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SHORT COMMUNICATION

Magnetic alignment in warthogs *Phacochoerus africanus* and wild boars *Sus scrofa*

Jaroslav ČERVENÝ *Department of Game Management and Wildlife Biology, Faculty of Forestry and Wood Sciences, Czech University of Life Sciences, 16521, Praha 6, Czech Republic. Email: cerveny@fld.czu.cz*
Hynek BURDA *Department of Game Management and Wildlife Biology, Faculty of Forestry and Wood Sciences, Czech University of Life Sciences, 16521, Praha 6, Czech Republic and Department of General Zoology, Faculty of Biology, University of Duisburg-Essen, 45117 Essen, Germany. Email: Hynek.Burda@uni-due.de*
Miloš JEŽEK *Department of Game Management and Wildlife Biology, Faculty of Forestry and Wood Sciences, Czech University of Life Sciences, 16521, Praha 6, Czech Republic. Email: jezekm@fld.czu.cz*
Tomáš KUŠTA *Department of Game Management and Wildlife Biology, Faculty of Forestry and Wood Sciences, Czech University of Life Sciences, 16521, Praha 6, Czech Republic. Email: kusta@fld.czu.cz*
Václav HUSINEC *Department of Game Management and Wildlife Biology, Faculty of Forestry and Wood Sciences, Czech University of Life Sciences, 16521, Praha 6, Czech Republic. Email: husinec.v@gmail.com*
Petra NOVÁKOVÁ *Department of Game Management and Wildlife Biology, Faculty of Forestry and Wood Sciences, Czech University of Life Sciences, 16521, Praha 6, Czech Republic. Email: novakovap@fld.czu.cz*
Vlastimil HART *Department of Game Management and Wildlife Biology, Faculty of Forestry and Wood Sciences, Czech University of Life Sciences, 16521, Praha 6, Czech Republic. Email: hart@fld.czu.cz*
Veronika HARTOVÁ *Department of Game Management and Wildlife Biology, Faculty of Forestry and Wood Sciences, Czech University of Life Sciences, 16521, Praha 6, Czech Republic. Email: nemcova.verca@seznam.cz*
Sabine BEGALL *Department of General Zoology, Faculty of Biology, University of Duisburg-Essen, 45117, Essen, Germany. Email: Sabine.Begall@uni-due.de*
E. Pascal MALKEMPER* *Department of Game Management and Wildlife Biology, Faculty of Forestry and Wood Sciences, Czech University of Life Sciences, 16521, Praha 6, Czech Republic and Department of General Zoology, Faculty of Biology, University of Duisburg-Essen, 45117, Essen, Germany. Email: Pascal.Malkemper@uni-due.de*

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*Correspondence author.

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ABSTRACT

Magnetic alignment (MA) results from the preference of animals to align themselves along the field lines of the geomagnetic field, a behavioural expression of a magnetic sense. MA is well documented for ruminants and might demonstrate a general magnetic sensory ability among artiodactyls. We measured body-axis alignment in 1614 foraging or resting wild boars *Sus scrofa*, 1849 wild boar beds, and 1347 warthogs *Phacochoerus africanus*, and found a highly significant north–south preference. The magnetic field was the only common denominator of all observations. Thus, we provide the first data suggesting a magnetic sense in the Suidae.

INTRODUCTION

Among ungulates in Europe, the wild boar *Sus scrofa* is the species with the largest population growth over the last few decades. The concomitant expansion of its geographic range has brought about several problems: crop damage, diseases, danger to people, etc. (Barrios-Garcia & Ballari 2012, Massei et al. 2015). To manage wild boar populations effectively and obtain a complete picture of the wild boar's movement ecology, detailed knowledge about its sensory biology and spatial cognition is crucial (Morelle et al. 2015). Wild boars possess very good orientation abilities and a well-developed spatial memory (Lozan 1995), use landmarks and scent marks (Bracke 2011), and may even have an internal map of space (Dardaillon & Beugnon 1987). The visual acuity of pigs is relatively poor (Zonderland et al. 2008), but their auditory and olfactory senses are well developed (Heffner & Heffner 1990, Maselli et al. 2014). However, olfactory cues are generally believed to be used only for small-scale orientation, and environmental acoustic cues are usually not temporally stable enough to build the foundation for an internal map of space (Geva-Sagiv et al. 2015). Visual landmarks and/or a global reference are needed. The geomagnetic field can provide such a global reference (Phillips 1996). Whether or not wild boars can sense the geomagnetic field and make use of it during navigation has not been addressed so far. Magnetic alignment (MA), the preference to align the body axis in a certain angle relative to the field lines of the geomagnetic field, is expressed by a variety of vertebrates during diverse behaviours, often during grazing and resting, and is regarded as a clear indicator of magnetoreceptive abilities (Begall et al. 2013).

Here, we screened for evidence of MA in two species of the suborder Suiformes. We observed wild boars directly in the field and measured their characteristic beds (Appendix S1) at several locations in the Czech Republic. In addition, to follow the idea that MA is as widespread among Suiformes as it is among ruminants, we performed direct observations on warthogs *Phacochoerus africanus* in six African countries.

METHODS

Sampling

Free-living foraging or resting wild boars and warthogs were directly observed by means of binoculars (at distances of 20–100 m), and the heading of each animal of the herd at the time of observation was recorded. Headings of moving animals were not taken until they began foraging or lay down to rest. Only the first heading of each animal of the herd was recorded. The preferred resting positions of wild boars were additionally assessed by measuring the alignment of the shallow oval pits they make to rest in (beds, Appendix S1). All headings were assessed by means of hand-held compasses; therefore we observed behaviour with respect to the local magnetic field lines (local declination values are listed in Appendix S2). The compass bearings were estimated to the nearest 5°. Beds or individuals that were <20 m away from each other were assigned to the same herd. In addition to the headings, environmental and other variables were noted: time of day, weather conditions, sky condition (only for warthogs, sunny or cloudy), wind direction and wind strength, habitat type, sex, and age of the animals. Three age classes (juvenile, subadult, and adult) were distinguished based on morphology, behaviour, and herd composition. Juveniles were always with their mother and sometimes with subadult siblings. Adults, except for breeding females, are mostly solitary.

In total, the alignment of 1614 directly observed wild boars (264 herds) and 1849 wild boar beds (323 herds) were measured at 31 different localities in the Czech Republic. Furthermore, 1347 warthogs (310 herds) were observed at 33 different localities in six African countries (Appendix S2).

Statistics

Circular statistics were carried out with Oriana 4.02 (Kovach Computing Services, Pentraeth, Wales, UK). For both species of suids we calculated a mean vector for each observed herd of animals or beds and then the grand mean at different localities, in different countries, during different seasons, under different weather conditions, for different observers, and at different times of the day. The method of doubling the angles was used to convert angular data into axial data prior to grand mean statistical analysis (Batschelet 1981).

First-order (Rayleigh test) statistics were employed to test the headings for significant deviations from random distribution. As the herd sizes were highly variable (Appendix S3), we did not weight the mean vectors according to their vector lengths when calculating second-order statistics. Relationships between latitude and MA were investigated by applying Pearson correlation. Whenever sample sizes differed significantly between different conditions, random subsamples of equal sizes were taken for comparisons. Differences between mean headings and distributions between groups (species, localities, etc.) were tested for significance by means of Watson-Williams *F*-tests and Watson U^2 tests, respectively.

RESULTS

The wild boars in the herds we observed had a highly significant axial preference to align themselves approximately along the magnetic north–south axis, with a slight shift towards east [first-order statistics of individual values: μ = 20°/200° ± 3° (mean axial vector orientation angle; 95% confidence interval), r = 0.299 (mean vector length), Rayleigh test: n = 1614, $P < 10^{-12}$, Z = 144.73; second-order statistics of herd means: μ = 21°/201° ± 5°, r = 0.605, Rayleigh test: n = 264, $P < 10^{-12}$, Z = 96.756; Fig. 1, Table 1].

A similar and equally strong axial north–south preference was revealed for the orientation of wild boar beds (first-order statistics of individual values: μ = 19°/199° ± 3°,

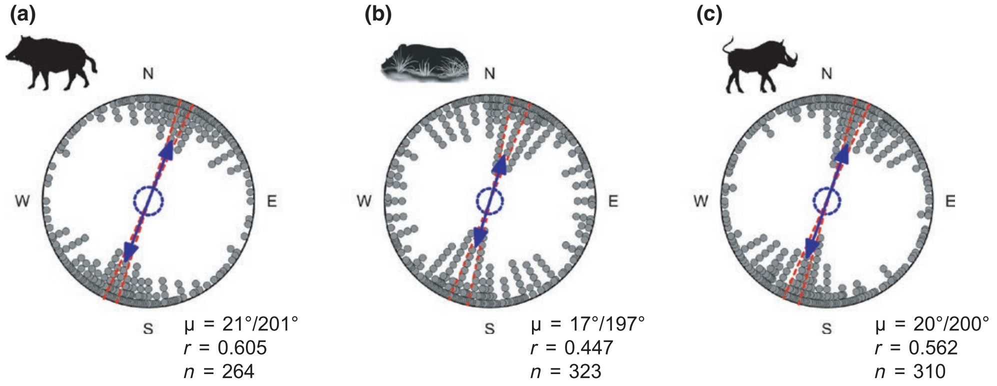

Fig. 1. Alignment of wild boars and warthogs, demonstrating the preference for an alignment roughly parallel to the north–south axis. (a) Directly observed wild boars. (b) Wild boar beds. (c) Warthogs directly observed in six different African countries. Each opposing pair of dots within the circle represents the mean axial direction of two herds. The double-headed arrows indicate the grand mean axial vector (μ) calculated over all herds' axial means. The lengths of the mean vectors (*r*) provide a measure of the degree of clustering in the distribution of the species' mean vectors. The dashed lines show the 95% confidence intervals and inner circles mark the 1% significance border of the Rayleigh test.

Table 1. Overview of alignment observations in wild boars *Sus scrofa* and warthogs *Phacochoerus africanus*. Second-order statistics were applied to the means of the herds. μ, mean vector; *r*, length of mean vector.

Species	Observation type	No. of herds	No. of animals	Localities	μ (axial)	Circular SD	*r*	*P* (Rayleigh test)
Sus scrofa	Direct	264	1614	25	21°/201°	29°	0.605	$<10^{-12}$
	Beds	323	1849	16	17°/197°	36°	0.447	$<10^{-12}$
Phacochoerus africanus	Direct	310	1347	33	20°/200°	31°	0.562	$<10^{-12}$

$r = 0.271$, Rayleigh test: $n = 1849$, $P < 10^{-12}$, $Z = 136.142$; second-order statistics of herd means: $\mu = 17°/197° \pm 5°$, $r = 0.447$, Rayleigh test: $n = 323$, $P < 10^{-12}$, $Z = 64.563$; Fig. 1, Table 1).

In warthogs, the same axial north–south preference became apparent (first-order statistics of individual values: $\mu = 19°/199° \pm 3°$, $r = 0.385$, Rayleigh test: $n = 1347$, $P < 10^{-12}$, $Z = 199.741$; second-order statistics of herd means: $\mu = 20°/200° \pm 4°$, $r = 0.562$, Rayleigh test: $n = 310$, $P < 10^{-12}$, $Z = 97.934$; Fig. 1, Table 1).

The time of the day, season, and weather conditions have no significant influence on the mean directional preferences of wild boars or warthogs (Appendices S4–S6). In wild boars but not warthogs, MA was more pronounced in males (Appendix S7) and in both species it was stronger in juveniles (Appendix S8) and in larger herds (Appendices S9 and S10); pairs showed antiparallel body orientation (Appendix S11). Furthermore, the ratio of north-heading to south-heading animals was dependent on the latitude of observations (Appendix S12).

DISCUSSION

We demonstrated MA, an indication of a magnetic sense, in two species of suids. Given the well-developed navigation skills of wild boars, it would not be surprising if they made use of a magnetic compass or even a map (Dardaillon & Beugnon 1987, Morelle et al. 2015). A magnetic sense would, for example, help boars put several feeding grounds into global perspective, therefore facilitating quick switching between them when needed (Phillips et al. 2010). Unlike landmark-based navigation, magnetic navigation is not affected by structural or seasonal changes in the environment; it represents an ideal strategy for species that need to react to environmental changes quickly. The wild boar is a highly flexible species (Keuling et al. 2008a, Podgórski et al. 2013). The warthog is generally considered to be a rather sedentary species; it inhabits small home ranges 64–374 ha (White 2010), compared to 175–6625 ha in wild boar (Keuling et al. 2008a,b). Nevertheless, warthogs would also benefit from a landmark-independent navigation system, for migration and for facilitated navigation and optimal space use within their home ranges. MA has been proposed as a means to prepare co-ordinated flight responses in herding animals (Begall et al. 2008, Hart et al. 2012), and as wild boars and warthogs are social animals that forage and rest in groups, MA might serve this function in these species. Antiparallel orientation of pairs can be interpreted as an antipredator strategy.

Given that the alignment of other ruminants is affected by magnetic disturbances such as the oscillating electromagnetic fields that emanate from high-voltage power lines (Burda et al. 2009, Kolbabová et al. 2015), it is reasonable to assume that wild boars and warthogs are also affected by such disturbances. It would be interesting to test whether or not they align themselves randomly when they are in the vicinity of electromagnetic disturbances. High-voltage power lines often border streets, so there may be a relationship between car accidents involving wild boars and the distance between electromagnetic disturbances and these crash sites. Collisions between wild boars and cars are very dangerous for the humans involved in the accident, and often result in human injuries or even death (Thurfjell et al. 2015).

In summary, given that the only stable reference available in all conditions was the geomagnetic field, we provide data supporting magnetoreception in Suiformes, thus adding to the continuously growing evidence for magnetoreception in large mammals (Begall et al. 2014).

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REFERENCES

Barrios-Garcia MN, Ballari SA (2012) Impact of wild boar (*Sus scrofa*) in its introduced and native range: a review. *Biological Invasions* 14: 2283–2300.

Batschelet E (1981) *Circular Statistics in Biology*. Academic Press, London, UK.

Begall S, Červený J, Neef J, Vojtěch O, Burda H (2008) Magnetic alignment in grazing and resting cattle and deer. *Proceedings of the National Academy of Sciences* 105: 13451–13455.

Begall S, Malkemper EP, Červený J, Němec P, Burda H (2013) Magnetic alignment in mammals and other animals. *Mammalian Biology* 78: 10–20.

Begall S, Burda H, Malkemper EP (2014) Magnetoreception in mammals. In: Naguib M (ed) *Advances in the Study of Behavior*, 45–88. Elsevier, Amsterdam, The Netherlands.

Bracke M (2011) Review of wallowing in pigs: description of the behaviour and its motivational basis. *Applied Animal Behaviour Science* 132: 1–13.

Burda H, Begall S, Červený J, Neef J, Němec P (2009) Extremely low-frequency electromagnetic fields disrupt magnetic alignment of ruminants. *Proceedings of the National Academy of Sciences* 106: 5708–5713.

Dardaillon M, Beugnon G (1987) The influence of some environmental characteristics on the movements of wild boar *Sus scrofa*. *Biology of Behaviour* 12: 82–92.

Geva-Sagiv M, Las L, Yovel Y, Ulanovsky N (2015) Spatial cognition in bats and rats: from sensory acquisition to multiscale maps and navigation. *Nature Reviews Neuroscience* 16: 94–108.

Hart V, Kušta T, Němec P, Bláhová V, Ježek M, Nováková P et al. (2012) Magnetic alignment in carps: evidence from the Czech Christmas fish market. *PLoS One* 7: e51100. doi:10.1371/journal.pone.0051100.

Heffner RS, Heffner HE (1990) Hearing in domestic pigs (*Sus scrofa*) and goats (*Capra hircus*). *Hearing Research* 48: 231–240.

Keuling O, Stier N, Roth M (2008a) Annual and seasonal space use of different age classes of female wild boar *Sus scrofa* L. *European Journal of Wildlife Research* 54: 403–412.

Keuling O, Stier N, Roth M (2008b) How does hunting influence activity and spatial usage in wild boar *Sus scrofa* L.? *European Journal of Wildlife Research* 54: 729–737.

Kolbabová T, Malkemper EP, Bartoš L, Vanderstraeten J, Turčáni M, Burda H (2015) Effect of exposure to extremely low frequency magnetic fields on melatonin levels in calves is seasonally dependent. *Scientific Reports* 5: 14206. doi:10.1038/srep14206.

Lozan A (1995) Study of the wild boar (*Sus scrofa* L.) memory in its orientative behaviour. *Journal of Mountain Ecology* 3: 130.

Maselli V, Polese G, Larson G, Raia P, Forte N, Rippa D et al. (2014) A dysfunctional sense of smell: the irreversibility of olfactory evolution in free-living pigs. *Evolutionary Biology* 41: 229–239.

Massei G, Kindberg J, Licoppe A, Gačić D, Šprem N, Kamler J et al. (2015) Wild boar populations up, numbers of hunters down? A review of trends and implications for Europe. *Pest Management Science* 71: 492–500.

Morelle K, Podgórski T, Prévot C, Keuling O, Lehaire F, Lejeune P (2015) Towards understanding wild boar *Sus scrofa* movement: a synthetic movement ecology approach. *Mammal Review* 45: 15–29.

Phillips JB (1996) Magnetic navigation. *Journal of Theoretical Biology* 180: 309–319.

Phillips JB, Muheim R, Jorge PE (2010) A behavioral perspective on the biophysics of the light-dependent magnetic compass: a link between directional and spatial perception? *Journal of Experimental Biology* 213: 3247–3255.

Podgórski T, Bas G, Jedrzejewska B, Sönnichsen L, Sniezko S, Jedrzejewski W et al. (2013) Spatiotemporal behavioral plasticity of wild boar (*Sus scrofa*) under contrasting conditions of human pressure: primeval forest and metropolitan area. *Journal of Mammalogy* 94: 109–119.

Thurfjell H, Spong G, Olsson M, Ericsson G (2015) Avoidance of high traffic levels results in lower risk of wild boar-vehicle accidents. *Landscape and Urban Planning* 133: 98–104.

White AM (2010) A pigheaded compromise: do competition and predation explain variation in warthog group size? *Behavioral Ecology* 21: 485–492.

Zonderland JJ, Cornelissen L, Wolthuis-Fillerup M, Spoolder HA (2008) Visual acuity of pigs at different light intensities. *Applied Animal Behaviour Science* 111: 28–37.

SUPPORTING INFORMATION

Additional supporting information may be found in the online version of this article at the publisher's web-site.

Appendix S1. The characteristic beds of wild boars.
Appendix S2. Magnetic alignment in wild boars and warthogs observed in different countries.
Appendix S3. Histograms showing the absolute occurrences of different herd sizes.
Appendix S4. Directional preferences of warthog herds observed under different weather conditions.
Appendix S5. Number of observations at different times of the day.
Appendix S6. Directional preferences observed at different times of the day and in different seasons.
Appendix S7. Male wild boars show stronger alignment than female wild boars.
Appendix S8. Juvenile pigs expressed stronger alignment.
Appendix S9. Magnetic alignment in wild boar and warthog herds of different size.
Appendix S10. Decreasing scatter in the alignment of warthogs with increasing herd size.
Appendix S11. Boxplots and histograms demonstrating vigilance behaviour in pigs resting in pairs.
Appendix S12. Decreasing numbers of north-heading pigs at southern latitudes.