A new hypothesis for the use of geomagnetic field orientation by terrestrial hatchlings and the question: Do these new insights about the geomagnetic field orientation by turtles require rethinking the practice of head-start programs for turtles and terrapins?

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Geomagnetic field (GMF) orientation has been recognized as an important aspect of navigation for several animal species, among them turtles. Evidence for the importance of GMF has been provided in particular for species in regard to natal homing over long distances (Luschi et al. 2007, Fuxjager et al. 2014, Brothers & Lohmann 2015). However, other turtle species seem to rely on GMF as well. In particular freshwater turtles, which are known for long distance migrations to their nesting sites, seem to rely on GMF for orientation. Two types of GMF that are probably used according to their specific habitats have been recognized (Kramer 1950): First, the use of the earth GMF to establish a geomagnetic field map for orientation and navigation, and second the use of the GMF in combination with a solar (or sun-) compass, mainly using UV-radiation for orientation (Lohmann et al. 2007, 2008, Congdon et al. 2015, Putman et al. 2015). In addition a third type of GMF, which may be considered as a subtype of the formerly described types, has been described for young snapping turtles (*Chelydra serpentina*) by Land-

Fig. 1
Blanding's turtles (*Emydoidea blandingii*) have been comparably well studied and the use of the earth geomagnetic field for orientation has been shown. Photo: Scott D. Gillingwater

LER et al. (2015). The authors show that young snapping turtles orient their body axis according to a magnetic field present at the low level Larmor frequency, which is a naturally occurring electromagnetic radiofrequency (see also comment in regard to radiotelemetric tracking of hatchlings by BIDMON 2015a). From a biological point of view Larmor frequency should be favored, because the perception of an electromagnetic field has several limitations related to the lipid rich cell membranes in living tissue – except for very low frequencies such as the Larmor frequency.

The above mentioned possibilities for the use of geomagnetic field orientation seem to be important at least for all turtle species or populations whose nesting sites are located at longer distances, so that the freshwater habitat will not be visible from the nesting site of these species either by day or night, e.g. *Glyptemys insculpta*, *Emydoidea blandingii* (WALDE et al. 2007, PATERSON et al. 2012), *Emys orbicularis* (SCHNEEWEISS & STEINHAUER 1998, SCHNEEWEISS et al. 1998, SCHNEEWEISS 2003).

Orientation of Sea Turtles

For some sea turtles it is known that the imprinting of the nest sites does not only take place at embryonic stages during development within the nest, as they use earth GMF also for their migration into the open sea after hatching (LUSCHI et al. 2007, LOHMANN et al. 2007, 2008, PUTMAN et al. 2011, PUTMAN et al. 2015). Whether this GMF orientation of sea turtles includes only some species or is only used during certain times, e. g. at the beginning of their journey, is still a matter of discussion, because some hatchlings rather seem to follow the prevailing sea current experienced during hatching season (PROIETTI et al. 2014). For these latter the geomagnetic imprinting towards the nesting site (place of birth) seems to be the most important one. After leaving the nest at night sea turtle hatchlings find their way to the water visually using UV-light (KAWAMURA et al. 2009) and once in the water they follow either the current or a GMF perceived beforehand in order to follow a predetermined route. However, sea turtles usually mate and fertilize their eggs shortly (only several sea miles) before reaching their nesting sites

Fig. 2
Hatchlings like this Blanding's turtle have a need for orientation information, because after hatching they have to find their way to the next freshwater habitat.
Photo: James H. Harding

Fig. 3a–b
For young snapping turtles (*Chelydra serpentina*) it has been shown that they make use of the Larmor frequency for orientation.
Photos: Scott D. Gillingwater (a), James H. Harding (b)

Fig. 4a–b
Not always are the nesting sites so close to the water like in that case. Turtle tracks from snappers (*Chelydra serpentina*) in the sand. Photos: James H. Harding

(e.g. Stiebens et al. 2013). That means the developing embryos would be only able to perceive the GMF for a relatively short period of time, namely the last miles before their mother reaches the nesting site at the beach. However, after hatching they still have the opportunity to perceive and imprint the GMF and its changes by establishing a magnetic map, which they experience during their journey through the atlantic- or pacific basin. This way they have the possibility to gain GMF information in order to find their way back to their place of birth either by this GMF map or the use of GMF information in combination with a solar compass (for details see the above cited literature).

Fig. 5
Wood turtles (*Glyptemys insculpta*) like many other terrapins migrate over long distances towards suitable nesting sites.
Photo: James H. Harding

Freshwater turtles and Terrapins

The situation is somewhat different for freshwater turtles, terrapins or certain populations which inhabit freshwater habitats far away from optimal nesting sites (Schneeweiss et al. 1998, Walde et al. 2007, Paterson et al. 2012) and where mothers are sometimes forced to change the nesting site as the old one is either destroyed or overgrown by dense vegetation. Such turtle species have two problems to solve: First, the female hatchlings have to remember the direction towards suitable nesting sites (place of hatching) and second, all hatchlings have to find the way back to the freshwater habitat. The only thinkable exception would be a nesting site is in a location from which a freshwater habitat can be found in either direction (e.g. an islet surrounded by water) so that the exact direction in which the hatchlings migrate is not important. This scenario, however, is rarely found and becomes even rarer in increasingly fragmented and/or agriculturally used land. Therefore, it is indispensable that the hatchlings have information about the direction where to find a suitable freshwater habitat, especially when they are unable to see the water from their place of birth. How difficult it is for freshwater turtles to find a suitable body of water without this pre-registered information has been described very well by Roth & Krochmal (2015, see also comment in Bidmon 2015b). In response to that knowledge Liboff (2015) formulated a hypothesis proposing that the geomagnetic information including low frequency which is perceived by the female (mother) turtle is somehow transferred via signals (e.g. hormones or transmitters or messenger RNA) into the egg in order to be available for the hatchling. Abraham Liboff is a physicist and focuses on certain theories about the magnetic field information transfer which are perceived by the mother turtle and then transferred into the eggs via certain until now non-specified components.

It is most likely that the embryos will sense the geomagnetic field in which their mother moves while still in utero.

Fig. 6a–b
An egg from a freshly deposited wood turtle clutch (*Glyptemys insculpta*) which was injured. The already present embryo with developing eyes is already clearly visible, even before a white spot is visible. Developing eye: blue arrow, head with brain: red arrow.
Photos: Hans-Jürgen Bidmon

Fig. 7a–b
In Quebec, Canada, female wood turtles have sometimes to migrate for extremely long distances between their freshwater habitat and their nesting sites (a) during which they have to overcome some obstacles (b).
Photos: Andrew D. Walde (a), Scott D. Gillingwater (b)

A new, alternative hypothesis relying on state-of-the-art research that is - in my opinion - very comprehensible from a biological point of view!

From my point of view the hypothesis that information about the GMF is transferred from the mother into the egg is difficult to understand - think of a female gravid turtle, which reaches her nesting site after a journey which lasts several days full with an usually already completed (shell covered) clutch of eggs in utero (e.g. Schneeweiss 2003 and Buhlmann & Osborn 2011), but is then forced to search for a new one. How should it now transmit that information about the new nesting site into the eggs (usually most eggs are covered with an eggshell long before they start migrating towards the nesting sites)? According to the theory the females could only provide the eggs with predetermined information in form of signal-components before the eggshell will be completed. Considering new findings about the adaptability of organisms to stochastically variable environments (Richardson 2010), this would be a rather unlikely scenario, even for a philopatric sea turtle. However, when referring to biologically consolidated knowledge that most if not all turtles contain developing embryos long before the eggshell is completed which even undergo a phase of dormancy within the oviducts induced by hypoxia after shell formation (for detail see: Rafferty & Reina 2012, Rafferty et al. 2013, Rings et al. 2015) it is be conceivable that embryos perceive the GMF their mother is walking in (Direct Embryonic Geomagnetic Field Perception Hypothesis). In such a scenario the embryo directly perceives the geomagnetic inclination values without the need of a signal transfer from the mother via the eggshell as proposed by Liboff (2015). An example how well the embryos are already developed in a freshly deposited wood turtle clutch (*Glyptemys insculpta*) at a time when no white spot (as a mark for continuing embryonic development) is visible is shown in Fig.6. It shows that the head and the pigmented eye-Anlagen are already clearly present. As a necessary condition for this embryonic GMF perception-hypothesis one has to assume that the neurons (or neuroblasts) in the brain or eyes sensing the GMF are already present. Such an assumption would have been pure speculation until June 2015 – but work of Vidal-Gadea et al. (2015) provides evidence of two GMF responsive neurons among the 302 neurons forming the nervous system of the so called vinegar eel, *Caenorhabditis elegans*. They clearly show that GMF-sensitive, functional neurons do exist already in worms (phyla: Nematoda). Since such neurons are already functionally present in much older phyla, the possibility exists that the CNS of early vertebrate embryos possess such neurons as well. At that point one could argue that these neurons may not be functional during the hypoxia induced dormancy within the oviducts (Rings et al. 2015). However, as we have learned from the vast amount of literature about hypoxic hibernation in freshwater turtles and terrapins (including hibernation within the eggs) such phases of dormancy are actively regulated by involving specialized patterns of gene expression and cerebral signaling which actively protect the CNS from hypoxic damage (Storey 2007, Biggar & Storey 2009, Hogg et al. 2014, Krivoruchko & Storey 2015, Jonz et al. 2015). Therefore, it is well conceivable that it may be a matter of physiological regulation to keep these GMF-sensitive neurons alert during that phase – just like those neurons, which have to kept later alert and functional during hibernation in order to respond to temperature or seasonal changes when waking up after winter.

The biological advantage of the Direct Embryonic Geomagnetic Field Perception Hypothesis is that the perception of information by the embryo remains very flexible, allowing the embryo to record and imprint stochastic directional changes which are executed by the gravid female turtle (mother) in response to non-predictable environmental changes even shortly before clutch deposition (see Schneeweiss 2003). According to this an active exchange of biological signal components, such as hormones or other transmitters, from the mother into the egg would be not necessary (and when eggshell formation is completed it would no longer be an option anyway). The only inherited information the hatchlings would need from their parents is that they have to hatch, leave the nest under certain environmental conditions and migrate. The direction for body align-

Fig. 8a–b
Water is essential for turtles (a), but also male specimens are migrating, like this wood turtle in Quebec, Canada (b). Photos: Scott D. Gillingwater (a), Andrew D. Walde (b)

Fig. 9
Hatchlings need to have information how to orient at the time of hatching, even when the mother had to change direction unexpectedly when the former nesting place was destroyed or lost. Photo: James H. Harding

ment (Landler et al. 2015) or orientation during migration would have been already imprinted at an early embryonal stage.

As it is well known from the literature such long migration routes of hatchlings are also influenced by a variety of environmental parameters in a species-dependent manner, such as temperature, air- and substrate humidity or availability of prey and others.

What are consequences of such patterns of GMF orientation for conservation biology and the management of turtles at the level of species and/or populations?

In accordance with the strong evidence for the use of GMF orientation several consequences in regard to their conservation management arise. One of the first refers to populations whose gravid females depend on long distance migration to reach their optimal and preferred nesting sites: Under that circumstances the only option would be the protection against predators of the clutches exactly at the site where they have been deposited, because only this can guarantee that the hatchlings will maintain the topographical relation between nesting site and migration route to their freshwater habitat. (Steel wire meshes, which could act as a Faraday cage, should be avoided as they may interfere with the continuous GMF-imprinting during development while in the nest). In such habitats it would probably be completely counterproductive to introduce foreign turtles or turtles which have been raised in an artificial head-start program, because the probability will be very high that they cannot find these optimal nesting sites since they are not aware of their existence and location. Their only option would be a non – targeted search (problems arising under these circumstances are well outlined by Roth & Krochmal 2015 and Bidmon 2015b). In such a situation head-start programs or relocation programs will only have a chance when in addition artificial nesting sites are provided close to the freshwater habitat, which the turtles could find by visual orientation. However, given such artificial supportive measures one will not be able to maintain the endogenous population with its unique adaptation to this habitat or environment. Such biological and biophysical parameters remained mainly unconsidered or neglected until now in head-start or reintroduction programs and one could speculate that this could be a reason why they have largely failed for species depending on long distance migrations towards specific nesting sites. Certainly, under such circumstances head-start programs may increase the

Fig. 10
One of the last females of the in Germany autochthonous European pond turtle (*Emys orbicularis*) on its long distance migration to the nesting site (see Fig. 11). Photo: Norbert Schneeweiß

number of adult individuals within the freshwater habitat, but when females after maturing are unable to locate suitable nesting sites, because of disorientation (towards the far away nesting sites which are unknown to them) it will not benefit population survival in the long term! From what we have learned so far about the use of GMF orientation, it can already be predicted that head-start and reintroduction programs will only be beneficial and successful for amphibian- and (reptile) turtle populations or species whose long term survival does not depend on long distance migrations guided by GMF orientation.

That is the most significant difference between migrating amphibians/reptiles and migrating birds or mammals, because offspring from migrating birds and mammals will learn their first long-distance orientation by following their parents. Comparably late they become imprinted to the GMF and its inclination changes, which they can later use for their own orientation during migration.

Fig. 11a–b
A south-facing slope at a forest glade which is more than 600 m (straight distance) away from the freshwater habitat serves as nesting site. The nest is covered by a protective wire mesh (a). From this nesting site the freshwater habitat is not visible due to the surrounding timber forest. A small hatchling which made the way back at the edge of the freshwater habitat (b). Photos: Norbert Schneeweiß

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Abstract

A new hypothesis for the use of geomagnetic field orientation by terrestrial hatchlings and the question: Force the new insights to rethink the practice of head-start programs for several turtles and terrapins?

Abstract

Here I discuss a new biological hypothesis of direct geo-electromagnetic field perception of early turtle embryos while the eggs are still in utero within the mother, in response to Liboff's (2015) hypothesis of geomagnetic field information information-transfer via molecular signals from the mother into the developing turtle egg. The new hypothesis pays attention to certain specific constraints such as a completed egg shell during the late phases of migrating towards the nest as well as the need to change this information if the well-known nesting sites are destroyed and have to be changed shortly before deposition, because such late unpredictable nest site change can involve additional long distance migrations according to the literature. This new alternative hypothesis is based on the very new discovery of specialized geomagnetic perception neurons in the vinegar eel, *Caenorhabditis elegans* which are the first indications that these specialized neurons exist in animals. In general the overwhelming new insights about the use of the geomagnetic field orientation by turtles provide the evidence for a need to drastically rethink the practice of head-start programs for enhancing turtle and terrapin populations at least when their long term survival depends on long distance migrations to suitable nesting sites.

Key words

Chelonia, Testudines, Emydidae, Direct embryonic geomagnetic field perception hypothesis, geomagnetic field, geomagnetic maps, head-start programs, conservation biology.