in five corvid species corresponding with the magnetic ~north-south axis while feeding, consistent with previous observational studies of SMA in free-roaming vertebrates (Begall et al. 2013, Červený et al. 2017, Nováková et al. 2017). First-order statistics revealed a strong magnetic alignment preference in the overall distribution of foraging birds, whereas corvid alignment, when pooled relative to the sun's azimuth, was indistinguishable from random. It should be noted that when the data was partitioned by species (and mixed-species groups), two groups with the fewest mean measurements failed to reach significance when pooled relative to the magnetic field, and may suggest that large sample sizes, but not necessarily large flock sizes, are needed to reveal SMA in free-roaming corvids. A similar sample size effect is shown for alignment relative to the sun in the partitioned distributions.

Consistent with first-order analyses, axial alignment responses of corvids in second-order analyses when pooled relative to the magnetic field (excluding flock sizes < 5 individuals), show robust magnetic orientation along the north-south axis. A weaker, yet significant alignment response is also present when data is pooled relative to sun position, suggesting that celestial cues may also contribute to SMA in corvids. In contrast, when combining all data regardless of flock size, the second-order analyses when pooled relative to the sun are indistinguishable from random, whereas magnetic alignment is again, highly significant.

Interestingly, no relationships were found between magnetic alignment and flock size, or between the time of day and orientation relative to the sun's azimuth, factors often expected to influence spatial behaviour. These data provide support for SMA in corvids, and given their ubiquitous geographical distribution coupled with their exceptional cognitive aptitude (Emery & Clayton 2004), corvids could play an important role in future studies designed to characterize the sensory mechanisms and the functional significance underlying SMA in free-roaming vertebrates.

Although observational studies of SMA have been criticized for lacking experimental power, to be subject to observer bias, and involve relatively simple measurement techniques, they do provide insight into the spatial behaviour of free-roaming animals in their natural environment, allow observers to collect large amounts of data, and do not require specialized equipment and facilities typically associated with laboratory studies of animal behaviour (Begall et al. 2013).

As shown in Fig. S1, the observer position relative to flock position was not symmetrically distributed across all magnetic directions. However, a comparison between observer position and magnetic alignment clearly shows that observer bias cannot account for the tightly clustered magnetic responses (compare variation between Fig. 1 and Fig. S1). Furthermore, since measurements were sampled from a variety of magnetic directions, other potential systematic biases in analysis techniques (e.g. error in the digital compass rosette), would not be additive, but rather should cancel out across the total distribution of measurements (Hart et al. 2012, Obleser et al. 2016, Červený et al. 2017, Nováková et al. 2017). In addition, observational biases and/or systematic biases in the analysis techniques would not be specific to analyses pooled relative to the magnetic field, and therefore should also be evident in the distributions pooled relative to the sun. However, the first-order analysis clearly shows robust alignment relative to the magnetic field, whereas alignment relative to the sun's azimuth is indistinguishable from random and no alignment tendency is evident.

As discussed previously, SMA has been shown for a diverse range of vertebrate and invertebrate taxa (Begall et al. 2013). However, the sensory mechanisms mediating these behaviours is much less clear. Theoretical and empirical studies provide support for two types of biophysical processes underlying magnetosensitivity in terrestrial animals. A magnetite-based mechanism (MBM) is thought to involve biogenic crystals of magnetite that "track", or rotate into alignment with the local magnetic field. If located inside sensory cells, these crystals could provide a sense of magnetic direction and/or intensity (Winklhofer & Kirschvink 2010). The MBM is thought to be sensitive to the polarity the magnetic field and pulse remagnetization treatments, unaffected by low-level radio-frequency fields, and function in the absence of light. Indeed, behavioural evidence consistent with a MBM comes from fixed alignment orientation exhibited by migratory birds. Responses were unaffected by weak broadband radio-frequency exposure in the low-MHz range and sensitive to the polarity, rather than to the inclination, of the magnetic field (Wiltschko et al. 2005). A separate study has shown effects of pulse remagnetization treatments on

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migratory orientation in adult migrants (Wiltschko et al. 1998). Taken together, these findings provide strong support for the involvement of a MBM underlying some forms of magnetosensitivity in birds.

In addition to a MBM, support for a chemical compass involving a class of specialized photopigments forming radical-pair intermediates sensitive to the axis of the magnetic field, comes from theoretical and empirical studies, and is thought to be mediated by the visual transduction pathway (Ritz et al. 2000, 2004, Phillips et al. 2010). Behavioural evidence for the so-called radical-pair mechanism (RPM) has been provided by a variety of vertebrate and invertebrate organisms, including several avian groups, where magnetic responses are 1) sensitive to the inclination, rather than polarity of the magnetic field, 2) disrupted by low-level radio-frequency fields in the MHz range, 3) affected by light, 4) and unaffected by pulse remagnetization treatments, all properties consistent with a radical-pair mechanism (Wiltschko & Wiltschko 2005). The RPM is thought to affect the sensitivity of specialized photoreceptors, and therefore, has been proposed to produce a 3-dimensional visual pattern of, e.g. light intensity and/or colour, superimposed on the animal's visual surroundings and fixed with respect to magnetic north (Phillips et al. 2010).

Phillips et al. (2010), have argued that a complex visual pattern like that thought to be produced by an RMP, may provide a "visual" coordinate frame superimposed on the visual field and fixed in alignment relative to magnetic north, that could be used to help encode spatial relationships, e.g. between visual landmarks in novel environments, and/or help to place independent spatial maps into register (Phillips et al. 2010). Furthermore, a visual pattern fixed relative to a global reference (e.g. magnetic field) may also be used to anchor path integration systems that are prone to accumulate errors, and therefore become unreliable over long-distance navigation without a fixed "compass" reference (Cheung et al. 2008). However, the biophysical properties of a MBM are also well-suited to stabilize path integration systems.

Spontaneous magnetic alignment has been proposed to coordinate the movement of social animals living in dense groups or flocks where space may be limited. For example, SMA has been observed in landing waterfowl and in the escape behaviours of free-roaming roe deer (Hart et al. 2013, Obleser et al. 2016). The authors of these studies propose that the magnetic field provides a reference frame with which to estimate the trajectory of water landings, using the inclination of the magnetic field during the descent, and promotes herd cohesiveness for unexpected escape responses where coordination of group behaviour may increase individual survival.

Here we show that SMA is expressed in feeding corvids. One possibility, as discussed in (Phillips et al. 2010), is that a "magnetic coordinate frame" could help to place adjacent patches of habitat into register. Similar to the functional significance proposed for SMA observed in grazing ungulates (Begall et al. 2008), magnetic alignment in feeding corvids may provide a reference frame to effectively and efficiently forage in large patches of homogenized habitat devoid of salient spatial features, and/or may help to place the relative locations of foraging patches into register to form a more comprehensive cognitive map. In addition to, or alternatively, SMA in foraging corvids could represent an adaptive escape strategy, coordinating the alignment of multiple individuals while attention is diverted from anti-predator or vigilance behaviours, as was suggested by (Obleser et al. 2016).

The current study adds to a growing list of free-roaming animals shown to exhibit SMA, however, future studies are clearly needed to identify the functional significance and sensory mechanisms mediating spontaneous alignment. Corvids, a widespread and remarkably intelligent avian taxon, could play a key role in providing insight into the adaptive significance underlying magnetic alignment. For example, corvids may be well-suited for laboratory experiments designed similar those used to study magnetic compass orientation in zebra finches in which birds encode the magnetic direction of a food reward (Pinzon-Rodriguez & Muheim 2017). We hope that that the evidence for SMA presented in the current study will inspire future research with corvids which may offer several advantages over more traditional models used in magnetoreception research.

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Supplementary online material

Fig. S1. Magnetic position of the observer during each mean measurement. Circular bearings on the periphery of the circle represent the magnetic position of the observer relative to the direction of each flock. Inner black circle shows the $p = 0.05$ significance cutoff and the black arrow shows the distribution's mean direction and its length corresponds to the strength of clustering around the distribution mean. First-order Rayleigh test statistics are as follows: n = 89, μ = 210°, r = 0.23, $p = 0.01$.

Table S1. Number of individuals and number of mean bearings obtained from each sample location.

Table S2. Second-order analyses pooled relative to magnetic north and relative to the sun's azimuth. Unlike Table 1 in the main text, these analyses include all independent measurements, regardless of flock size (http://www.ivb.cz/folia_zoologica/supplemetarymaterials/painter_et_al._fig._s1,_table_s1,_s2.docx).

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