Directional preference may enhance hunting accuracy in foraging foxes

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Red foxes hunting small animals show a specific behaviour known as ‘mousing’. The fox jumps high, so that it surprises its prey from above. Hearing seems to be the primary sense for precise prey location in high vegetation or under snow where it cannot be detected with visual cues. A fox preparing for the jump displays a high degree of auditory attention. Foxes on the prowl tend to direct their jumps in a roughly north-eastern compass direction. When foxes are hunting in high vegetation and under snow cover, successful attacks are tightly clustered to the north, while attacks in other directions are largely unsuccessful. The direction of attacks was independent of time of day, season of the year, cloud cover and wind direction. We suggest that this directional preference represents a case of magnetic alignment and enhances the precision of hunting attacks.

Keywords: fox; hunting behaviour; magnetoreception; magnetic alignment

1. INTRODUCTION

Recently, we reported that in the absence of strong extrinsic and intrinsic influences, grazing and resting cattle and deer prefer to orient their body axes in roughly north–south directions, i.e. they tend to align along the geomagnetic field (GMF) lines [1]. No such directional preference was recorded in animals under high-voltage power lines, where the GMF is disturbed, providing direct support for the hypothesis of magnetic alignment [2]. Magnetic alignment may be a more widespread phenomenon among animals than previously thought, which raises questions about its biological significance.

The functions of magnetic alignment may be manifold. The interaction between magnetosensation and homeostatic, neurovegetative and metabolic functions has been proposed (cf. [3]) but empirical and experimental evidences to support this possibility are lacking. Magnetic alignment in ruminants may help to synchronize movement of individuals in herds. However, magnetic alignment is even more prominent in resting and sleeping animals, and here it is more difficult to explain. Maintaining a certain magnetic direction may provide a constant directional reference for spatial orientation (cf. [1,2,4]). It can also serve as a basic tool for cognitive mapping of everyday surroundings and learning new landmarks (cf. [5–7]).

Here, we report a case of compass preference, exhibited in another behavioural context. Red foxes (Vulpes vulpes) hunting rodents show a specific behaviour known as ‘mousing’. The fox jumps high, so that it surprises its prey by striking from above. Although the sensory mechanisms of prey location have not been explicitly studied, observations of foraging foxes suggest that hearing plays a decisive role. Prior to an attack, foxes move forward very slowly and deliberately, with ears erect, cocking their heads from side to side indicating that they are paying careful attention to auditory cues. Preliminary observations, obtained prior to this study, suggested that the body direction of foxes as they attack their prey was non-random.

2. MATERIAL AND METHODS

Mousing behaviour was observed by 23 experienced wildlife biologists and hunters in 84 wild red foxes (V. vulpes) in 65 localities in the Czech Republic, in different habitats, between April 2008 and September 2010, and at different times of day. The body orientation of a fox while preparing for a jump was recorded in 95 hunting series, in which a total of 592 hunting jumps were observed. Body orientation was measured with a compass with accuracy of 1° with the angle indicating the head direction. In 200 jumps, the immediate success or failure of the attack could be clearly determined. We calculated means over repeated measures of individuals that were used in further analysis (second-order statistics). We analysed the heading direction of jumps with respect to the height of vegetation or snow cover, time of the day, season of the year, observer, sex and age of the fox, and other relevant variables. The Rayleigh test was used to test for the significant deviation from a random distribution (see electronic supplementary material for details).

3. RESULTS

A hunting series lasted on average 19 min (±18 min; ranging from a few seconds up to 88 min) and involved on average seven (±17; 1–31) mousing jumps. Foxes preparing for the jump showed a preference to head for the north-eastern direction (figure 1a). Analysis of all jumps in all hunting series revealed highly significant deviation from randomness (43 ± 86°, n = 592, r = 0.322; Z = 61.3; p < 10−12). Directions of jumps were not correlated either with the absolute or relative time of day or with the day or season of the year (see the electronic supplementary material). There was no significant difference between mean heading of all jumps in low vegetation cover (where the fox would be likely to see its prey; figure 1e) compared with those in high vegetation or snow cover (figure 1b). However, north-east-oriented jumps (and particularly in high cover) tended to be more successful than jumps in other directions (figure 1 and the electronic supplementary material). In other words, a large majority (74%) of successful attacks in high cover were confined to a cluster centred about 20° clockwise of magnetic north with a small (15%) secondary cluster at due south, while attacks in other directions were largely unsuccessful. In fact, high cover attacks performed within the angular segment of 340°–40° were highly successful (72.5%), and those within the segment of 160°–220° had success of 60 per cent, while attacks...
initiated in other magnetic alignments had a success rate under 18 per cent.

4. DISCUSSION
The tight clustering of preferred (and particularly of successful) attack directions cannot be explained by an effect of light cues (sun position, celestial polarized light pattern, asymmetrical lighting, etc.) since observations were carried out at different times of day, at different seasons of the year, under overcast (most often) and clear skies (see electronic supplementary material for detail). Nor was this clustering a response to wind direction, which varied from observation to observation, and rarely came directly from the north or south. Note also that recordings were made by different observers at a number of different locations. Clustering of successful jumps in high vegetation or higher snow cover, where visual guiding of attacks is unlikely, is highly significant (figure 1c), showing that directional heading has a profound effect on hunting success under conditions in which visual information is not available to augment auditory cues. In low vegetation, where the prey can be spotted also by sight, directional heading seems to play a less decisive role (figure 1f).

In the absence of any other source of directional information that can explain the non-random alignment of fox predatory attacks and, in particular, the precise alignment of successful attacks on prey in high cover and under snow, we propose that these responses are another case of alignment with respect to GMF. In contrast to magnetic alignment responses in other animals where the adaptive significance of the behaviour remains a mystery [3], in foxes, the relationship between attack direction and attack success provides a valuable clue to the adaptive significance of this behaviour. The question then is why should alignment with respect to an absolute (presumably magnetic) reference have such a profound impact on attack success and, in particular, why should this relationship be more pronounced in high cover that limits the use of visual cues to guide predatory attacks?

A variety of animals have been shown to derive azimuth (‘compass’) information from the horizontal component of GMF (cf. [3]). The vertical component (course and slope of field lines) of GMF (inclination) varies geographically between 0° at the equator and vertical ±90° at poles and it can allow animals to distinguish between the ‘equatorward’ and ‘poleward’ ends of the magnetic axis (e.g. [8,9]). The predictable spatial variation in inclination has also been shown to provide some animals with one coordinate (roughly corresponding to north–south position) of a bicoordinate ‘magnetic map’ or geographical position sense [10]. The other coordinate may be provided by geographically specific intensity (strength) of the GMF (cf. [11]). Within the home range of a non-migratory species like the red fox, however, inclination and intensity are effectively constant and unlikely to be used for differential ‘micro-scale’ geographical position determination. However, the inclination of the magnetic field might be used also to derive information about relative horizontal distance (see [7] and the electronic supplementary material). Here, we suggest that mousing red foxes may use the magnetic field as a ‘range finder’ or targeting system to measure distance to its prey and thus increase the accuracy of predatory attacks.

Figure 1. Angular data revealing the north-east alignment of mousing foxes. The direction of the arrow represents the mean vector of angular data (μ), length of the arrow represents the r-value (length of the mean vector), and inner circles indicate the 0.05 level of significance. (a) Analysis of all individual values (n = 592 jumps), μ = 43°, r = 0.322; upper row (b–d) analysis of individual values of direction of mousing jumps in high vegetation or snow cover; lower row (e–g) direction of jumps in low cover; all jumps (b,c), known successful jumps (c,f), and known unsuccessful jumps (d,g) were analysed separately. See electronic supplementary material for details. Each triangle in (a) represents four observations (i.e. separate data points) ((b) three observations; (e) two observations; (c,d,f,g) one observation).
When hunting for prey in high cover or under snow, foxes are unable to use visual cues to augment auditory cues to target prey. Other predators that specialize on small mammals, and rely primarily on auditory cues to locate prey, have evolved specialized mechanisms to increase the accuracy of prey localization. For example, barn owls have asymmetrically positioned ears with the right ear-canal opening higher than the left one. This asymmetry allows the barn owl to determine the elevation of a sound by comparing sound intensity and time differences between its two ears [12]. The present findings suggest that foxes may have evolved a different solution to this problem. First, the fox tilts its head when attending to sounds produced by a potential prey, creating thus asymmetric position (different height above the ground) of both ear-canals. Secondly, as suggested here on the base of the model presented by Phillips et al. [7], a fox that approaches an unseen prey along a northward compass bearing could estimate the distance of its prey by moving forward until the sound source is in a fixed relationship to the magnetic field, e.g. it coincides with the inclination of the magnetic field. This would consistently place the fox at a fixed distance from its prey, allowing it to attack using a highly stereotyped leap (see electronic supplementary material). Thus, when visual information is limited, using the magnetic compass to provide a more accurate estimate of distance from the prey could account for the dramatic increase in predatory success of attacks aligned to the north and south field (J. B. Phillips & M. S. Painter 2010, personal communication). If so, this would be the first documented case of an animal using magnetic compass input to estimate distance, rather than direction.

A magnetic targeting system, as proposed above, could be mediated by a magnetite-based compass mechanism like that used by subterranean mole-rats (cf. [13]). An alternate possibility is a magnetic compass mechanism based on a light-dependent radical pair reaction mediated by specialized photoreceptors in the retina [14,15]. Evidence for such a photoreceptor-based magnetic compass mechanism has led to speculation that the GMF may be perceived as a pattern of light intensity of colour superimposed on the animal’s surroundings [14]. If so, the three-dimensional pattern [7] could provide a ‘targeting’ system as proposed here. Note that unlike the targeting system used by a jet fighter pilot, such a magnetic coordinate system would be fixed in alignment with respect to magnetic north. A fox moving in a fixed direction when approaching its prey (i.e. moving to the north), could approach until a specific component of the visual pattern generated by the magnetic compass is superimposed on the source of the sound from the prey, so that it could initiate an attack from a fixed distance. Note that unlike a magnetite-based magnetic compass, a magnetic targeting system that produces a three-dimensional ‘visual’ pattern, which is axially symmetrical [14], might also be used for targeting prey when aligned to the south, which could explain the secondary clusters of successful attacks to south (figure 1 and the electronic supplementary material).

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