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Direction indicator and magnetic compass-aided tracking of the sun by flamingos?

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Abstract. Animals use to align their body axis with respect to different cues (e.g. sun position, wind direction, magnetic field lines) and signals (informing about source of interest) in diverse behavioural contexts. Existence of alignment indicates ability to sense such cues or signals and its study can enlighten the mechanism of their sensing. Global cues (sun position, magnetic field) might provide a directional reference (direction/heading indicator) for organization of the mental map and/or for coordinated take-off. The existence of a common direction indicator may be of importance especially in birds living in large colonies and having impeded maneuverability. We measured the direction of the body axis (alignment) in flamingos of four species at 18 localities in zoological gardens and in the wild in altogether eight countries during different seasons of the year and at different times of the day. The measurements were taken from photographs in a blinded way. Flamingos in Europe showed a significant preference to align towards South during all recorded stationary activities (grooming, resting, standing) while those from Kenya tended to head towards North. On the contrary, the distribution of body alignments during locomotor activities (walking, wading, feeding) was random. Under overcast weather, and especially in the morning hours, magnetic South or North were better predictors of heading than sun position. We interpret our findings as evidence for a magnetic alignment in flamingos (depending on the weather condition) and suggest that its main function might be seen in information rather than in energy interaction. Under windless conditions, sun position and magnetic field may provide a common reference direction, i.e. a direction indicator. Visual cues (if available) and vision are in birds probably more dominant in spatial orientation than magnetic cues and magnetoreception. Magnetoreception might be "switched on", when visual sensing of relevant cues is impeded.

Key words: Phoenicopteridae, magnetoreception, magnetic alignment, sun compass

Introduction

Alignment, i.e. the preferred body orientation with respect to given environmental cues (e.g. solar position, wind or water currents) or certain signals (communicative, alert or prey), occurs in animals of diverse taxa in different behavioural contexts and is familiar to nature observers. It brings energetic benefits, helps to acquire information or to avoid sensory noise (overstimulation). Its study has a heuristic potential because its expression is evidence for purposive (unconscious or conscious) behaviour and, above all, also for physiological capacity to sense the respective cues or signals (Begall et al. 2013). For group-living animals, a congruent alignment might facilitate e.g. coordinated keeping the course during group landings (Hart et al. 2013a) or the escape from a predator (Hart et al. 2012, Obleser et al. 2016) and it might serve the calibration and reading of the cognitive map of space (e.g. Collett & Baron 1994, Hart et al. 2013b). Concordantly with the idea of a common direction indicator (heading indicator) synchronising group movement, (magnetic) alignment was more pronounced in groups than in solitary individuals (Hart et al. 2012, Hart et al. 2013a, b, Červený et al. 2016).

Birds of many species across many taxa congregate in huge groups (colonies, flocks, swarms). While the advantages of group living (e.g. breeding, foraging, migration) have been widely discussed in textbooks of behavioural ecology, the emerging problems of living in groups have attracted less attention of scholars. Apart from the apparent problem of competition for resources, a main problem is the synchronisation of movement to avoid collisions during different activities, and especially during take-off and

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landing. For example, landing (especially) on water is problematic for heavier birds with longer braking distances as it is not possible to actively change the course of the last phase of landing ("landing roll") to avoid an imminent collision. A recent study (Hart et al. 2013a) addressed the necessity for flocks of water fowl to have a common direction indicator for landing on water under windless conditions and suggested that the geomagnetic field lines can provide such a cue.

Here, we test the hypothesis that flamingos possess a common direction indicator. Flamingos are, because of several reasons, unique for such testing. They belong to the largest birds living in huge dense colonies that can amount to more than 20000 individuals (Bucher et al. 2000). They permanently live in these colonies, i.e. not only during the breeding season. They are widely distributed in tropical and subtropical regions between latitudes 34° S and 46° N (Cramp & Simmons 1977). Besides that they are popular birds kept in most zoological gardens across the world. Most flamingos are migratory; some populations undertake journeys of 3000-4000 kilometres or more, whilst others are sedentary and show a high level of philopatry (Johnson 1989). Flamingos are good flyers, but due to their large body size they need long distances for taking off and "landing roll". Given their abundance and the density of their colonies, a common reference direction indicator to synchronise their activities seems to be a necessity.

To test the hypothesis that flamingos exhibit preferences for a certain magnetic compass direction, a phenomenon which would indicate magnetoreception, we measured the body alignment during feeding, walking, standing, resting, and comfort behaviour in four flamingo species. We hypothesized that under windless conditions, the distribution of the recorded body directions (headings) is not random (i.e. a certain compass direction is preferred).

Material and Methods

Sampling

Altogether 413 high-resolution photographs representing 34322 snapshots of individual birds (including repeated measures of the same individuals at different times and partly at different places) belonging to four flamingo species (lesser flamingo *Phoeniconaias minor*, American flamingo *Phoenicopterus ruber*, Chilean flamingo *Phoenicopterus chilensis* and greater flamingo *Phoenicopterus roseus*) were taken between July 2005 and January 2015, during different months and at different times of day at 18 localities in eight countries (Table 1). Locality, species, date, time, weather (sunny or partly cloudy versus overcast or rainy), and the direction, measured by a hand-held compass, and in some cases also by an integrated camera compass, in which the photo was taken were recorded for each photograph. Most daytimes were represented (as apparent from represented solar azimuths, Fig. 1-3).

Data analysis and statistics

The pictures were analysed by three members of our team (D. Kořanová, F. Čapek, L. Pleskač), who were blinded for the true direction in which the photos were taken. They measured the directional bearings on the screen with respect to the top of the photograph (being set as 0°) of all birds that could be clearly recognized. For each measured flamingo its activity was assigned to one of the following activities: stationary (resting, standing, grooming) or locomotor (walking and feeding) (cf. Fig. 1 and 2 for typical silhouettes). The coded photographs were analysed with Microsoft PowerPoint in a three-step procedure (cf. supplementary material Fig. S1). First, arrows were drawn along the median body axes of every bird visible in the photograph (the arrow

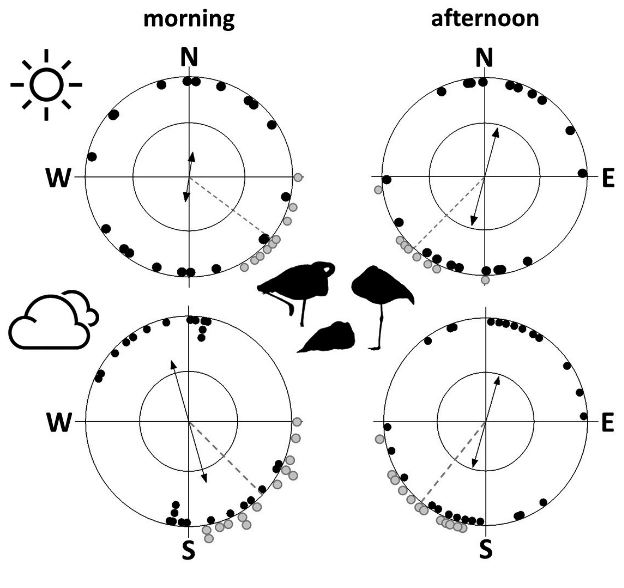

Fig. 1. Alignment of flamingos with respect to the magnetic North during stationary activities (resting and comfort behaviour) in Europe under sunny (upper row) and overcast (lower row) weather conditions in the morning (left column) and afternoon (right column). Each pair of opposite black dots within the outer circle represents the mean axial vector for one particular locality based on mean vectors of flocks photographed at the given locality at different times within the given daytime period. The double-headed arrow indicates the grand mean axial vector (μ) calculated over all axial means. The length of the mean vector (r) provides a measure of the degree of clustering in the distribution of the mean vectors. The inner circle marks the 0.05 level of significance border of the Rayleigh test. The mean solar azimuths (and thus also times of the day) represented in each sample are represented by gray dots outside the outer circle. The dashed line represents the grand mean of solar azimuths and thus also expected mean vector of alignments if the birds were heading towards the sun. See Table 2 for statistics.

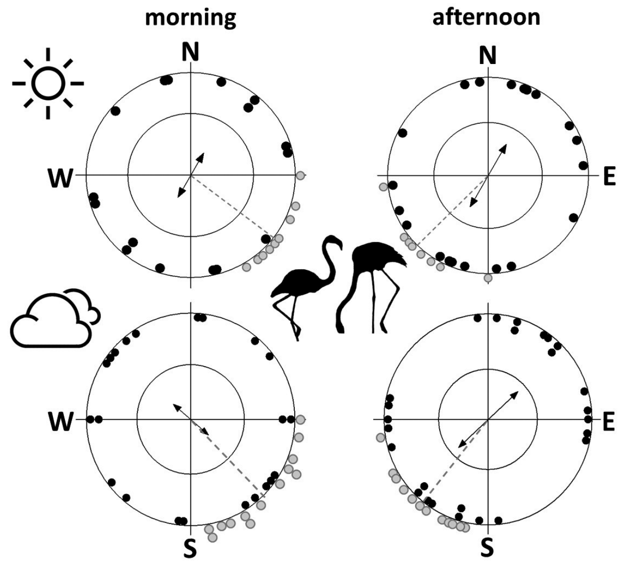

Fig. 2. Alignment of flamingos with respect to the magnetic North during locomotor activities (resting and comfort behaviour) in Europe under sunny (upper row) and overcast (lower row) weather conditions in the morning (left column) and afternoon (right column). Each pair of opposite black dots within the outer circle represents the mean axial vector for one particular locality based on mean vectors of flocks photographed at the given locality at different times within the given daytime period. The double-headed arrow indicates the grand mean axial vector (μ) calculated over all axial means. The length of the mean vector (r) provides a measure of the degree of clustering in the distribution of the mean vectors. The inner circle marks the 0.05 level of significance border of the Rayleigh test. The mean solar azimuths (and thus also times of the day) represented in each sample are represented by gray dots outside the outer circle. The dashed line represents the grand mean of solar azimuths and thus also expected mean vector of alignments if the birds were heading towards the sun. See Table 3 for statistics.

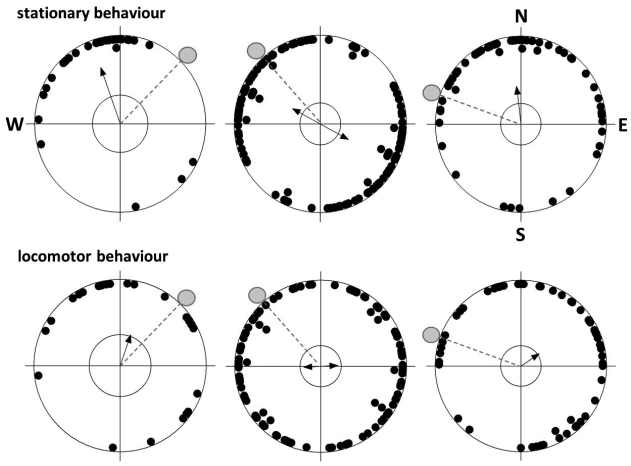

Fig. 3. Alignment of flamingos with respect to the magnetic North during stationary behaviours (resting, grooming, upper row) and locomotor activities (resting and comfort behaviour, lower row) in Kenya under overcast weather conditions in the morning (sun azimuth, represented by the gray dot outside the outer circle of 45°, left column), early afternoon (sun azimuth 320°, middle column) and late afternoon (sun azimuth 290°, right column). Black dots within the outer circle represent the mean angular (in the case of sun azimuths 45° and 290°) or axial (pairs of opposite dots in the case of sun azimuth 320°) vector for one particular flock photographed at different days within the given daytime period. The (double-headed) arrow indicates the grand mean angular (axial) vector (μ) calculated over all angular or axial means. The length of the mean vector (r) provides a measure of the degree of clustering in the distribution of the mean vectors. The inner circle marks the 0.05 level of significance border of the Rayleigh test. The dashed line represents the expected mean vector of alignments if the birds were heading towards the sun. See Table 4 for statistics.

direction was marked by the head position) and each activity category was analysed separately. Secondly, the underlying photograph was removed and replaced by a compass rosette divided radially into 36 ten-degree segments. The compass rosette was oval-transformed to compensate for the perspective distortion of the photographs. Thirdly, each arrow was moved to the centre of the rosette and its azimuthal direction was determined by the nearest 10° mark. Subsequently, the topographic bearings were back-transformed to true magnetic bearings (= magnetic alignment) and subsequently also with respect to solar azimuth (= solar alignment) by a researcher (P. Nováková), who knew the true compass bearing of the respective photographs. Circular statistics were carried out with Oriana 4.02 (Kovach Computing). Since birds in one group or flock are, with respect to their directionality, not independent units, we calculated means over all the bearings of flamingos showing the same behavioural pattern on each photograph. From the mean vectors for each photograph a grand mean vector was calculated for each flock at a given place and given time. Note that each photograph/flock records a unique situation differing from that recorded in another photograph/another flock in at least one, mostly in several of the following parameters: locality and site, date, time of the day, and/or weather. Furthermore, photographs were taken from different compass azimuths. In most photographs, most flamingos were resting, standing, or grooming (stationary behaviours), only about 14 % (in Kenya) and about 26 % (in Europe) of the flamingos were assigned as performing locomotor activities.

From means for each unique situation (photograph) we calculated separate grand means for Kenya, diverse European localities, and Europe, for stationary and locomotor activities, overcast and sunny conditions, for a.m. and p.m. periods in diverse respective combinations. First order statistics (Rayleigh test) were employed to test for significant deviations from random distribution.

We related the bearings with respect to magnetic North (= 0°) and to the sun azimuth (= 0°). The sun azimuth for each locality and given time was calculated according to the NOAA solar position calculator (http://www.esrl.noaa.gov/gmd/grad/solcalc/azel.html). Circular diagrams were plotted in Oriana 4.02. We calculated mean alignment vectors for a.m. and

Table 1. Localities and sample sizes of sampled flamingos.

Country	Locality	Latitude	Longitude	Stationary activities number of measured photos (birds)		Locomotor activities number of measured photos (birds)		Total number of measured photos (birds)
				sunny	overcast	sunny	overcast	
Kenya	Lake Bogoria	0.245611° N	36.100917° E	0	134 (24004)	0	127 (3808)	134 (27812)
Czech Republic	Dvůr Králové Zoo	50.434493° N	15.799439° E	3 (37)	0	3 (14)	0	3 (51)
Czech Republic	Jihlava Zoo	49.396546° N	15.599223° E	3 (79)	7 (116)	3 (18)	5 (35)	10 (248)
Czech Republic	Liberec Zoo	50.777894° N	15.080334° E	3 (30)	4 (75)	3 (13)	4 (9)	7 (127)
Czech Republic	Ohrada Zoo	49.042406° N	14.421774° E	9 (144)	24 (488)	6 (20)	20 (145)	33 (797)
Czech Republic	Plzeň Zoo	49.763846° N	13.365027° E	12 (37)	8 (94)	2 (11)	5 (20)	20 (162)
Czech Republic	Prague Zoo – Locality I.	50.115717° N	14.409078° E	12 (365)	27 (867)	8 (50)	22 (242)	39 (1524)
Czech Republic	Prague Zoo – Locality II.	50.116075° N	14.407179° E	10 (298)	13 (313)	11 (106)	11 (119)	23 (836)
France	Rhône Delta, Camargue	43.530121° N	5.048250° E	30 (601)	0	26 (254)	0	30 (855)
Germany	Dortmund Zoo	51.473592° N	7.469867° E	0	12 (56)	0	10 (17)	12 (73)
Germany	Duisburg Zoo	51.435494° N	6.809691° E	12 (97)	11 (70)	12 (19)	10 (21)	23 (207)
Germany	Gruga-Park Essen	51.428727° N	6.988961° E	0	9 (29)	0	9 (46)	9 (75)
Great Britain	Paignton Zoo	50.425296° N	3.580848° W	6 (24)	19 (372)	2 (7)	18 (68)	25 (471)
Hungary	Budapest Zoo	47.519946° N	19.080702° E	0	4 (99)	0	4 (80)	4 (179)
Spain	Isla Canela	37.178761° N	7.385807° W	1 (4)	11 (62)	1 (17)	8 (109)	12 (192)
Spain	Marismas del Odiel	37.240908° N	6.997423° W	21 (372)	0	21 (153)	0	21 (525)
Spain	Coto Donana	37.001034° N	6.389730° W	0	3 (24)	0	0	3 (24)
Switzerland	Basel Zoo	47.547773° N	7.578777° E	0	5 (107)	0	5 (57)	5 (164)
Sum Europe	17 localities			122 (2088)	157 (2772)	98 (682)	131 (968)	279 (6510)
Sum: 8 countries	18 localities			122 (2088)	291 (26776)	98 (682)	258 (4776)	413 (34322)

p.m. sun azimuths separately. For graphical illustration only more significant results of either angular or axial analyses were selected.

Results

Circular statistics based on average means for particular activities at particular photographs showed significant alignment of flamingos' heading approximately southwards or along the North-South axis in Europe and northwards in Kenya during stationary behaviours (Table 2, 4, Fig. 1 and 3), but less significant orientation during locomotion (walking and feeding; Table 3, 4, Fig. 2 and 3). The alignment was more prominent during overcast than during sunny conditions and during overcast conditions it was highly significant in the morning hours. Generally, alignment deviated in the course of the day less from the N-S axis than it deviated from the actual sun azimuth. There was no correlation between the direction in which a photograph was taken and the mean heading of birds measured on that particular photograph ($r = -0.003$ for angular data and $r = -0.0966$ for axial data). Under the overcast conditions flamingos seemed to track the course of the sun and to head towards it. However, the deviation angle of the mean alignment axis from the North-South axis during stationary activities was markedly smaller (on average 20°) than that from the sun azimuth (on average 40°). The mean bearings of flamingos on the northern and the western shores of Lake Bogoria, Kenya, did not significantly differ and pointed northwards (Fig. 4).

Discussion

Technical considerations

The question to be answered is whether the findings could have been influenced by the method of sampling and measurement. We argue against this possibility.

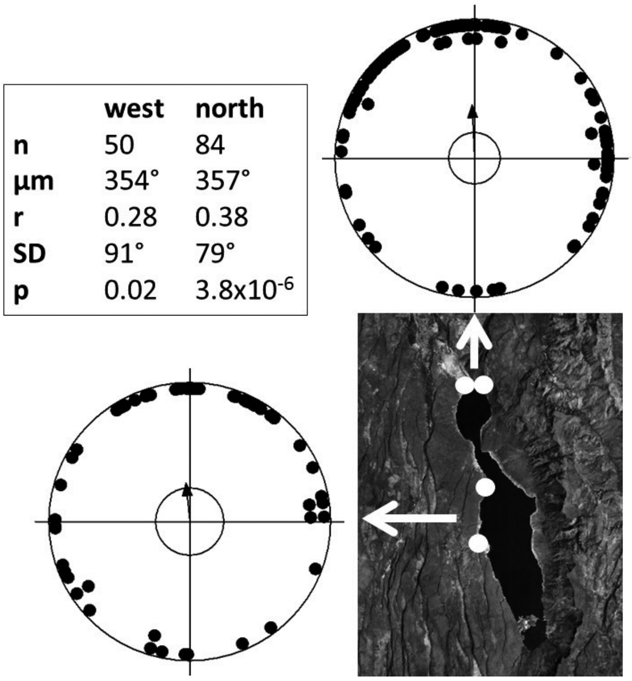

Fig. 4. Map of Lake Bogoria, Kenya (source Wikipedia) with shown positions of localities at the northern and western shore where photographs of flamingos for measurement were taken. Note that although Lake Bogoria is situated at geographic equator, the geomagnetic equator runs almost 1000 km northwards. Circular graphs show alignment of flamingos with respect to the magnetic North during stationary behaviours (resting, grooming, upper row) at the northern shore (above right) and at the western shore (below left). Black dots within the outer circle represent the mean angular vector for one particular flock photographed at different daytime periods. The arrow indicates the grand mean angular vector (µ) calculated over all angular means. The length of the mean vector (r) provides a measure of the degree of clustering in the distribution of the mean vectors. The inner circle marks the 0.05 level of significance border of the Rayleigh test. See frame for statistics.

Although errors in estimating the angular value of body direction of birds which are not aligned exactly parallel or perpendicular to the direction of photographing cannot be excluded due to distorted perspective of the picture, this kind of errors would result in rather quadrimodal distribution of values, due to parallel and perpendicular directions acting as value attractors. Since all the directions of photographs were represented in our sample, a random distribution of bearings would be a possible result of too rough measurements from photographs. There would be no reason, why one particular axis should be preferred. In fact, all the directions of photographs, when analysed separately provided the same result: flamingos aligned their body axis roughly along the N-S axis during resting (Table 2, Fig. 1 and 3). Thus the error of measurement represents noise (scatter of values) but is not systematically cumulative to one attractor value. It should be further noted that the researchers who measured the directions of the flamingos did not know the true direction of the photo and the measurements were thus blind. Besides that, should our observation be only an artifact of accuracy there would not be a difference between stationary and locomotor activities as all birds on the photo are "fixed" and thus "stationary".

Although some bird individuals (especially those photographed in zoos) were measured several times, the records were done at different times, at different places, under different weather conditions and during different activities. Thus, the repeated recordings do

Table 2. Circular statistics for axial bearings in flamingos displaying stationary activities (standing, resting, grooming), for localities in Europe, and separately for overcast and sunny weather and morning and afternoon hours. Magnetic alignment refers to bearing respective to the magnetic North (= 0°); solar alignment refers to bearings respective to the actual sun position (= 0°) calculated for the given locality, date and time of observation. It is apparent that mean vectors counted for magnetic alignment deviate for about 15° from the North-South axis, those for solar alignment deviate for about 30° from the respective sun azimuth. See Fig. 1 for illustration.

Weather	overcast				sunny			
Time (solar azimuths)	morning (70°-170°)		afternoon (180°-270°)		morning (70°-170°)		afternoon (180°-270°)	
Number of observations means of localities/ flocks/birds	13/74/1546		13/83/1226		10/71/1209		10/51/879	
Alignment	magnetic	solar	magnetic	solar	magnetic	solar	magnetic	solar
Mean vector **(µ)**	164°/344°	29°/209°	16°/196°	155°/335°	8°/188°	41°/221°	14°/191°	154°/334°
Length of mean vector (r)	0.602	0.453	0.455	0.553	0.250	0.336	0.507	0.336
Circular standard deviation	29°	36°	36°	31°	48°	42°	33°	42°
95 % Confidence interval (–/+) for µ	147°-181°	4°-54°	351°-41°	136°-174°	269°-107°	354°-87°	349°-39°	108°-201°
99 % Confidence interval (–/+) for µ	141°-186°	356°-61°	344°-49°	130°-180°	238°-138°	340°-102°	341°-47°	93°-215°
Rayleigh test (Z)	4.710	2.669	2.687	3.970	0.625	1.129	2.574	1.130
Rayleigh test (*p*)	0.007	0.067	0.065	0.016	0.547	0.332	0.073	0.331

Table 3. Circular statistics for axial bearings in flamingos displaying locomotor activities (walking, wading, feeding), for localities in Europe, and separately for overcast and sunny weather and morning and afternoon hours. Magnetic alignment refers to bearing respective to the magnetic North (= 0°); solar alignment refers to bearings respective to the actual sun position (= 0°) calculated for the given locality, date and time of observation. It is apparent that mean vectors counted for magnetic alignment and solar alignment deviate on average for about 40° from the North-South axis or from the respective sun azimuth respectively. See Fig. 2 for illustration.

Weather	overcast				sunny			
Time (solar azimuths)	morning (70°-170°)		afternoon (180°-270°)		morning (70°-170°)		afternoon (180°-270°)	
Number of observations means of localities/ flocks/ birds	11/62/456		13/69/512		8/59/430		10/39/252	
Alignment	magnetic	solar	magnetic	solar	magnetic	solar	magnetic	solar
Mean vector **(μ)**	131°/311°	105°/285°	47°/227°	9°/189°	29°/209°	106°/286°	30°/210°	170°/350°
Length of mean vector (r)	0.223	0.179	0.385	0.401	0.246	0.526	0.367	0.250
Circular standard deviation	50°	53°	40°	39°	48°	32°	41°	48°
95 % Confidence interval (–/+) for μ	344°-277°	*****	16°-78°	339°-38°	63°-356°	79°-133°	350°-70°	71°-269°
99 % Confidence interval (–/+) for μ	298°-324°	*****	6°-88°	330°-48°	320°-99°	71°-142°	337°-82°	39°-300°
Rayleigh test (Z)	0.547	0.354	1.928	2.09	0.484	2.217	1.347	0.624
Rayleigh test (*p*)	0.59	0.711	0.146	0.123	0.631	0.107	0.266	0.547

Table 4. Circular statistics for angular or axial bearings (results with higher respective significance are presented) with respect to the magnetic North (= 0°) in flamingos displaying stationary (standing, resting, grooming) or locomotor activities (walking, wading, feeding) observed at Lake Bogoria in Kenya. Note that all observations in Kenya were made under overcast conditions, separately in the morning (sun azimuth 45°), in the early and late afternoon (sun azimuths 320° and 290° respectively). See Fig. 3 for illustration.

Type of behaviour	stationary			locomotor		
Solar azimuth	45°	320°	290°	45°	320°	290°
Data type	Angles	Axial	Angles	Angles	Axial	Angles
Number of observations means of flocks/birds	28/1524	53/12939	53/9541	23/101	51/2074	53/1633
Mean vector (μ)	340°	118°/298°	353°	19°	87°/267°	56°
Length of mean vector (r)	0.677	0.369	0.434	0.376	0.197	0.258
Circular standard deviation	51°	40°	74°	80°	52°	94°
95 % Confidence interval (–/+) for μ	321°-359°	104°-133°	329°-17°	336°-61°	59°-115°	14°-97°
99 % Confidence interval (–/+) for μ	315°-5°	100°-137°	322°-24°	323°-74°	50°-124°	1°-110°
Rayleigh test (Z)	12.814	7.205	9.999	3.257	1.977	3.517
Rayleigh test (*p*)	6.09×10^{-7}	7.43×10^{-4}	4.55×10^{-5}	0.037	0.139	0.030

not represent pseudoreplication within the context of our hypothesis that flamingos express either solar alignment (expected: changes of alignment at different times of the day at the same locality, and congruent changes at different localities at the same sun position) or magnetic alignment (expected: no differences between mean vectors for localities and times of the day). Accordingly, means of individual bearings of birds in one group (flock) were calculated for each locality, each activity, each weather condition, and diverse solar azimuths (times of the day) separately and in combinations. Recognizing and assigning behaviour to one of the given locomotor and stationary categories is in flamingos easy and unequivocal (cf. silhouettes at the Fig. 1 and 2).

Results

The non-random alignment of birds can be generally explained by three factors: wind direction, sun position and magnetic field. All these factors can potentially serve also as direction indicators. We exclude wind direction as a common global denominator since all our observations were made under windless conditions.

Since locomotion is goal-oriented, any sun or magnetic alignment might be masked by the respective motivation. Sun (or magnetic) alignment seems to have in flamingos rather an information than a thermoregulatory function. Flamingos track the sun and "look into it" rather than being perpendicularly oriented towards it (e.g. for sun basking).

Interpretation and conclusions

We suggest that magnetic alignment calibrated by solar alignment or solar alignment compensated and corrected by magnetic alignment under overcast conditions might serve (under windless conditions) as a "direction (heading) indicator". This alignment might be an expression of the flamingos' readiness to take off in a given direction, e.g. if the flock was suddenly surprised. In this case, it would be thus the basis of the so-called nonsense orientation, i.e. a strong tendency to fly in one direction, unrelated to any homing ability (Matthews 1961). Thake (1981) explained this phenomenon in the context of escape behaviour, arguing that "birds whose preferred orientations are sufficiently similar to those of birds around them to allow flocking to occur have an advantage over birds whose preferred orientations make flocking difficult". Magnetic field and/or solar azimuth may also provide a reference direction to arrange the mental map (cf. Collett & Baron 1994). (It is easier to rotate the body than to perform a mental rotation of the spatial map – similarly we turn our paper map so that the north points upwards or forwards and we align accordingly, and similarly dogs seem to align when marking their territories and memorizing the marked places, Hart et al. 2013b). It should be pointed out that the hypothesis of direction indicator (nonsense orientation) does not try to compete with complex models explaining coordinated synchronized movement and direction changes in swarms and flocks of insects, fish or birds (Couzin et al. 2005, Buhl et al. 2006, Katz et al. 2011). A direction indicator applies in situations when the manoeuvrability is limited (e.g. in heavier birds and/or during landing or take-off) and or when the sight control ("what does my neighbour do") is impeded (e.g. during a simultaneous take-off from positions hidden in dense vegetation or of animals distributed over a large-scale area).

We assume that there is hierarchy in cues which serve as direction indicators related also to hierarchy in efficacy of senses which register and process them. Because of aerodynamic reasons, the most efficient direction indicator for take-off or landing should be wind direction. If there is no wind, sun may provide an unequivocal direction indicator. Magnetoreception is probably a sense which has a lower rank in hierarchy of senses and is attended to, only in a novel environment and after cues perceived by other more dominant senses are not available or their sensing is impeded. Under sunny days continuous visual monitoring of the actual sun position is arguably easier and faster than monitoring of any cardinal magnetic direction by magnetic sense. This might be the reason why under overcast conditions, when sun position could not be visually determined, more flamingos were trying to "get into the line" with the magnetic field "in order to be ready". Still unclear is, however, why this alignment was more prominent in the morning hours (a.m.) than in the afternoon and evening (p.m.).

It would be surely of interest to study body orientation of flamingos at night, under disturbed magnetic fields, either due to geomagnetic storms (cf. Hart et al. 2013b) or due to electromagnetic pollution (cf. Engels et al. 2014), and, of course, to analyse actual directions of take-offs and landings (cf. Hart et al. 2013a).

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Literature

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Supplementary online material

Fig. S1. Analysis of coded photographs with Microsoft PowerPoint in a three-step procedure (http://www.ivb.cz/folia_zoologica/supplemetarymaterials/novakova_et_al._fig._s1.pdf).