

**BIOCHEMISTRY.** For the article “Expression of Globo H and SSEA3 in breast cancer stem cells and the involvement of fucosyl transferases 1 and 2 in Globo H synthesis,” by Wen-Wei Chang, Chien Hsin Lee, Peishan Lee, Juway Lin, Chun-Wei Hsu, Jung-Tung Hung, Jin-Jin Lin, Jyh-Cherng Yu, Li-en Shao, John Yu, Chi-Huey Wong, and Alice L. Yu, which appeared in issue 33, August 19, 2008, of *Proc Natl Acad Sci USA* (105:11667–11672; first published August 6, 2008; 10.1073/pnas.0804979105), the authors note that in the Abstract, line 8, “29/31” should have appeared as “29/40.” Additionally, in Table 1, last column, second row from the bottom, “77.5” should have appeared as “72.5.” These errors do not affect the conclusions of the article. The corrected table appears below.

**Table 1. A comparison of Globo H and SSEA3 expression in BCSCs and non-BCSCs**

Glycan and population	No. of patients	Positive		
		No.	Range*	% of total
<b>Globo H<sup>†</sup></b>				
Total	41	25	14.3–75.2	61.0
Non-BCSCs	41	25	24.4–79.2	61.0
BCSCs	40 <sup>‡</sup>	8	9.7–71.0	20.0
<b>SSEA3<sup>†</sup></b>				
Total	40	31	5.9–66.4	77.5
Non-BCSCs	40	29	24.3–70.4	72.5
BCSCs	40	25	5.0–58.4	62.5

Globo H or SSEA3 expression was determined by flow cytometry as described in *Materials and Methods*. BCSCs were defined as CD45<sup>+</sup>CD24<sup>−</sup>CD44<sup>+</sup> cells, and non-BCSCs were defined as the remaining populations of CD45<sup>+</sup> cells.

\*Range was calculated as percentage of positive cells in total cells.

<sup>†</sup>Among the 53 tumor samples, 28 were examined for the expression of both Globo H and SSEA3, 13 were tested for Globo H only, and the remaining 12 were tested for SSEA3 only.

<sup>‡</sup>Tumor cells from 1 of the 41 patients showed an absence of CD24<sup>−</sup>CD44<sup>+</sup> subpopulation.

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**ECOLOGY.** For the article “Magnetic alignment in grazing and resting cattle and deer,” by Sabine Begall, Jaroslav Červený, Julia Neef, Oldřich Vojtěch, and Hynek Burda, which appeared in issue 36, September 9, 2008, of *Proc Natl Acad Sci USA* (105:13451–13455; first published August 25, 2008; 10.1073/pnas.0803650105), the authors note that due to a printer’s error, on page 13454, right column, in *Analysis of Body Position of Deer (Field Observation)*, the first sentence, “Body position of 2,974 deer (in 227 localities) was recorded in the Czech Republic” should instead read: “Body position of 2,974 deer (in 241 localities) was recorded in the Czech Republic.” Additionally, on page 13455, right column, in *Sun Position and Roe Deer Orientation*, the first sentence “The position of the sun could be deviated by the exact time of the day” should instead read: “The position of the sun could be determined by the exact time of the day.”

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**MEDICAL SCIENCES.** For the article “Uncovering G protein-coupled receptor kinase-5 as a histone deacetylase kinase in the nucleus of cardiomyocytes,” by Jeffrey S. Martini, Philip Raake, Leif E. Vinge, Brent DeGeorge, Jr., J. Kurt Chuprun, David M. Harris, Erhe Gao, Andrea D. Eckhart, Julie A. Pitcher, and Walter J. Koch, which appeared in issue 34, August 26, 2008, of *Proc Natl Acad Sci USA* (105:12457–12462; first published August 18, 2008; 10.1073/pnas.0803153105), the authors note that the author name Brent DeGeorge, Jr., should have appeared as Brent R. DeGeorge, Jr. The author line has been corrected online. The corrected author line and related author contributions footnote appear below.

**Jeffrey S. Martini, Philip Raake, Leif E. Vinge, Brent R. DeGeorge, Jr., J. Kurt Chuprun, David M. Harris, Erhe Gao, Andrea D. Eckhart, Julie A. Pitcher, and Walter J. Koch**

Author contributions: J.S.M., D.M.H., A.D.E., J.A.P., and W.J.K. designed research; J.S.M., P.R., L.E.V., B.R.D., and E.G. performed research; J.S.M. and D.M.H. contributed new reagents/analytic tools; J.S.M., B.R.D., J.K.C., D.M.H., A.D.E., and W.J.K. analyzed data; and J.S.M. and W.J.K. wrote the paper.

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**MICROBIOLOGY.** For the article “Purported nanobacteria in human blood as calcium carbonate nanoparticles,” by Jan Martel and John Ding-E Young, which appeared in issue 14, April 8, 2008, of *Proc Natl Acad Sci USA* (105:5549–5554; first published April 2, 2008; 10.1073/pnas.0711744105), the authors note that on page 5550, right column, line 3, “P:Ca ratio” should have appeared as “Ca:P ratio.” This error does not affect the conclusions of the article.

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**PLANT BIOLOGY.** For the article “Enhanced photoprotection pathways in symbiotic dinoflagellates of shallow-water corals and other cnidarians,” by Jennifer McCabe Reynolds, Brigitte U. Bruns, William K. Fitt, and Gregory W. Schmidt, which appeared in issue 36, September 9, 2008, of *Proc Natl Acad Sci USA* (105:13674–13678; first published August 29, 2008; 10.1073/pnas.0805187105), the authors note that due to a printer’s error, on page 13674, right column, second full paragraph, line 6, “maximum quantum yield as  $F_v/F_m = F_m - F_0$ ” should have appeared as “maximum quantum yield as  $F_v/F_m$ , where variable fluorescence,  $F_v = F_m - F_0$ .”

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# Magnetic alignment in grazing and resting cattle and deer

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**We demonstrate by means of simple, noninvasive methods (analysis of satellite images, field observations, and measuring “deer beds” in snow) that domestic cattle ( $n = 8,510$  in 308 pastures) across the globe, and grazing and resting red and roe deer ( $n = 2,974$  at 241 localities), align their body axes in roughly a north-south direction. Direct observations of roe deer revealed that animals orient their heads northward when grazing or resting. Amazingly, this ubiquitous phenomenon does not seem to have been noticed by herdsman, ranchers, or hunters. Because wind and light conditions could be excluded as a common denominator determining the body axis orientation, magnetic alignment is the most parsimonious explanation. To test the hypothesis that cattle orient their body axes along the field lines of the Earth’s magnetic field, we analyzed the body orientation of cattle from localities with high magnetic declination. Here, magnetic north was a better predictor than geographic north. This study reveals the magnetic alignment in large mammals based on statistically sufficient sample sizes. Our findings open horizons for the study of magnetoreception in general and are of potential significance for applied ethology (husbandry, animal welfare). They challenge neuroscientists and biophysicists to explain the proximate mechanisms.**

grazing behavior | magnetic alignment | magnetoreception | resting behavior | spatial orientation

Farmers and attentive nature and countryside observers know that most cattle and sheep, when grazing, face the same way. Many of them ask for the reason and which factors determine the direction in which they align. The farmers’ wisdom and experience indicate that cattle face into the wind, whereas sheep face away from the wind; the animals expose the maximum body surface area to the sun when sun basking in cold but sunny times of the day. Several scientific studies also addressed alignment of grazing cattle and sheep from the point of behavioral thermoregulation, i.e., they focused on alignment under suboptimal weather conditions. Thus it was confirmed that cattle stand perpendicular to the sun on cold, sunny days, especially in the early morning, maximizing the surface area exposed to short-wave radiation and gaining heat. On the other hand, cattle orient parallel with strong winds during winter, which minimizes the area exposed to convective heat loss associated with wind (e.g., ref. 1 and references therein). However, to the best of our knowledge, the farmers’ wisdom and scientific studies have not provided answers (and even do not address the question) about which factors determine common alignment of cattle (and sheep) within one herd under favorable, nonstressful conditions (windless, sunless days, with optimal or near-optimal temperature). Furthermore, apparently there is no information whether the cattle show any common alignment during night grazing periods and when resting. Also to the best of our knowledge, no scientific study (or common hunters’ wisdom) addresses whether wild ruminants (like deer) also predictably align when grazing or resting.

In this study, we address these questions by combining several methodical approaches. First, we recorded body alignment of

cattle in satellite images provided by Google Earth. In this manner we received scan-sampling data on alignment of animals in diverse localities across the globe and in diverse times, making it unlikely that effective direction of each of the factors (wind, sun, and temperature) was a common key factor of the alignment in all places and times. Second, we observed alignment in grazing and resting roe deer at different times of the day (even at night) in diverse localities, under diverse climatic conditions. Third, we analyzed the alignment of “beds” (body prints in snow of resting animals) of red deer and roe deer. We demonstrate that in all cases the animals tend to show a roughly north-south (N-S) body alignment, and we argue that a further extrinsic cue, the magnetic field of the Earth, has to be considered as a factor affecting spatial orientation in cattle and deer.

Magnetoreception is a widespread, although enigmatic, sensory ability. Behavioral experiments have demonstrated that diverse animals, including representatives of six vertebrate classes, can use the magnetic field of the Earth as a cue for spatial orientation (2). Among mammals, robust evidence for magnetic compass orientation has been obtained only recently for, thus far, just a few rodent species (3–7) and one bat species (8). Magnetic compass orientation has been suggested also for humans and some larger mammals, such as horses and cetaceans. Its evidence is, however, questionable and mainly only anecdotal (2). Surely, the investigation of magnetic orientation in large mammals under reproducible controlled laboratory conditions involving sufficiently large sample sizes is difficult, if not impossible. While most experiments on mammalian magnetic orientation have been based on the study of homing or learning achievements, spontaneous (innate) magnetic behavioral responses (and their subsequent manipulation) have remained largely unstudied and untapped (but see the study of magnetoreception in mole-rats in refs. 3, 4, and 9–11).

## Results

**Body Position of Cattle.** Body axes of cattle (*Bos primigenius*) of 308 evaluated herds/pastures (displayed on satellite images in Google Earth) showed a significant deviation from random distribution (Rayleigh test,  $P < 0.00001$ ) with a preference for a rough N-S direction (mean vector:  $5.4^\circ/185.4^\circ$  with geographic north as reference). Because declination was small for most pastures chosen (i.e., magnetic north being close to geographic north), cattle were also roughly N-S oriented with respect to magnetic north (mean vector:  $6.4^\circ/186.4^\circ$ ,  $P < 0.00001$ ). Taken the pastures separately, cattle show significant axial body orientation with a mean vector of  $1.2^\circ/181.2^\circ$  in Europe,  $3.7^\circ/183.7^\circ$  in Asia,  $12.1^\circ/192.1^\circ$  in Australia,  $30.9^\circ/210.9^\circ$  in Africa,  $32.0^\circ$

Author contributions: J.Č. and H.B. designed research; S.B., J.Č., O.V., and H.B. performed research; S.B. and J.N. analyzed data; and S.B. and H.B. wrote the paper.

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**Table 1. Basic circular statistics for axial directions of cows from six continents**

Continent	Mean vector		Circular SD	Rayleigh test, Z	Rayleigh test, P	No. of herds	No. of cattle
	$\mu$	r					
Africa	30.9°/210.9° (17.6–44.1)	0.608	28.6°	12.21	0.00000157	33	972
Asia	3.7°/183.7° (353.5–13.9)	0.784	14.2°	15.35	0.00000008	25	291
Australia	12.1°/192.1° (359.4–24.7)	0.668	25.7°	12.49	0.00000088	28	1,019
Europe	1.2°/181.2° (350.0–12.4)	0.422	30.9°	19.78	< 0.00000001	111	1,488
North America	347.5°/167.5° (159.1–176.0)	0.634	27.4°	29.33	< 0.00000001	73	3,034
South America	32.0°/212.0° (21.4–42.7)	0.675	25.4°	17.33	0.00000001	38	1,706
All herds	6.4°/186.4° (0.7–12.2)	0.486	34.4°	72.77	<0.00000001	308	8,510

Body positions of cows were estimated by using Google Earth mapping services. For each herd a mean vector has been calculated that was used for further analysis. The mean vector is characterized by its angle ( $\mu$ ) and its length ( $r$ ).  $\mu$  is given as XX°/XX° (N-S). Values in parentheses represent the 99% confidence intervals (with reference to north only).

212.0° in South America, and 347.5°/167.5° in North America (Table 1 and Fig. 1A; all data with reference to magnetic north). To evaluate whether geographic or magnetic north better predicts cattle orientation, we separately evaluated pastures originating from localities with naturally high positive and negative declination values. The mean vectors calculated for localities with high positive and negative declination differed significantly when geographic north was used as a reference ( $U^2 = 0.39$ ;  $P < 0.001$ ). When using magnetic north as a reference the difference between the mean vectors was not significant ( $U^2 = 0.15$ ;  $P > 0.1$ ), indicating that magnetic north is a much better predictor for the observed alignment to N-S than geographic north (Table 2).

Cattle's body orientation was independent from sun position because no significant correlation between axial shadow direction (as an indicator for sun position) and the cattle's body axes have been found (circular correlation;  $r = 0.159$ ;  $n = 103$  herds).

**Body Position of Deer.** Body axes of grazing roe deer (*Capreolus capreolus*) deviate significantly from random distribution (Rayleigh test,  $P < 0.00001$ ) revealing alignment to approximately N-S direction (mean vector: 9.0°/189.0°,  $r = 0.81$ ,  $n = 152$  herds); when resting, they align their body axis along 10.7°/190.7°,  $r = 0.93$ , ( $n = 28$  herds). Also body axes of grazing European red deer (*Cervus elaphus*) showed a significant deviation from

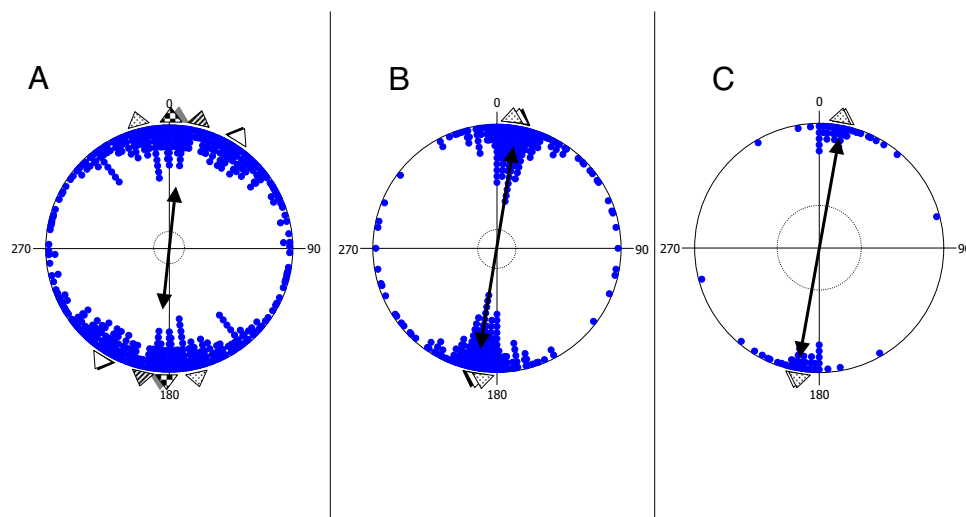
random distribution (Rayleigh test,  $P < 0.00001$ ) and were directed in a roughly N-S direction (9.7°/189.7°,  $r = 0.86$ ;  $n = 16$  herds). Deer beds in the snow, i.e., body prints of resting or sleeping animals, were in the same range (roe deer: 7.6°/187.6°,  $r = 0.86$ ,  $n = 21$  herds; red deer: 10.5°/190.5°,  $r = 0.9$ ,  $n = 24$  herds) (Table 3 and Fig. 1B and C).

Direct observations revealed that the majority of grazing and resting deer face northward (angular data for roe deer: 13.2°,  $r = 0.62$ ,  $n = 166$  herds; angular data for red deer: 34.3°,  $r = 0.47$ ,  $n = 16$  herds). When looking around and checking the surroundings, the animals just turn their heads but do not change the direction of their body axis. They change their body direction for short periods when moving to the next grazing place.

There was no significant correlation between the body position of roe deer and the time of day representing the position of the sun (circular correlation:  $r = 0.002$ ).

**Discussion**

Although the detailed dates of the satellite images are not provided by Google Earth, most views were apparently made on cloudless sunny days, judging from short shades, mainly around midday. Based on the vegetation, all images from Europe and the United States originated from summer times, and those from the southern continents covered both dry and rainy seasons. Given



**Fig. 1.** Axial data revealing the N-S alignment in three ruminant species under study. (A) Cattle. (B) Roe deer. (C) Red deer. Each pair of dots (located on opposite sites within the unit circle) represents the direction of the axial mean vector of the animals' body position at one locality. The mean vector calculated over all localities of the respective species is indicated by the double-headed arrow. The length of the arrow represents the  $r$ -value (length of the mean vector), dotted circles indicate the 0.01-level of significance. Triangles positioned outside the unit circle indicate the mean vectors of the cattle data subdivided into the six continents (dotted: North America; gray: Asia; checkered: Europe; striped: Australia; black: Africa; white: South America) (A) and the mean vectors of resting (black) and grazing (white) deer, and of deer beds (dotted) (B: roe deer; C: red deer).

**Table 2. Geographic north versus magnetic north as references for body orientation of cattle originating from localities with naturally high declination values**

Declination	Geographic north mean vector		Magnetic north mean vector		No. of herds	No. of cattle
	$\mu$	$r$	$\mu$	$r$		
Positive	11.7°/191.7°(4.1–19.2°)	0.85	358.7°/178.7°(350.7–6.7°)	0.83	31	1,052
Negative	333.3°/153.3°(318.5–348.1°)	0.85	347.5°/167.5°(332.7–2.3°)	0.85	11	223

The data for localities with positive and negative declination values are analyzed separately to minimize the effect of compensation. Only herds with a significant mean vector ( $P < 0.05$ ) were considered in the analysis. Both grand mean vectors were highly significant (Rayleigh test,  $P < 0.000000001$ ).  $\mu$  is given as XX°/XX° (N-S). Values in parentheses represent the 99% confidence intervals (with reference to north only).

the number and variety of localities distributed geographically, ecologically, and over time, the apparently calm weather situation, and the high position of the sun, the direction of the wind and the position of the sun are unlikely to be of major influence on the cattle's body orientation in our sample. They play, if at all, only a minor role and may be the "exceptions to the rule" (i.e., cases, when the animals were not aligned in a N-S direction).

**Wind.** If the wind was the primary factor determining alignment of the evaluated cattle, it has to be presumed that there were windy (and not windless) conditions in most of the 308 sampled pastures distributed geographically and in time. We had to presume furthermore that winds were strong and blowing mainly from northern or southern directions. This is highly improbable, because in the Northern Hemisphere westerlies and in the Southern Hemisphere "south eastern trades" are prevailing, and generally, airflow is deflected by the Coriolis force and tends to follow more east–west (E-W) direction rather than N-S (*Encyclopedia of the Atmospheric Environment*, [www.ace.mmu.ac.uk/eae/Climate/Older/Wind\\_Belts.html](http://www.ace.mmu.ac.uk/eae/Climate/Older/Wind_Belts.html)). Concordantly, wind atlases show that prevailing winds in the respective countries are variable throughout the year and mostly westerly. Regionally and locally, weaker winds are, however, highly variable throughout the year. Taken together, should wind be the determining factor of alignment, either random distribution of body orientation would be expected (if winds were weak or negligible, as probably was the situation in most cases), or the cattle would be oriented in west–east or northwest–southeast (if winds were strong and cattle were facing into the wind).

The wind factor can be excluded also for alignment of resting deer, because deer search for wind-protected places deep in the forests to rest (and even if it is windy, the wind in the forest is dampened and changes its direction locally and unpredictably). Most beds were fresh, originating from the previous night.

Climatic data for those particular nights indicate windless situations or winds blowing from different directions. Because the direct observation of grazing and resting deer took place mainly during windless days (or during days when the wind was negligible and in any case blowing from different directions at different recording times and localities), the influence of wind can be excluded as well.

**Sun.** Theoretically, the sun may influence body alignment in three different ways: thermoregulation, sun compass, and looking away to avoid dazzling. Sun basking is displayed by animals on cold, sunny days, mostly in the morning (when shades are long), after cold nights. Animals are standing so that they do not shade each other, and mostly are not grazing. No images that would suggest sun basking were found. Cattle facing heat stress do not graze, and they look for cover in tree shade, etc., if available. There were no images in our sample that would raise suspicion that the cattle were heat-stressed. We observed sun basking in roe deer; yet these records were not included into the analysis. In all observations of grazing or resting red and roe deer that were included into the analyses behavioral thermoregulation could be clearly excluded. Thermoregulation as an alignment-determining factor can be excluded in night observations and alignment of night deer beds.

The sun compass is known to play an important role in navigation (but not in alignment) of e.g., insects and migratory songbirds. It is known that these animals can perceive polarized light so that they can orient by means of a sun compass even on cloudy days (cf. refs. 12 and 13 and references therein). The animals known to perceive polarized light and use the sun compass (primarily for long-distance navigation) are basically diurnal, with vision being a dominant sense. On the contrary, ruminants are active throughout the day with several nocturnal grazing periods, also in deep winter. Moreover, although clear

**Table 3. Basic circular statistics for axial directions of deer from the Czech Republic**

Deer position	Mean vector		Circular SD	Rayleigh Test Z	Rayleigh Test p	No. of herds	No. of deer
	$\mu$	$r$					
Red deer							
All localities	10.2°/190.2° (4.4–16.0)	0.88	14.3°	31.17	<0.0001	40	1,062
Beds	10.5°/190.5°	0.90	13.0°	19.52	<0.0001	24	917
Grazing	9.7°/189.7°	0.86	16.0°	11.68	<0.0001	16	145
Roe deer							
All localities	9.1°/189.1° (5.8–12.3)	0.83	17.4°	139.07	<0.0001	201	1,912
Beds	7.6°/187.6°	0.86	15.9°	15.44	<0.0001	21	430
Grazing	9.0°/189.0°	0.81	18.6°	99.75	<0.0001	152	1,080
Resting	10.7°/190.7°	0.93	10.7°	24.35	<0.0001	28	402

Body positions were estimated for grazing and resting red and roe deer (direct observations) or from snow tracks of resting animals (beds). The mean vector is characterized by its angle ( $\mu$ ) and its length ( $r$ ). Values in parentheses below the mean vectors represent the 99% confidence intervals (with reference to north only).

behavioral evidence is still missing, the retinal parameters speak clearly against the capacity of polarized light perception (L. Peichl and H. Wässle, personal communication). Facing away from the sun, to avoid dazzling, could play a role in the morning or late afternoon, when the sun is low, and would result in E-W orientation of animals. This aspect can be clearly excluded in most of the satellite images (short shades), all of the direct observations (most of them being done on cloudy days), night observations, and deer beds.

Furthermore, there was no correlation between the position of roe deer and the time of day when the observation took place, meaning that the position of the sun had no influence on deer orientation.

**Magnetic Field.** Because climatic factors like wind, sun, or temperature were apparently not common directional key factors explaining ubiquitous alignment, we conclude that the magnetic field is the only common and most likely factor responsible for the observed alignment. Our analysis of cattle at localities with naturally high positive and negative declinations (compare Table 2) clearly provides the crucial proof in favor of the Earth's magnetic field being the responsive cue.

**Magnetic Alignment.** Magnetic alignment is a spontaneous behavioral expression of magnetoreception that appears particularly in resting animals when body orientation is not controlled by other factors (2). Earlier laboratory studies confirmed a certain preference for alignment to the magnetic field lines for several insect groups like flies, termites, and honey bees (14–17); further studies are reviewed in ref. 2. Among vertebrates, fishes (namely goldfish and eel) represent the only group for which alignment behaviors have been reported (2, 18). Recently, it was reported that pigeons show a tendency to align their flight in directions relative to the intensity of the geomagnetic field (19). In contrast to the easy recording of body alignment, its statistical evaluation is of a less trivial character. Alignment data are bimodal or quadrimodal, and usually  $<2/3$  of the observed individuals express it (2). Magnetic alignment *per se* does not require magnetoreception, i.e., conscious sensing of the geomagnetic field, and it does not necessarily imply the use of a magnetic compass for spatial long-distance orientation and navigation. Nevertheless, it surely requires some kind of magnetoreception. Observations made on grazing roe deer, and evaluation of fresh deer beds, where head and rear ends of the bed are easily recognizable, suggest that the recorded phenomenon represents not just a simple bimodal magnetic alignment of the body axis but even head orientation in the northern direction. Similarly, the angular analysis of data for grazing red deer revealed that the majority of animals orient their heads northward. However, within groups of animals, approximately one-third of the deer orient their heads southward, resulting in a grand mean vector of  $34^\circ$  (angular analysis). This differential alignment may represent an antipredatory behavior, as in the region of recordings, the lynx occurs.

The biological significance of the shown magnetic alignment remains enigmatic. It has been speculated that maintaining a symmetric position to the field lines somehow influences certain physiological processes (ref. 2 and references therein). Indeed, in humans the rapid eye movement latency is shortened in the E-W position of sleepers compared with the N-S position (20), and statistically significant differences in the EEG of normal subjects have been found, depending on whether the subjects sit facing the N-S or E-W direction (21). Maintaining a certain magnetic direction may provide also a constant directional reference for spatial orientation, which might be useful e.g., after disturbance and fast escape. Noteworthy, all of the studied ruminants are social animals, with large home ranges, moving over large distances, originally in habitats (dense forests or grassland)

without apparent landmarks. Our results call for an in-depth study of this phenomenon and challenge neuroscientists, biochemists, and physicists to study the proximate mechanisms and biological significance of magnetic alignment. It is amazing that this ubiquitous conspicuous phenomenon apparently has remained unnoticed by herdsman and hunters for thousands of years.

## Materials and Methods

**Analysis of Body Position of Cattle Using Google Earth.** We determined the axial directions of 8,510 cattle of 308 randomly selected localities (pastures) from six continents: Africa (Morocco, South Africa), Asia (India), Australia, Europe (Belgium, Denmark, France, Germany, Ireland, Netherlands, Russia, United Kingdom), North America (Connecticut, Kansas, Massachusetts, Montana, New York, Oregon, Texas), and South America (Argentina) by using satellite images freely available at Google Earth mapping services. Care was taken to evaluate only pastures in the flat country. The recordings include both sexes and diverse races of both dairy and beef cattle. The resolution of most satellite images in Google Earth did not allow clear and fast distinction between the individuals' head and rear, so records were confined to the body axis. Also, we did not distinguish between grazing, resting, and moving individuals. Chosen eye altitude depended on resolution and ranged between 45 and 1,730 m. Images of bad resolution and pastures located near the sea, at the hillside, or near human settlements were not selected. Screenshots of the chosen pastures were copied from Google Earth and pasted into Microsoft Powerpoint. Cattle moving on trails or standing at feeding troughs or watering places and calves being close to (suckler) cows were excluded from further analysis. We marked the cattle's longitudinal axis by drawing a straight line with the Powerpoint drawing tools and estimated for each animal separately its direction to the nearest  $5^\circ$  by overlaying a circular scale with  $10^\circ$  steps. Because we could not always distinguish the animals' front and rear, bidirectional analysis was the method of choice [i.e., data are doubled (modulo 360) before being analyzed, and the resulting mean vector is then back-converted, thus ranging in the interval ( $0^\circ$ ;  $180^\circ$ )]. Cattle of the same herd might not orient independently of each other, and we therefore calculated a single mean vector per pasture that was used in further analysis (Rayleigh test). All axial values are reported as  $XX^\circ/XX^\circ$  (N–S).

To estimate whether geographic north or magnetic north better predicts the body alignment, we investigated pastures at localities with high declination (Connecticut:  $-14.8^\circ$ ; Massachusetts:  $-14.7^\circ$ ; New York:  $-14^\circ$ ; Australia:  $+8^\circ$ ;  $+12.3^\circ$ ; Montana:  $+10^\circ$ ;  $+14.8^\circ$ ; Oregon:  $+17.5^\circ$ ). Watson's  $U^2$  test was used to test for significant differences between the two mean vectors representing alignment in cattle from localities with high negative and high positive declination. This test was conducted for geographic north and magnetic north separately.

Satellite images provided by Google Earth are oriented with respect to geographic north, and to correct the mean vectors for declination we used the following formula to obtain mean vectors (with respect to magnetic north):  $\text{mean vector}_{\text{magneticN}} = (\text{mean vector}_{\text{geogrN}} - \text{mean declination}) \text{ modulo } 180$ . We used the online calculator of the National Geophysical Data Center ([www.ngdc.noaa.gov/seg/geomag/jsp/IGRFWMM.jsp](http://www.ngdc.noaa.gov/seg/geomag/jsp/IGRFWMM.jsp)) to calculate magnetic parameters for each locality separately for the period 2000–2007 (step size: 1 year) and averaged the declination for the respective 8 years. The corrected mean vectors were then tested for uniformity by using the Rayleigh test with  $Z = n^2$  (significance level set to  $\alpha = 0.01$ ). As repetitions of the "experiments" with the same herd of cattle are impossible, only first-order statistics could be performed. Calculations were performed (i) for all localities together and (ii) for each continent separately.

**Sun Position and Cattle Orientation.** To evaluate a possible influence of the sun position and the cattle's body position, we performed a circular correlation for these parameters. We determined the sun position indirectly by evaluating the shadow direction. Only those images have been chosen where the shadow direction could be clearly identified ( $n = 103$  localities).

**Analysis of Body Position of Deer (Field Observation).** Body position of 2,974 deer (in 227 localities) was recorded in the Czech Republic. Axial directions of deer were based on measuring beds of animals that had rested in the snow (roe deer:  $n = 430$  in 21 localities; red deer:  $n = 917$  in 24 localities) and on direct snapshot observations of grazing and resting deer (roe deer:  $n = 1,080$  in 152 localities, red deer:  $n = 145$  in 16 localities). Recorded red deer beds were distributed in deep forests of the Sumava Mountains National Park that represent undisturbed localities chosen by deer for overwintering for generations. Grazing roe deer were observed at different times in the winter of

2007/2008 in a variety of habitats, in localities encompassing both the national park area and the agricultural landscape in the center of the Czech Republic. Animals that were obviously sun-basking were not taken into account. The animals did not notice the observer, or, being habituated, did not apparently react to him. Only records of resting or grazing (i.e., undisturbed) animals were analyzed. Standing and moving animals were not considered. Climatic data (wind, sun, temperature) had been recorded on the day the observation of grazing deer took place or the day before we measured the deer beds.

All directions were measured  $\pm 5^\circ$  with a compass. Only for the directly observed grazing and resting deer we distinguished between front and rear (angular data). All other data are bidirectional. However, to compare data for resting and grazing roe deer with those for beds, we classified all data as axial. As with the cattle, only one mean vector per deer locality was taken into

account to obtain statistical independence. Again, the Rayleigh test was applied to test for significant deviations from uniform distribution of the mean vectors.

All circular statistics were calculated with Oriana 2.0 (Kovach Computing).

**Sun Position and Roe Deer Orientation.** The position of the sun could be deviated by the exact time of the day. Circular correlation has been tested for the parameters time of day and roe deer position.

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1. Olson BE, Wallander RT (2001) Orientation of beef cattle grazing foothill winter range in Montana. *Proc W Sect Amer Soc Animal Sci* 52:1–6.
2. Wiltschko R, Wiltschko W (1995) *Magnetic Orientation in Animals* (Springer, Berlin).
3. Burda H, Marhold S, Westenberger T, Wiltschko W, Wiltschko R (1990) Magnetic compass orientation in the subterranean rodent *Cryptomys hottentotus* (*Bathyergidae*, *Rodentia*). *Experientia* 46:528–530.
4. Burda H, et al. (1991) Magnetic orientation in subterranean mole rats of the super-species *Spalax ehrenbergi*: Experiments, patterns, and memory. *Isr J Zool* 37:182–183.
5. Deutschlander ME, et al. (2003) Learned magnetic compass orientation by the Siberian hamster, *Phodopus sungorus*. *Anim Behav* 65:779–786.
6. Kimchi T, Terkel J (2001) Magnetic compass orientation in the blind mole rat *Spalax ehrenbergi*. *J Exp Biol* 204:751–758.
7. Muheim R, Edgar NM, Sloan KA, Phillips JB (2006) Magnetic compass orientation in C57BL/6 mice. *Learn Behav* 34:366–373.
8. Holland RA, Thorup K, Vonhof M, Cochran WW, Wikelski M (2006) Bat orientation using Earth's magnetic field. *Nature* 444:653–702.
9. Marhold S, Wiltschko W, Burda H (1997) A magnetic polarity compass for direction finding in a subterranean mammal. *Naturwissenschaften* 84:421–423.
10. Némec P, Altmann J, Marhold S, Burda H, Oelschläger HAH (2001) Neuroanatomy of magnetoreception: The superior colliculus involved in magnetic orientation in a mammal. *Science* 294:366–368.
11. Wegner RE, Begall S, Burda H (2006) Magnetic compass in the cornea: Local anaesthesia impairs orientation in a mammal. *J Exp Biol* 209:4747–4750.
12. Wehner R (1976) Polarized-light navigation by insects. *Sci Am* 23:106–115.
13. Muheim R, Phillips JB, Akesson S (2006) Polarized light cues underlie compass calibration in migratory songbirds. *Science* 313:837–839.
14. Becker G, Speck U (1964) Examinations on magnetic field orientation in Diptera. *Z Vergl Physiol* 49:301–340.
15. Becker G (1963) Resting position according to magnetic direction, magnetic orientation in termites. *Naturwissenschaften* 50:455.
16. Altman G (1981) Investigation of magnetotaxis of the honey bee, *Apis mellifica* L. *Anz Schädlingskd Pflanzenschutz Umweltschutz* 54:177–179.
17. Becker G (1964) Reactions of insects on magnetic fields, electric fields, and the atmosphere. *Z Angew Entomol* 54:75–88.
18. Becker G (1974) Influence of the Earth's magnetic field on the directional behavior of gold fish. *Naturwissenschaften* 61:220–221.
19. Dennis TE, Rayner MJ, Walker MM (2007) Evidence that pigeons orient to geomagnetic intensity during homing. *Proc R Soc London Ser B* 274:1153–1158.
20. Ruhenstroth-Bauer G, Rüter E, Reinertshofer TH (1987) Dependence of a sleeping parameter from the N-S or E-W sleeping direction. *Zeitschr Naturf C* 42:1140–1142.
21. Ruhenstroth-Bauer G, et al. (1993) Influence of the Earth's magnetic field on resting and activated EEG mapping in normal subjects. *Int J Neurosci* 73:195–201.