Spatial orientation of the Philippine bent-toed gecko (*Cyrtodactylus philippinicus*) in relation to its home range*

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Abstract. As is well known, many animals are able to orientate themselves in the earth's magnetic field. However, to date there is no evidence that squamate reptiles are able to perceive the earth's magnetic field. Here, we demonstrate the homing performance of the Philippine bent-toed gecko (*Cyrtodactylus philippinicus* STEINDACHNER, 1867) after displacing individuals from their home ranges. The observed number of returns is significantly larger than expected from a random selection of directions after displacement (2-tailed exact binomial test, P<0.01). Additionally, we suggest from experiments with an Emlen funnel that these geckos are able to perceive a change in the local magnetic field, which would hint at the use of the earth's magnetic field for orientation purposes (bootstrap test, P<0.05). Moreover, the data presented here suggest that these geckos are able to orientate themselves when displaced, and that sensing of the earth's magnetic field may be a component of the homeward orientation mechanism. Our results represent the first indication that squamate reptiles can perceive changes in the earth's magnetic field, and may be able to extract from it cues for orientation.

Key words. Squamata, Gekkonidae, homing performance, magnetic perception, earth magnetic field.

Introduction

The earth's magnetic field provides a constant source of information for the orientation of animals. It has been shown that a number of animals align their direction of movement with an internal magnetic compass (WILTSCHKO & WILTSCHKO 1995). Moreover, they possess the ability to recognize the polarity of the magnetic vector. These phenomena have been investigated in many vertebrates and invertebrates (e.g., reviewed in WILTSCHKO & WILTSCHKO 1995, VÁCHA et al. 2008). However, the phenomenon of magnetic compass orientation has not yet been verified for any squamate reptile (Röll 2007 pers. comm., Wiltschko 2008 pers. comm.). The use of the earth's magnetic field for long-distance orientation in reptiles has been demonstrated for turtles (e.g., LOHMANN & LOHMANN 1993). Moreover, evidence for magnetic short-distance orientation has been found in homing experiments with young American alligators (Alligator mississippiensis) by RODDA (1984) and in the nocturnal palmate newt Lissotriton helveticus (DIE-GO-RASILLA et al. 2008).

The present pilot study is based on data that were collected during the conduct of homing experiments using the Philippine bent-toed gecko (*Cyrtodactylus philippinicus*) on Panay Island, in the vicinity of the Research Station "Sibaliw" of the Philippine Endemic Species Conservation Project (PESCP). We determined the homing rate of *C. philippinicus* to test if the animals return to their home ranges after being translocated. Such behaviour has previously been demonstrated for several types of reptiles, including lizards (e.g., WEINTRAUB 1970, FREAKE 2001, LETTINK 2007). To this end, we translocated captured specimens of *C. philippinicus* from within and around the research station to a distant site, and observed whether or not they returned home.

Here, we studied whether these geckos were able to perceive changes in the earth's magnetic field. More specifically, we demonstrate that *C. philippinicus* is able to detect an experimental change of the local magnetic north-south polarity. Our results are the first to indicate that squamate reptiles (*C. philippinicus*) are able of perceiving changes in the earth's magnetic field.

Materials and methods

The Research Station "Sibaliw" is located near the western edge of the forest of the NW peninsula of Panay Island, in the Municipality of Buruanga (11°49'11.6"N, 121°58'0.5"E) (Fig. 1). We performed several translocation experiments on bent-toed geckos, *C. philippinicus*. These experiments differed with respect to season and point of release. Specif-

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Figure 1. Right: Panay Island. The research station is located on the NW Panay peninsula. Left: The research station and its environment. 1: generator house, 2: volleyball field, 3: toilet, 4: frog tub, 5: research station, 6: quarantine cages, 7: bird cages, 8: washing place, 9: shower cabin, 10: mice cages, 11: "release tree 100 m" (2005/2006), 12: arena (2006), 13: "release tree 150 m" (2005), 14: "release tree 100 m" (2007), 15: arena (2007), "......": trail.

ically, we performed tests in the dry season of 2005 (January to April) and the rainy seasons of 2006 (August to October) and of 2007 (September to December). We translocated specimens captured in and around (radius < 25 m) the research station, to three different release trees at a distance of approximately 100 m and 150 m to the east, and 100 m to the north-northeast, respectively (Fig. 1). In total, we displaced 66 geckos that were marked on the back with a number painted with a fluorescent dye. Transportation was accomplished in closed buckets, allowing us to exclude visual orientation and learning via visual clues during displacement. The area in which we searched for the geckos included the research station and its surroundings, so that approximately 3600 m² were covered. This area lay within a sector with an angle of 18° (2005), 48° (2006) and 44° (2007) opening toward the research station with the vertex being the release site (Fig. 1). Every night we searched for several hours for geckos that had returned. To calculate the home ranges of the animals, we used the widely accepted minimum convex polygon method. For our tests concerning the possible perception of the earth's magnetic field, we constructed a circular arena, based on the idea of an Emlen Funnel (EMLEN & EMLEN 1966). The arena measured 50 cm in diameter with a wall height of 25 cm. Blue plastic foil above the arena shielded it from rain

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and a free view of the sky. We designed the arena in such a manner that would enable us to observe the behaviour of the animals, focusing on their attempts to escape, but the geckos were not able to climb the walls. In the experiments, there was always only one gecko in the arena. Since the animals are nocturnal, the search for geckos, the displacements as well as the magnetic field tests were carried out at night.

We performed the experiment at two different locations, next to the respective release trees at a distance of ~120 m from the research station. We observed escape attempts under "normal" conditions or those employing a manipulated magnetic field. In order to manipulate the local magnetic field in the arena, we placed bar magnets under the arena so that the N/S-axis was reversed by 180°. This was confirmed with a compass. In total we observed 25 geckos under natural and 11 under disturbed magnetic field conditions. Each observation period lasted 90 min. Four Geckos observed under the disturbed magnetic field conditions are also included in the geckos used under natural magnetic conditions. The periods of rest between tests performed with the same individual lay between 13 and 21 days. We recorded the direction of any attempt of a gecko to leave the arena by trying to climb the wall (subsequently called "escape attempt direction").

Results

Home ranges

Through repeated re-captures and re-sightings of geckos around the research station the sizes of three home ranges could be estimated in 2005 and of another seven in 2007. They comprised approximately 15 to 86 m² (2005) and 2 to 35 m^2 (2007).

The homing performance of the displaced geckos

First, we examined the question of whether displaced geckos are capable of finding their original home. To this end, we analysed three data sets. The 2005 sample comprised 22 individuals, of which 8 returned to their area of capture, i.e., the research station and its surroundings. They were re-discovered by searching in a sector bounded by an angle of 18°, with the release tree being the vertex, i.e., in the same sector in which the entire sample had been captured. They returned within periods of between 4 and 36 days from their release site. The observed number of returns is significantly different from random direction dispersal for which only 1.1 returning animals would be expected (2-tailed exact binomial test, P<0.001 (cf. SACHS 1984)).

The 2006 sample consisted of 31 individuals, of which 13 were re-captured or re-sighted within the bounds of a 48° sector. They returned within 2 to 51 days after release. Again, the observed ratio of returners/non-returners of 0.42 is significantly different from the expected ratio of 0.13 (2-tailed exact binomial test, P<0.001). Similarly, for the 2007 sample of 13 individuals, of which six were re-captured within the bounds of a 44° sector, the difference from random dispersal is significant as well (2-tailed exact binomial test, P<0.01). Hence, the results of all three samples support unequivocally the idea that the geckos returned back home non-randomly.

Evidence for the geckos perceiving the earth magnetic field

The arena was divided into thirty-six 10°-sectors of a circle. Each escape attempt was assigned to one of these 36 sectors. We collected four separate data sets, distinguished by observation period (and accordingly observation location), and magnetic field conditions. The data sets consist of observations of the escape attempt directions (EADs) in natural local magnetic field conditions (301 and 144 EADs) and in experimental distorted magnetic field conditions (109 and 128 EADs). Because several escape attempts were recorded during a single test, i.e., with the same animal during one night's observation, independence of the data cannot be assumed. However, an autocorrelation analysis of the sequences of successive EADs for the individual animals indicated only marginal correlations between the EADs (average autocorrelation between 2 subsequent EADs ≈ 0.2 , between EADs with 1 or 2 other attempts in between ≈ 0). Statistical analysis revealed that the samples of EADs in the natural magnetic field and in the rotated magnetic field were significantly non-uniformly distributed (Rayleigh's test: natural field P=0.013 (2006), P=0.10 (2007); rotated magnetic field P=0.10 (2006) and P=0.025 (2007)). Fig. 2 shows the EADs in the natural and rotated magnetic fields for the 2006 and 2007 samples. Note, that the mean EADs are not orientated towards the station, but are different between the natural and rotated magnetic field.

To analyse the potential difference in the observed distributions of EADs we compared them statistically, both for 2006 and 2007. A standard χ^2 -test yields only a first indication of a difference of the overall distributions disturbed vs. normal (P=0.3 (2006) and P=0.06 (2007)). However, we note that the χ^2 -test may not perform well because we had less than 5 observations in some direction bins (BAT-SCHELET 1981). To overcome this problem we analysed the specific alternative that modification of the magnetic field changed the average direction of escape attempts of the geckos. To this end, we performed a bootstrap test (e.g., EFRON 1979) that is particularly well-suited for this kind of analysis and needs no further assumptions. The differences between the mean angles of the EADs in the observed samples for natural and modified magnetic fields were 107.7° (2006) and 121.1° (2007). Our bootstrap test indicates how probable this observed difference is: if both samples were drawn from the same distribution, they have the same true mean direction. For this reason we drew random samples matching the original sample sizes for the natural and disturbed magnetic field conditions. Each random sample is distributed in the same way as the data for the natural field in the respective trial are. In this manner we simulated 1000 sets of artificial data for each original data set, determined the absolute difference of the mean directions in each set, and observed how often the resulting difference exceeds the actual one. The bootstrap test yielded P=0.044 (2006) and P=0.029 (2007), respectively. We conclude that the observations for the distorted and normal field cases follow distributions with markedly different mean angles.

Discussion

Our experiments on homing using 66 bent-toed geckos strongly hinted at directional homing by the geckos, thus excluding a random search as an explanatory mechanism. The idea of piloting with the help of learnt landmarks can be strongly dismissed for the following reasons: First, we can assume that the geckos resident at the research station and its surroundings arrived from all directions and not only from a strip of land connecting the research station with the release site. Second, looking at the estimated home range sizes (n=10), not even the largest (86 m^2) is large enough to provide the landmarks required for piloting. GRUBER & HENLE (2004) demonstrated in translocation experiments that the nocturnal arboreal gecko Gehyra variegata is capable of orientation using visual cues for short distance movements (the original home tree was still visible after translocation). Visual cues from the research station can be definitely excluded due to the distance between the research station and the release trees, even in view of the adaptation of the gecko eye to their nocturnal lifestyle and a good orientation in darkness (e.g., RÖLL

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Natural magnetic field 2007

Distorted magnetic field 2007

Figure 2. Distribution of EADs of the geckos in 2006 and 2007 for the natural (left) and the distorted (right) magnetic fields. The arrows in the centre represent the mean resultant vectors.

2000, ROTH & KELBER 2004). Acoustic cues are also unlikely, not least due to variable weather conditions. Moreover, since geckos predate mainly on insects, the short-distance sense of acoustic is of paramount importance especially for hunting (CHOU et al. 1988) and also in intraspecific social contexts (MARCELLINI 1977). Regarding other sensorial cues, olfactory and compass orientation cues are most likely. It is not possible to discriminate between these two senses in this study, but our data indicate at least magnetic reception to be involved in the home orientation found. Geckos have been shown to have well-developed nasal chemical senses, which are used for fundamental activities like feeding, shelter selection, conspecific interactions, predator avoidance, mate choice and reproduction (DIAL et al. 1989, COOPER & BURGHARDT 1990, MASON & GUTZKE 1990, see SCHWENK 1993 for more references, DIAL & SCHWENK 1996). There is no evidence in the literature for olfactory long-distance orientation of geckos. Moreover, ZURI & BULL (2000) showed that olfaction and vomerolfaction are no major cues for home-range maintenance in sleepy lizards (Tiliqua rugosa) and SCHWENK (1993) concluded that olfaction is involved particularly in the detection of food and predators, and vomerolfaction in the exploration of novel stimuli and in reproductive behaviour.

Navigation has been shown to be affected by little-understood local effects, i.e., influences from a particular release site chosen (WILTSCHKO & WILTSCHKO 1995, PERRY & GARLAND 2002). Employing two different release sites makes the hypothesis improbable that a local effect underlies the homing of bent-toed geckos. Among potential cues enabling the geckos to locate their original homes are landmarks and the earth's magnetic field. Collectively, a close scrutiny of the capture site, consideration of the distance from the release site, and an assessment of a sample of home ranges allow us to exclude the idea of homing via landmarks or directly perceived cues from the home ranges (see above). This points to cues from the earth's magnetic field as an alternative explanation of the observed homing behaviour even though olfaction s. l. cannot be excluded at present.

We analysed the data pertaining to the escape attempts of the geckos obtained under different magnetic fields using a number of statistical tests. These showed that the geckos have markedly different mean directions during their escape attempts in the distorted magnetic field when

compared to the natural magnetic field. Moreover, the escape attempts are significantly non-uniformly distributed. Our most powerful test was the bootstrap test that showed a difference between the mean escape attempt directions. Nevertheless, the differences in mean directions for the natural and the manipulated magnetic fields for the years 2006 and 2007 are only 107° and 121°, respectively. If we assume that the geckos orientate themselves only via the magnetic field, we would expect a difference of approximately 180°. This may point to additional orientating cues being superimposed on the magnetic orientation mechanism. Note that a superposition of cues of different origin would reduce the probability of rejecting our null hypothesis, and hence render our tests conservative in this respect. Such additional cues may also explain why the mean escape directions in the natural and distorted magnetic fields were not orientated towards the station.

To summarise, we showed that this forest gecko is able to return home after displacement from its home range. Importantly, we showed that the orientation of the geckos in a test arena is related significantly to the local earth's magnetic field. Specifically, escape behaviour changed when the magnetic field was modified, which demonstrates the ability of the geckos to perceive the magnetic field. While we assume that magnetic cues may play a role in homing, our study does not provide evidence of other cues potentially used. Identification of other cues than those provided by the magnetic field will thus be an important question in our ongoing research.

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