Assessing reliance on vector navigation in the long-distance oceanic migrations of green sea turtles

Abbreviated title: Vector navigation in green turtle oceanic migrations

Abstract

Vector navigation, i.e. maintaining a constant heading for a given amount of time, is hypothesized to provide a viable basis for the navigational feats of a number of long-distance animal migrants. Since animals following this strategy are subject to drift by wind or by ocean current, performing long migrations relying on vector navigation is particularly challenging. We tested whether vector navigation could be involved in the migrations of green turtles (*Chelonia mydas*) that migrate between the remote Ascension Island and Brazil. To this aim, a novel approach was followed using individual-based numerical models to simulate migratory trajectories of virtual turtles that were compared to actual routes reconstructed by satellite. Simulated post-nesting migrations from Ascension revealed that weak currents enabled modeled turtles to reach the Brazilian coast, but only for a limited range of headings around due West. This conclusion was corroborated by comparing modeled trajectories with the actual routes of previously tracked turtles, with a bee-line vector navigation strategy providing the best fit, although a true navigation strategy directed to the landfall site produced similar results. Finally, we tested if a vector navigational strategy was feasible for the pre-breeding migration from Brazil towards Ascension, but modeled routes mostly failed to reach the island or a larger area around it, with individuals drifting away under the influence of currents. We conclude that Ascension turtles can take advantage of vector navigation when migrating towards a wide target like the Brazilian coast, while the demanding prebreeding migration likely requires more complex navigational systems.

Keywords: navigational strategies, individual-based models, migration, clock and compass

Lay summary

We modeled the oceanic migration of turtles nesting in the remote Ascension Island to gain insights into the unknown mechanisms of open sea navigation. We show that a simple strategy of maintaining a single heading for a given amount of time can account for the turtles' postnesting migrations directed to targets along the Brazilian coast, while for pre-breeding migrations aimed at reaching the isolated Ascension Island, reliance on more complex, map-like systems seems crucial.

Introduction

During their life cycle, a variety of animals undertake prolonged migration extending over hundreds of km to reach their reproductive sites or foraging/wintering areas (Alerstam et al. 2003). How animals navigate during these movements has fascinated scientists for many years and has resulted in a considerable number of studies addressing this problem. Despite this intense scientific interest, our understanding of how migrants find their way during their long-distance movements is still limited. A number of navigational hypotheses have been put forward in the past (e.g. Wallraff 1991; Freake et al. 2006; Chapman et al. 2011; Guilford et al. 2011; Lohmann et al. 2008a; Endres et al. 2015), but direct evidence for any such hypothesis is still limited, challenged further by the difficulties in studying the subject in natural conditions (Lohmann et al. 2008b; Hussey et al. 2015; Kays et al. 2015).

The actual navigational mechanism used by a given animal migrant will largely depend on its ability to obtain information regarding the surrounding environment. To address this point, two main strategies have been suggested: vector and true navigation (Wallraff 1991; Able 2001; Bingman and Cheng 2005). In the latter case, the animal relies on a variety of positional cues to develop a sort of map, through which it can determine the direction to the final goal and adjust its headings during migration (Kramer 1961). This constitutes a powerful navigational mechanism allowing the animal to diagnose and correct for extensive off-route deflections so as to reach the goal from any location, although continually following a map sense can be inefficient or even lead to failure in strong flow conditions (Alerstam 1979; Chapman et al. 2011). When relying on a vector navigation strategy, the migrant does not have such a complete control on its route, but follows a spatiotemporal program providing information about the distance and direction of the target (Berthold 1991), by keeping a certain heading for a certain amount of time it should reach its final goal or at least the general vicinity. The key difference between the two systems is that animals relying on vector navigation are fully subject to the effects of environmental conditions encountered during their migratory journeys, and in particular, to winds or sea currents that may cause the animal to drift away from its intended route (Berthold 1991; Chapman et al. 2011). Despite these limitations, vector navigation is considered a viable strategy to explain the navigational feats of a number of long-distance migrants spanning from butterflies to birds, also given that it can be more energy-efficient compared with a continuous goal navigation for migrants moving in weak or balanced flows (McLaren et al 2014). Evidence consistent with reliance on vector navigation derived from interpretation of empirical data on orientation responses of captive birds (Berthold 1991), of recoveries of tagged animals (Mouritsen 1998; Mouritsen et al. 2013) or of reconstructed migratory routes (Gschweng et al. 2008; Yoda et al. 2017), with only two studies having employed models to evaluate the feasibility of vector navigation in birds (Stoddard et al. 1983; McLaren et al. 2014).

In the marine environment, sea turtles provide well-known examples of long-distance migrations directed to specific destinations, as their marked philopatry leads them to return to the same site to breed typically every 2-3 years, and then to return to their individually-specific foraging grounds (reviewed by Luschi et al. 2003; Southwood and Avens 2010). These migrations, which often are directed to a small breeding island or an isolated foraging area in the middle of the ocean (e.g. Girard et al. 2006; Hays et al. 2014), are particularly challenging, since marine animals move in areas devoid of fixed reference points, and so are unable to assess the current drift they are exposed to (Lohmann et al. 2008a; Sale and Luschi 2009; Chapman et al. 2011). While the general features of turtle migrations are being revealed through satellite telemetry (reviewed by Godley et al. 2008), the navigational mechanisms underlying these migratory performances are still largely unknown. The results of specific experiments performed in the laboratory and under natural conditions (e.g. Lohmann et al. 2004; Luschi et al. 2007), suggest that turtles may rely on a true navigation mechanism (Kramer 1961), likely based on geomagnetic information, that would allow most of the navigational performances known in tracked turtles, including their ability to compensate for artificial displacements (e.g. Lohmann et al. 2004; Luschi et al. 2001; 2007; Hays et al. 2003; Girard et al. 2006; Benhamou et al. 2011). However, it is unclear whether migrating turtles continuously rely only on this mechanism, which may even be counterproductive in some cases (Chapman et al. 2011). Under some conditions, for instance when heading to large targets such as an offshore foraging area or a continental coast (Papi et al. 2000; Sale and Luschi 2009) they may utilize other strategies, and satellite reconstructions of oceanic postnesting migratory routes have indeed shown that sometimes turtles do not directly head to their individually-specific foraging sites, but follow a bi-phasal process, whereby they first quickly cross the open sea to reach coastal or neritic waters and then make evident course corrections to reach their destination (Hays et al. 2002; 2013; Hawkes et al. 2012). In such cases, reliance on vector navigation cannot be excluded to account for the recorded turtle behaviour.

A possible way to study the navigation mechanisms underlying animal migrations is to take a modeling approach. For instance, Lagrangian virtual particle tracking has allowed the generation of relevant, although indirect, information on otherwise inaccessible processes like the passive dispersal patterns of small non-active swimmers, such as fish larvae, small invertebrates or turtle hatchlings (e.g. Putman et al. 2012; Casale and Mariani 2014; Baltazar-Soares et al. 2014; Fossette et. al. 2015; Young et al. 2012; Davis et al. 2015; Scott et al. 2017). When tracking data on individual migratory routes are available, individual-based models can be applied to infer information on the cues used for compass orientation during migrations (Åkesson and Bianco 2015; 2017), or on the navigational strategies employed by tracked migrants (e.g. Åkesson et al. 2003, McLaren et al. 2014; 2016; Hays et al. 2014; Åkesson and Bianco 2015; 2017; Bracis and Muller 2017).

In the present study we extended this modeling approach to the case of animals migrating towards a specific destination in the oceanic environment, by focusing on one of the most iconic animal migration, that of the green turtles (*Chelonia mydas*) breeding at Ascension Island in the South Atlantic Ocean (7.57° S, 14.22° W). Upon completing the nesting process, Ascension turtles migrate to foraging sites located along the Brazilian coast, thus undertaking an amazing postnesting migration of >2000 km in the open ocean (Carr 1975; Luschi et al. 1998; Hays et al. 2002). Oceanic migrations directed to specific sites represents a most challenging feat of migratory navigation, not only for sea turtles (Lohmann et al. 2008b; Sale and Luschi 2009), but also for other open-sea migrants showing fidelity to specific sites (Bonadonna et al. 2003; Bingman and Cheng 2005; Luschi 2013), such as fish (e.g. Jorgensen et al. 2010; Block et al. 2005; 2011), seabirds (e.g. Jouventin et al. 1994; Croxall et al. 2005; Weimerskirch et al. 2012), seals (e.g. Le Beouf et al. 2000; Bonadonna et al. 2001; Block et al. 2011) or whales (Horton et al. 2017, Durban and Pitman 2011). To test whether vector navigation can account for the navigational feats of Ascension turtles, we used spatially-explicit numerical models and followed a three-step approach, first modeling the postnesting migrations of virtual turtles migrating using a vector navigation strategy, then evaluating which navigational strategy produces trajectories best fitting with the actual routes previously reconstructed for tracked turtles, and finally modelling the pre-breeding migrations of turtles migrating from Brazil to Ascension following a vector navigation strategy to assess if this could successfully direct turtles to their remote destination.

Methods

To develop the models, we referred to information obtained from eleven female green turtles that have been tracked by satellite in years 1997, 1998, 2001 and 2009 during their post-nesting migrations from Ascension (Tab. 1; Fig. S1; Luschi et al. 1998; Papi et al. 2000; Hays et al. 2002; Witt et al. 2010). Details on transmitter models, weights, attachment methods and data filtering procedures can be found in the original papers. In brief, turtles were tracked by means of the Argos System, and the locations obtained were subjected to a filtering process to discard erroneous data. The resulting tracks were then interpolated with a fixed sampling period of 6 h to obtain locations evenly spaced in time. Turtles tracked in 2009 were equipped with a Fastloc Argos-GPS transmitter, but for our analysis only Argos locations were considered and then interpolated, so to have data fully comparable to the other turtles.

Daily ocean current data were obtained for the migratory period of each female from the Global Hybrid Coordinate Ocean Model (hycom.org), with a spatial resolution of 1/12° (approx. 8 km). This model merges remote-sensing data (satellite altimetry and sea surface temperature data) and *in situ* measurements (e.g. drifters) to derive both a reanalysis and a forecast of global ocean currents (Fossette et al. 2012) and is widely used for studies of sea turtle spatial behaviour (e.g. Putman and Mansfield 2015; Briscoe et al. 2016). Since migrating green turtles travel in the upper layers of the water column (Hays et al. 2001), the most superficial layer depth of 0-2 m was selected from the model. In the area considered, currents are generally weak in the latitudinal band 5-10°S (Brown 1990), becoming stronger in the region north of 5°S.

A preliminary analysis was carried out to estimate the water-related speed of each turtle using ARGOS data on movements and HYCOM current values. This was undertaken according to the procedures developed by Gaspar et al. (2006) and Galli et al. (2012): the turtle velocity vector deriving from its active swimming was derived by subtracting the current velocity vector encountered along the migratory route from the ground-based velocity obtained from the tracking data at each location. The results of this analysis (Fig. S2, S3), showed that turtles mostly migrated in a generally weak current field, with their swimming velocities always being much higher than currents (overall mean current speeds over the turtle courses: 0.8±0.5 km·h^{-1} vs. mean active swimming speed 2.6±0.7 km·h^{-1}; n=11; Table 1). As a consequence, their ground-based movements were therefore quite representative of the turtle's active swimming for most part of their route, and it was only when approaching the Brazilian coast that they encountered somewhat stronger currents (see examples in Fig. S4).

The navigational models were developed in R (R Development Core Team, 2017) creating a custom function simulating the migration of a virtual turtle leaving from a defined starting point at Ascension or in Brazil and then moving by keeping one single heading during the whole migration (see also Painter and Hillen 2015). In all cases, and positions of modeled turtles were updated every six hours (4 virtual fixes/day). No attempt was made to introduce compass errors in the model, given that no information on the accuracy of sea turtle compasses is available (Lohmann et al. 2008b).

Phase 1: modeling postnesting migrations from Ascension Island to Brazil

Modeled turtles moved from the same starting point (14.414°W, 7.919°S; the main nesting beach at Ascension) for 40 days (mean migration length of previously tracked turtles), at a travel speed corresponding to the minimum value of the mean active swimming speeds recorded in the different turtles (2.2 km·h^{-1}). Simulations were run twice a month (starting on day 1 and 15) between March and July (likely temporal window of departure; Godley et al. 2002) and repeated for 13 years (from 1997 to 2009), to account for variability in ocean conditions. For each starting date, 9 different westward headings were tested, ranging from 250° to 290°, in 5° increments, for a total of 1170 simulations.

A simulation was considered successful if it ended up in a target area (up to 50 km offshore along the Brazilian coast from 5°S to 15°S; Fig. S1). This area included the foraging sites of all previously tracked turtles and the landfall points where turtles first reached the coast, that are in areas where green turtles are known to aggregate when foraging (Carr 1975; Proietti et al. 2009; Gonzales-Carman et al. 2016).

Phase 2: comparing modeled vs. actual routes

Individual-based models were employed to assess which navigational strategy produced simulations best representing the routes reconstructed for the 11 turtles tracked by satellite. Models were run with parameters specific for each individual: starting point, day/year of departure, migration length (days), travel speed (mean of the estimated swimming speeds).

Migration using a vector navigation strategy was simulated with modeled turtles moving from Ascension Island keeping a single heading for the total migration length. Four possible headings were tested: the beeline angle between the turtle starting point and landfall (simulations V.LF), and the three best migration headings revealed by the previous analysis (simulations V.270°, V.275° and V.280°). In four cases, the heading used for V.LF simulations was 270° (Table 1), and the simulation V.270 was therefore not run. Furthermore we modeled a true navigation strategy, in which modeled turtles were assumed to adjust their movement direction every 24 hours in order to reach their final goal (Painter and Hillen 2015), which was constituted by the first landfall along the Brazilian coast (simulations true.LF) and by the final foraging grounds (simulations true.FG). This last simulation could only be performed for the six turtles in which the foraging grounds had been identified thanks to a prolonged tracking duration (Table 1). To facilitate comparison with simulated tracks the real turtle tracks were interpolated with a time interval of 6 hours.

The difference between the various simulations and the actual routes was assessed by calculating two values: i) the difference in date of arrival in an individually-specific target area (extending 100 km N and S from the turtle's landfall and 50 km offshore); ii) a measure of Route Diversity (RD) expressed as the mean distance (in km) between corresponding fixes of simulated and real routes. To compute the first variable, three categories were defined: 1) simulations arriving the same day as the turtle (best ones), 2) those arriving 2-9 days later or earlier, and 3) those not arriving at the target (worst ones). To calculate RD, the distance between corresponding fixes of simulated and real routes, was calculated throughout the modeled migration.

We used R and the package lme4 (Bates et al. 2015) to model RD per type of simulated navigational strategies using a Gaussian linear mixed model (LMM) with a logarithmic link function. Turtle ID was included as random factor to account for repeated measures of the same individual.

Phase 3: Modeling pre-nesting migrations from Brazil to Ascension Island

Finally, we also investigated the feasibility of a vector navigation during pre-breeding migrations by modeling trajectories from Brazil to Ascension Island. No tracking data are yet available for this migration, so general information derived from the geography of the migration area was used to set the simulation parameters: travelling headings ranged from 80° to 100° in 5° increments, 10 starting points were selected in Brazil inside the target area used in step 1, and the migration duration was set to 80 days. All simulations had the same travel speed (2.2 km·h^{-1}; as for phase 1 simulations), and were run starting twice a month, on day 1 and 15 from October to February between 1996 and 2009, resulting in 7000 simulations in total. These specific months were chosen on the basis of the presence of nesting turtles at Ascension Island (mostly from December to June; Godley et al. 2001), and considering that each female remains at the island for at least 2 months to lay successive egg clutches. A simulation was considered successful if it reached a final target constituted by an area of 20 km around Ascension Island plus a sector extending for 100 km towards NW (see Fig. 6). This irregular target was identified based on the outcomes of previous displacement experiments (Luschi et al. 2001; Hays et al. 2003) showing that turtles displaced from Ascension preferentially returned to the island only from the Northwest, likely employing wind-borne cues transported in that direction from the SE-blowing trade winds).

Results

Phase 1: modeling postnesting migrations from Ascension Island to Brazil

The results showed that modeled turtles consistently reached Brazil relying on a vector navigation when keeping a heading between 270° and 280° (Fig.1). Simulations with headings 270° or 275° mostly reached the target area (Fig. S1), while simulations with heading 280° failed in some cases. In these cases modeled turtles followed quite straight routes and were able to reach the target moving in a generally weak current field (see also Brown 1990), being deviated by stronger Northward currents only when getting close to the Brazilian coast. Unsuccessful simulations failed to reach the target because they ended up too far north or encountered head currents that prevented them completing the migration in 40 days. No differences among different starting dates were evident in the rate of success of simulations with successful headings (Fig. 1).

Phase 2: comparing modeled vs. actual routes

As shown in Fig. 2, the results were quite variable among individuals. In some cases (turtles 15119 and 66770) none of the strategies produced routes similar to the turtle route, while in other cases the routes derived from one or more of the simulated strategies fitted largely (turtles 25476 and 94593) or partially (turtles 15122 and 67769) with the real routes. It is worth noting that when modeled turtles following a vector strategy arrived close to the Brazilian coast at latitudes between 6° and 12°S, their routes always displayed a final northward curved segment (Fig. 2a, 2c, 2e, 2f, 2h), deriving from the action of strong currents just before reaching the coast.

To quantitatively compare the outcome of the different strategies, we first considered the arrival dates in target areas. As expected, true navigation strategies produced simulations that mostly reached the target, but they often did so some days earlier or later than the real turtle (Fig. 3).

Among the alternative vector strategies, V.LF produced the best results while V.280 simulations did not reach the target area in 10 cases out of 11.

These results were partly mirrored when considering Route Diversity (RD) values. The routes deriving from V.LF strategy turned out to have a small median RDs, comparable to those of the true navigation strategy heading to landfall (true.LF) (Fig. 4). Conversely, the values of the true navigation strategy heading towards the turtle's foraging ground (true.FG) generated much worse results. The linear mixed model revealed significant differences among the strategies, with all three vector (V.270°, V.275° and V.280°), and the true.FG strategies being significantly different from the V.LF one (Fig. 4; Table S1). Conversely, true.LF simulations were not significantly different from those with the V.LF vector strategy.

Phase 3: modeling pre-nesting migrations from Brazil to Ascension Island

The outcomes of the pre-nesting simulations were quite different from those of phase 1, and their success was highly dependent on the heading considered. Simulated routes with heading 95° or 100° (Fig. S5) resulted in a very low success rate in all the starting dates considered; simulations with 90° heading were slightly better, but with different outcomes depending on the starting location, with a percentage of success that rarely reached 50%. A strong effect of currents was generally noticed, especially for the northernmost starting points, likely deriving from the time of the year and areas considered in these simulations. These simulations often entered a strong current field north of 5°S, and were then either drifted North or even prevented from reaching the longitude of the island. For instance, modeled turtles leaving from 5°S in January, often ended up in the dynamic current field north of the Brazilian bulge, and their single-heading routes sometimes displayed curved or circuitous segments (Fig. S6). On the other hand, the simulations starting from lower latitudes were subjected to lesser current drift, which was however sufficient in most cases to cause them to miss the target, likely because of its small size.

The simulations with more Northerly headings were more successful (Fig. 5). For simulations with 80° heading, the percentage of success was highly dependent on the starting point. Only when starting from latitudes 9.1° and 9.5°, the modeled turtles reached the area around Ascension Island in >40% of cases with peaks of >70% success for several combinations of starting points and dates (Fig. 5a). The best outcomes were those of simulations with an 85° heading (Fig. 5b, 6) for which a larger range of starting points and dates produced routes reaching the final goal, even if the mean percentage of success was below 55% for all latitudes.

Discussion

Vector navigation has been proposed as a feasible navigational strategy for several long-distance migrants (Stoddard et al. 1983; Berthold 1991; Mouritsen 1998; Mouritsen et al. 2013, Gschweng et al. 2008; McLaren et al. 2014; Yoda et al. 2017). This hypothesis has been mostly put forward for the movements of juvenile or inexperienced individuals in terrestrial environments but has never been considered for the many cases of migrations taking place in the ocean. The present findings contribute to fill this gap showing that vector navigation is a viable strategy also to account for long-distance migrations taking place in the open sea and directed to a specific site. Our phase 1 results showed that Ascension turtles can reach Brazil within the expected time frame (40 d) by relying on a simple vector mechanism. The models of phase 2 further confirmed this pattern for the specific cases of the 11 migrating turtles considered. The outcome of phase 1 simulations may not be surprising, given that modeled turtles aimed at a wide target constituted by a large stretch of the Brazilian coast (Fig. S1). However, the effects of current drift during a prolonged oceanic migration has never been previously evaluated in detail and may indeed be substantial during travels of several weeks, inducing large off-route deflections and leading turtles to miss even a wide target. Indeed, our simulations have revealed how reliance on vector navigation leads to successful migrations only within a limited range of westward headings (270°-280°), while otherwise the turtles drift away from the target or are delayed in reaching it. This shows that current drift may have a significant effect on the ability to reach even a large target. Finally, it is interesting to note that the success rate of reaching Brazil was not dependent on the starting date: this may be advantageous for turtles leaving Ascension as they would not need to change their heading depending on their departure date.

This conclusion was supported by phase 2 simulations, as the real turtle routes were best simulated by a vector navigation with a heading corresponding to the beeline to the landfall site (V.LF strategy). This heading was therefore different in the various turtles (Table 1). The other headings we tested in phase 2 simulations, that were identical in different turtles, produced modeled tracks less similar to the actual routes, even if these headings were the best ones identified in phase 1. The best vector navigation heading may, thus differ in different individuals, which is a reasonable possibility. Since we do not know exactly how the heading to be followed is chosen in different individuals, we cannot exclude that some turtles may head in a direction different from the safest ones (i.e. towards West in our case), which would then lead to apparently inefficient routes, for instance encompassing open sea legs longer than needed or pointing away from the final destination. In birds and butterflies, vector navigation is proposed to involve following endogenous, genetically determined headings (Berthold 1991; Mouritsen et al. 2013), but it is unclear whether this may happen in turtles as well, given the complexity of their life cycles (Musick and Limpus 1997; Hays et al., 2010; Scott et al. 2014). The turtles we tracked, though, had performed the migration a number of times, and may then have developed a preferred migratory route to follow, likely resulting in a further increase in variations in migratory headings, as well as in landfall sites (see also below), depending on previous individual experiences. In birds, inter-individual variability in routes are often proposed to result from the first migrations, e.g. among raptors (Sergio et al. 2014) or seabirds (Guilford et al. 2011).

It is noteworthy that another strategy representing the turtle routes well was true navigation towards landfall (true.LF), which once again seems to stress an importance of the landfall site, that may indeed be meaningful for migrating turtles. Turtles may, after breeding, return to the same site from where they departed several months previously. However, most tracked turtles did not stop at that site once reaching the coast, but continued moving along the coastline up to hundreds of km, to reach their final destination, with only one turtle (ID 15122; Fig. 2f) having her foraging site in the same area where she made landfall. It seems therefore doubtful that tracked turtles aimed at reaching that specific landfall site at the end of the open-ocean migration. A similar tendency to avoid stopping at the first location along a coast after an open-sea crossing, has been shown for other turtles during postnesting migrations (e.g. Cheng 2000; Hays et al. 2002; 2014, Snape et al. 2016).

The second kind of true-navigation strategy we simulated was certainly more meaningful since it assumed that turtles would head towards their specific foraging grounds, to which they have been shown to demonstrate site fidelity (Limpus et al. 1992; Read et al. 2014, Shimada et al. 2014, Broderick et al. 2007; Shimada et al. 2016). The actual degree of individual fidelity to foraging grounds in green turtles is not fully assessed: the available information derives from repeated recoveries of tagged turtles (Meylan 1982; Limpus et al. 1992; Read et al. 2014) and from tracking of repeated migrations of the same individual (Broderick et al. 2007; Shimada et al. 2016) and, as such, only shows fidelity over a limited time span (a few years maximum). The individual turtles' routes were generally poorly represented by true.FG simulations, as could be expected by considering that most turtles did not head towards their final destination, but made landfall quite far from it (see above). Such a biphasal migratory strategy has been shown for other green turtle populations (e.g. Cheng 2000; Broderick et al. 2007; Hays et al. 2013; 2014).

Overall, the degree of similarity between simulated and real routes in phase 2 simulations was often quite low (Fig. 2), in line however with similar studies comparing actual vs. simulated routes (Hays et al. 2013, Mc Laren et al. 2014, 2016). A number of factors may have contributed to these discrepancies. For instance, we ran the simplest model possible and so we made no effort to include any variation in the turtle swimming speed during the trip nor any steering inaccuracy, also given the lack of information on the accuracy of turtle compasses (Lohmann et al. 2008b). More importantly, modeled currents may not have been accurately estimated, given the limits in the spatial and temporal resolution of the present ocean circulation models (e.g. Putman et al. 2016; Cardona and Hays 2018), so that the currents used for our models may have thus differed from those actually experienced by the tracked turtles. Such inaccuracies in modeled currents will have affected our other simulations at a much lesser extent, since in those cases we aimed at modeling the effects on turtle migrations of the average currents occurring in a given period/area, and reliable information is provided by circulation models in this respect (Fossette et al. 2012). A weak correspondence between modeled and real routes could have also been obtained if real turtles would have been able to detect the currents flow they were moving in, thus compensating for the induced drift (Chapman et al. 2011). We consider this possibility quite unlikely, since most studies on the subject have shown that turtles are unable to perceive current drift during open ocean navigation (discussed in Galli et al. 2012; see also Kobayashi et al. 2014; Putman et al. 2015), and the evidence in other marine animals is very limited (Horton et al. 2011).

The simulations of the pre-reproductive migrations were not as successful as those of phase 1, even when a target larger than the actual size of the island was considered on the basis of the outcomes of previous experiments (see Methods above). Evidently, the impact of current drift during long oceanic migrations makes it too difficult to reach a remote target in the ocean only relying on a vector navigation strategy. The main reason leading to the low success rate of modeled routes can be attributed to a combination of the small size of the target and of the presence of currents flowing west or southwestward and thus against the general movement direction. Unfortunately, no turtles have been tracked migrating to Ascension Island, and therefore there are no data to compare with the simulated trajectories. Based on the outcomes of the simulation, however, it is difficult to imagine that turtles may find Ascension only by keeping a single heading with no means to compensate or correct for drift. In these conditions, hypothesizing a reliance on some kind of true navigation seems inescapable, although the precision of such navigation may not necessarily be high, since regional and local cues may be used for the final approach (e.g. Åkesson et al. 2003). At present, no turtle migrating to an isolated oceanic breeding site has ever been tracked, but useful hints can be deduced from the relatively few cases in which turtles have been tracked while migrating to foraging grounds located offshore or at oceanic islands (Papi et al. 1995; Hawkes et al. 2012; Hays et al. 2014; Parker et al. 2015; Balazs et al. 2017). While in some cases tracked turtles pinpointed their target with fair accuracy, sometimes they followed non-directed or looping courses, apparently revealing difficulties in locating the target, in line with the findings of displacement experiments with turtles nesting on oceanic islands (Luschi et al. 2001; 2007; Hays et al. 2003; Girard et al. 2006; Benhamou et al. 2011).

In conclusion, the present results allow us to depict an overall picture of the navigational strategies employed by Ascension turtles during their oceanic migrations (Åkesson et al. 2003). For the post-breeding migration, reliance on a vector navigation strategy is sufficient to reach the wide target constituted by the Brazilian coast, with turtles first aiming at reaching a site along the coast that may not necessarily be the final goal represented by the individual foraging site. The migratory direction chosen for this leg, which may differ between individuals, is not always the one leading to the final destination nor are the turtles determining the shortest and quickest route to reach the continental coast. The poor performances of simulations directed towards the individual foraging sites indicate that Ascension turtles do not need to rely on true navigation towards the final target during the postnesting migrations, although our results cannot exclude the turtle reliance on a strategy of true navigation towards the landfall site during the postnesting migration. This strategy will not necessarily lead to more a efficient or direct migratory routes than when following a vectorial navigation, as it is known that a partial drift compensation, that involves keeping an heading away from the goal direction and thus a non-continuous redirection to a goal, constitutes the most advantageous strategy in some conditions (e.g. predictable flows, see Chapman et al. 2011 for an extensive discussion). However, partial compensation has never been shown to be employed by marine navigators (e.g. Girard et al. 2006; Hays et al. 2013; see also Chapman et al. 2011). By contrast, the outcomes of phase 3 simulations clearly show how such a simple vector strategy is not sufficient to guide the pre-breeding migrations aimed at finding the small remote island. In this most challenging situation, turtles will likely have to switch to other, more powerful mechanisms such as long-range maps (Wallraff 1991; Lohmann et al. 2008a) to arrive at least in the vicinity of the remote island, where regional and local cues may then be needed to pinpoint their final target (Hays et al. 2003; Åkesson et al. 2003).

Under such scenario, the navigation system of Ascension turtles would therefore represent a further example of a coexistence of different navigational mechanisms in the same animal, that are used in different migrations or segments of the migratory journey to accomplish different orientation tasks (Bingman and Cheng 2005; Lohmann et al. 2008b). Our conclusions have far-reaching implications for our understanding of animal navigation in the ocean, as they highlight how even following the simple strategy of keeping a constant course for a given amount of time may allow an ocean-dwelling migrant to safely reach its destination, at least when there is an initial wide target to reach. Reliance on a vectorial navigation strategy should therefore be taken into account when considering other cases of long distance migrations and fidelity to specific locations that have been shown in a variety of marine animals (Block et al. 2011; Luschi 2013).

References

Able KP. 2001. The concepts and terminology of bird navigation. J. Avian Biol. 32:174-183.

Åkesson S, Broderick AC, Glen F, Godley BJ, Luschi P, Papi F, Hays GC. 2003. Navigation by green turtles: which strategy do displaced adults use to find Ascension Island? Oikos 103:363-372.

Åkesson S and Bianco G. 2015. Assessing vector navigation in long-distance migrating birds. Behav. Ecol. 27:865-875.

Åkesson S and Bianco G. 2017. Route simulations, compass mechanisms and long-distance migration flights in birds. J. Comp. Physiol. A 203:475-490.

Alerstam T, Hedenström A, Åkesson S. 2003. Long-distance migration: evolution and determinants. Oikos 103:247-260.

Balazs GH, Parker DM, Rice MR. 2017. Ocean pathways and residential foraging locations for satellite tracked green turtles breeding at French Frigate Shoals in the Hawaiian Islands1. Micronesica 4:1-19.

Baltazar-Soares M, Biastoch A, Harrod C, Hanel R, Marohn L, Prigge E, Evans D, Bodles K, Behrens E, Böning CW, Eizaguirre C. 2014. Recruitment Collapse and Population Structure of the European Eel Shaped by Local Ocean Current Dynamics. Curr. Biol. 24 :104-108.

Bates D, Maechler M, Bolker B, Walker S. 2015. Fitting Linear Mixed-Effects Models Using lme4. J. Stat. Softw. 67:1-48.

Benhamou S, Sudre J, Bourjea J, Ciccione S, De Santis A, Luschi P. 2011. The Role of Geomagnetic Cues in Green Turtle Open Sea Navigation. PLoS ONE 6:e26672.

Berthold P. 1991. Spatiotemporal programmes and genetics of orientation. In: Berthold P. Orientation in Birds. Basel, Boston, Berlin: Birkhäuser. p. 86-105.

Bingman VP and Cheng K. 2005. Mechanisms of animal global navigation: comparative perspectives and enduring challenges. Ethol. Ecol. Evol. 17:295-318.

Block BA, Teo SLH, Walli A, Boustany A, Stokesbury MJW, Farwell CJ, Weng KC, Dewar H, Williams TD. 2005. Electronic tagging and population structure of Atlantic blue fin tuna. Nature 434:1121–1127.

Block BA, Jonsen ID, Jorgensen SJ, Winship AJ, Shaffer SA, Bograd SJ, Hazen EL, Foley DG, Breed GA, Harrison A-L, Ganong JE, Swithenbank A, Castleton M, Dewar H, Mate BR, Shillinger GL, Schaefer KM, Benson SR, Weise MJ, Henry RW, Costa DP. 2011. Tracking apex marine predator movements in a dynamic ocean. Nature 475:86–90.

Bonadonna F, Lea MA, Dehorter O, Guinet C. 2001. Foraging ground fidelity and route-choice tactics of a marine predator: the Antarctic fur seal *Arctocephalus gazella*. Mar. Ecol. Prog. Ser. 223:287–297.

Bonadonna F, Benhamou S, Jouventin P. 2003. Orientation in “featureless” environments: the extreme case of pelagic birds. In: Berthold P, Gwinner E and Sonnenschein E. Avian Migration. Springer, Berlin, Germany. p. 367–377.

Bracis C and Mueller T, 2017. Memory, not just perception, plays an important role in terrestrial mammalian migration. Proc. R. Soc. B 284:20170449.

Briscoe DK, Parker DM, Balazs GH, Kurita M, Saito T, Okamoto H, Rice M, Polovina JJ, Crowder LB. 2016. Active dispersal in loggerhead sea turtles (*Caretta caretta*) during the 'lost years". Proc. R. Soc. B 283:20160690.

Broderick AC, Coyne MS, Fuller WJ, Glen F, Godley BJ. 2007. Fidelity and over-wintering of sea turtles. Proc. R. Soc. B 274:1533–1539.

Brown CW. 1990. The Significance of the South Atlantic Equatorial Countercurrent to the Ecology of the Green Turtle Breeding Population of Ascension Island. J. Herpetol. 24:81.

Cardona L, Hays GC. 2018. Ocean currents, individual movements and genetic structuring of populations. Mar. Biol. 165:10.

Carr A. 1975. The Ascension Island green turtle colony. Copeia 1975:547-555.

Casale P, Mariani P. 2014. The first 'lost year' of Mediterranean sea turtles: dispersal patterns indicate subregional management units for conservation. Mar. Ecol. Prog. Ser. 498:263-274.

Chapman JW, Klaassen RHG, Drake VA, Fossette S, Hays GC, Metcalfe JD, Reynolds AM, Reynolds DR, Alerstam T. 2011. Animal orientation strategies for movement in flows. Curr. Biol. 21:R861-R870.

Cheng I-J. 2000. Post-nesting migrations of green turtles (*Chelonia mydas*) at Wan-an Island, Penghu Archipelago, Taiwan. Mar. Biol. 137:747-754.

Croxall JP, Silk JRD, Phillips RA, Afanasyev V, Briggs DR. 2005. Global circumnavigations: tracking year-round ranges of nonbreeding albatrosses. Science 307:249–250.

David C, Vaz S, Loots C, Antajan E, van der Molen J, Travers-Trolet M. 2015. Understanding winter distribution and transport pathways of the invasive ctenophore *Mnemiopsis leidyi* in the North Sea: coupling habitat and dispersal modelling approaches. Biol. Invasions 17:2605-2619.

Durban JW and Pitman RL. 2012. Antarctic killer whales make rapid, round-trip movements to subtropical waters: evidence for physiological maintenance migrations?. Biol. Lett. 8:274–277.

Endres CS, Putman NF, Ernst DA, Kurth JA, Lohmann CMF, Lohmann KJ. 2016. Multi-Modal Homing in Sea Turtles: Modeling Dual Use of Geomagnetic and Chemical Cues in Island-Finding. Front. Behav. Neurosci. 10:19.

Fossette S, Putman NF, Lohmann KJ, Marsh R, Hays GC. 2012. A biologist's guide to assessing ocean currents: a review. Mar. Ecol. Prog. Ser. 457:285-301.

Fossette S, Gleiss AC, Chalumeau J, Bastian T, Armstrong CD, Vandenabeele S, Karpytchev M, Hays GC. 2015. Current-oriented swimming by jellyfish and its role in bloom maintenance. Cur. Biol. 25:342-347.

Freake MJ, Muheim R, Phillips JB. 2006. Magnetic Maps in Animals: A Theory Comes of Age. Q. Rev. Biol. 81: 327-347.

Galli S, Gaspar P, Fossette S, Calmettes B, Hays GC, Lutjeharms JRE, Luschi P. 2012. Orientation of migrating leatherback turtles in relation to ocean currents. Anim. Behav. 84:1491-1500.

Gaspar P, George JC, Fossette S, Lenoble A, Ferraroli S, Le Maho Y. 2006. Marine animal behaviour: neglecting ocean currents can lead us up the wrong track. Proc. R. Soc. B 273:2697-2702.

Girard C, Sudre J, Benhamou S, Roos D, Luschi P. 2006. Homing in green turtles Chelonia mydas: oceanic currents act as a constraint rather than as an information source. Mar. Ecol. Prog. Ser. 322:281-289.

González-Carman V, Bruno I, Maxwell S, Álvarez K, Albareda D, Acha EM, Campagna C. 2016. Habitat use, site fidelity and conservation opportunities for juvenile loggerhead sea turtles in the Río de la Plata, Argentina. Mar. Biol. 163:20.

Godley BJ, Broderick AC, Hays GC. 2001. Nesting of green turtles (*Chelonia mydas*) at Ascension Island, South Atlantic. Biol. Conserv. 97:151-158.

Godley BJ, Broderick AC, Frauenstein R, Glen F, Hays GC, 2002. Reproductive seasonality and sexual dimorphism in green turtles. Mar. Ecol. Prog. Ser. 226:125-133.

Godley BJ, Blumenthal JM, Broderick AC, Coyne M, Godfrey MH, Hawkes LA, Witt MJ. 2008. Satellite tracking of sea turtles: Where have we been and where do we go next? Endanger. Species Res. 4:3-22.

Gschweng M, Kalko EKV, Querner U, Fiedler W, Berthold P. 2008. All across Africa: highly individual migration routes of Eleonora's falcon. Proc. R. Soc. B 275:2887-2896.

Guilford T, Åkesson S, Gagliardo A, Holland RA, Mouritsen H, Muheim R, Wiltschko R, Wiltschko W, Bingman VP. 2011. Migratory navigation in birds: new opportunities in an era of fast-developing tracking technology. J. Exp. Biol. 214:3705-3712.

Hawkes L., Tomás J, Revuelta O, León Y, Blumenthal J, Broderick A, Fish M, Raga J, Witt M, Godley BJ. 2012. Migratory patterns in hawksbill turtles described by satellite tracking. Mar. Ecol. Prog. Ser. 461:223-232.

Hays GC, Åkesson S, Broderick AC, Glen F, Godley BJ, Luschi P, Martin C, Metcalfe JD, Papi F. 2001. The diving behaviour of green turtles undertaking oceanic migration to and from Ascension Island: dive durations, dive profiles and depth distribution. J. Exp. Biol. 204:4093-4098.

Hays GC, Broderick AC, Godley BJ, Lovell P, Martin C, McConnell BJ, Richardson S. 2002. Biphasal long-distance migration in green turtles. Anim. Behav. 64:895-898.

Hays GC, Åkesson S, Broderick AC, Glen F, Godley BJ, Papi F, Luschi P. 2003. Island-finding ability of marine turtles. Proc. R. Soc. B 270:S5-S7.

Hays GC, Fossette S, Katselidis KA, Mariani P, Schofield G. 2010. Ontogenetic development of migration: Lagrangian drift trajectories suggest a new paradigm for sea turtles. J. R. Soc. Interface 7:1319-1327.

Hays GC, Christensen A, Fossette S, Schofield G, Talbot J, Mariani P. 2013. Route optimisation and solving Zermelo's navigation problem during long distance migration in cross flows. Ecol. Lett. 17:137-143.

Hays GC, Mortimer JA, Ierodiaconou D, Esteban N. 2014. Use of long-distance migration patterns of an endangered species to inform conservation planning for the world's largest marine protected area. Conserv. Biol. 6:1636-1644.

Horton TW, Holdaway RN, Zerbini AN, Hauser N, Garrigue C, Andriolo A, Clapham PJ. 2011. Straight as an arrow: humpback whales swim constant course tracks during long-distance migration. Biol. Lett. 7:674–679.

Horton TW, Hauser N, Zerbini AN, Francis MP, Domeier ML, Andriolo A, Costa DP, Robinson PW, Duffy Clinton AJ, Nasby-Lucas N, Holdaway RN, Clapham PJ. 2017. Route fidelity during marine megafauna migration. Front. Mar. Sci. 4:422.Hussey NE, Kessel ST, Aarestrup K, Cooke SJ, Cowley PD, Fisk AT, Harcourt RG, Holland KN, Iverson SJ, Kocik JF. 2015. Aquatic animal telemetry: a panoramic window into the underwater world. Science 348:1255642.

Jorgensen SJ, Reeb CA, Chapple TK, Anderson S, Perle C, Van Sommeran SR, Fritz-Cope C, Brown AC, Klimley AP, Block BA. 2009. Philopatry and migration of Pacific white sharks. Proc. R. Soc. B 277:679–688.

Jouventin P, Capdeville D, Cuenotchaillet F, Boiteau C. Exploitation of pelagic resources by a non-flying seabird—satellite tracking of the king penguin throughout the breeding cycle. 1994. Mar. Ecol. Prog. Ser. 106:11–20.

Kays R, Crofoot MC, Jetz W, Wikelski M, 2015. Terrestrial animal tracking as an eye on life and planet. Science 348:aaa2478.

Kobayashi DR, Farman R, Polovina JJ, Parker DM, Rice M, Balazs GH. 2014 “Going with the flow” or not: evidence of positive rheotaxis in oceanic juvenile loggerhead turtles (*Caretta caretta*) in the South Pacific Ocean Using Satellite Tags and Ocean Circulation Data. PLoS One, 9(8), e103701.

Kramer G. 1961. Long-distance orientation. In: Marshall AJ. Biology and Comparative Physiology in Birds. New York: Academic Press. p. 341-371.

Le Boeuf BJ, Crocker DE, Costa DP, Blackwell SB, Webb PM, Houser DS. 2000. Foraging ecology of northern elephant seals. Ecol. Monogr. 70:353–382.

Limpus CJ, Jeffery DM, Parmenter CJ, Reimer D, McLachlan N, Webb R. 1992. Migration of Green (*Chelonia mydas*) and Loggerhead (*Caretta caretta*) Turtles to and from Eastern Australian Rookeries. Wildl. Res. 19:347-358.

Lohmann KJ, Lohmann CMF, Ehrhart LM, Bagley DA, Swing T. 2004. Geomagnetic map used in sea-turtle navigation. Nature 428:909-910.

Lohmann KJ, Lohmann CMF, Endres CS. 2008a. The sensory ecology of ocean navigation. J. Exp. Biol. 211:1719-1728.

Lohmann KJ, Luschi P, Hays GC. 2008b. Goal navigation and island-finding in sea turtles. J. Exp. Mar. Biol. Ecol. 356:83-95.

Luschi P, Hays GC, Del Seppia C, Marsh R, Papi F. 1998. The navigational feats of green sea turtles migrating from Ascension Island investigated by satellite telemetry. Proc. R. Soc. B. 265:2279-2284.

Luschi P, Åkesson S, Broderick AC, Glen F, Godley BJ, Papi F, Hays GC. 2001. Testing the navigational abilities of ocean migrants: displacement experiments on green sea turtles (*Chelonia mydas*). Behav. Ecol. Sociobiol. 50:528-534.

Luschi P, Hays GC, Papi F. 2003. A review of long-distance movements by marine turtles, and the possible role of ocean currents. Oikos 103:293-302.

Luschi P, Benhamou S, Girard C, Ciccione S, Roos D, Sudre J, Benvenuti S. 2007. Marine turtles use geomagnetic cues during open-sea homing. Curr. Biol. 17:126-133.

Luschi P. 2013. Long-Distance Animal Migrations in the Oceanic Environment: Orientation and Navigation Correlates. ISRN Zool. 2013:1–23.

McLaren JD, Shamoun-Baranes J, Dokter AM, Klaassen RHG, Bouten W. 2014. Optimal orientation in flows: providing a benchmark for animal movement strategies. J. R. Soc. Interface 11:20140588-20140588.

McLaren JD, Shamoun-Baranes J, Camphuysen CJ, Bouten W. 2016. Directed flight and optimal airspeeds: homeward-bound gulls react flexibly to wind yet fly slower than predicted. J. Avian Biol. 47:476-490.

Mouritsen H. 1998. Modelling migration: the clock-and-compass model can explain the distribution of ringing recoveries. Anim. Behav. 56:899-907.

Mouritsen H, Derbyshire R, Stalleicken J, Mouritsen OØ, Frost BJ, Norris DR. 2013. An experimental displacement and over 50 years of tag-recoveries show that monarch butterflies are not true navigators. Proc. Natl. Acad. Sci. U.S.A. 110:7348-7353.

Musick J.A. and Limpus C. 1997. Habitat utilization and migration in juvenile sea turtles. In: Lutz PL and Musick JA. The biology of sea turtles. Boca Raton, New York, London, Tokyo: CRC Press, Inc. p.137-164.

Painter, K. J., and Hillen, T. 2015. Navigating the flow: individual and continuum models for homing in flowing environments. J. R. Soc. Interface, 12, 20150647.

Papi F, Liew HC, Luschi P, Chan EH. 1995. Long-range migratory travel of a green turtle tracked by satellite: evidence for navigational ability in the open sea. Mar. Biol. 122:171-175.

Papi F, Luschi P, Åkesson S, Capogrossi S, Hays GC. 2000. Open-sea migration of magnetically disturbed sea turtles. J. Exp. Biol. 203:3435-3443.

Parker DM, Balazs GH, Frutchey K, Kabua E, Langridrik M, Boktok K. 2015. Conservation considerations revealed by the movements of post-nesting green turtles from the Republic of the Marshall Islands, Micronesica 3:1-9.

Proietti MC, Lara-Ruiz P, Reisser JW, Pinto L da S, Dellagostin OA, Marins LF. 2009. Green turtles (*Chelonia mydas*) foraging at Arvoredo Island in Southern Brazil: Genetic characterization and mixed stock analysis through mtDNA control region haplotypes. Genet. Mol. Biol. 32:613-618.

Putman NF, Scott R, Verley P, Marsh R, Hays GC. 2012. Natal site and offshore swimming influence fitness and long-distance ocean transport in young sea turtles. Mar. Biol. 159:2117-2126.

Putman NF and Mansfield KL. 2015. Direct evidence of swimming demonstrates active dispersal in the sea turtle "Lost Years". Cur. Biol. 25:1221-1227.

Putman NF, Lumpkin R, Sacco AE, Mansfield KL. 2016. Passive drift or active swimming in marine organisms? Proc. R. Soc. B. 283:20161689.

R Development Core Team (2017). R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. ISBN 3-900051-07-0, URL http://www.R-project.org.

Read TC, Wantiez L, Werry JM, Farman R, Petro G, Limpus CJ. 2014. Migrations of Green Turtles (*Chelonia mydas*) between Nesting and Foraging Grounds across the Coral Sea. PLoS ONE 9, e100083.

Sale A and Luschi P. 2009. Navigational challenges in the oceanic migrations of leatherback sea turtles. Proc. R. Soc. B. 276:3737-3745.

Scott R, Marsh R, Hays GC. 2014. Ontogeny of long distance migration. Ecology 95:2840–2850.

Scott R, Biastoch A, Agamboue PD, Bayer T, Boussamba FL, Formia A, Godley BJ, Mabert BDK, Manfoumbi JC, Schwarzkopf FU, Sounguet G-P, Wagner P, Witt MJ. 2017. Spatio-temporal variation in ocean current-driven hatchling dispersion: Implications for the world’s largest leatherback sea turtle nesting region. Divers. Distrib. 23:604-614.

Shimada T, Aoki S, Kameda K, Hazel J, Reich K, Kamezaki N. 2014. Site fidelity, ontogenetic shift and diet composition of green turtles *Chelonia mydas* in Japan inferred from stable isotope analysis. Endanger. Species Res. 25:151-164.

Shimada T, Limpus C, Jones R, Hazel J, Groom R, Hamann M. 2016. Sea turtles return home after intentional displacement from coastal foraging areas. Mar. Biol. 163:8.

Southwood A and Avens L. 2010. Physiological, behavioral, and ecological aspects of migration in reptiles. J. Comp. Physiol. B 180:1-23.

Snape RTE, Broderick AC, Çiçek BA, Fuller WJ, Glen F, Stokes K, Godley B.J. 2016. Shelf life: neritic habitat use of a turtle population highly threatened by fisheries. Divers. Distrib. 22:797-807.

Stoddard PK, Marsden JE, Williams TC. 1983. Computer simulation of autumnal bird migration over the western North Atlantic. Anim. Behav. 31:173-180.

Yoda K, Yamamoto T, Suzuki H, Matsumoto S, Müller M, Yamamoto M. 2017. Compass orientation drives naïve pelagic seabirds to cross mountain ranges. Curr. Biol. 27:R1152-R1153.

Young CM, He R, Emlet RB, Li Y, Qian H, Arellano SM, Van Gaest A, Bennett KC, Wolf M, Smart TI. 2012. Dispersal of deep-sea larvae from the intra-American seas: simulations of trajectories using ocean models. Integr. Comp. Biol. 52:483-496.

Witt MJ, Åkesson S, Broderick AC, Coyne MS, Ellick J, Formia A, Hays GC, Luschi P, Stroud S, Godley BJ. 2010. Assessing accuracy and utility of satellite-tracking data using Argos-linked Fastloc-GPS. Anim. Behav. 80:571-581.

Wallraff HG.1991. Conceptual Approaches to Avian Navigation System. In: Berthold P. Orientation in Birds. Basel, Boston, Berlin: Birkhäuser. p. 128-165.

Table 1. Summary data of tracked turtles. The asterisks show the turtles for which the foraging ground was identified.

Turtle ID	Year of tracking	Starting date of migration	Duration of migration (days)	Mean active speed (km·h^{-1})	Beeline heading (°)
6611	1997	12 May	36	2.5	270
6614	1997	22 June	40	2.4	273
4394*	1998	02 June	40	2.3	262
4395	1998	29 June	31	2.9	270
15119*	2001	13 June	33	2.5	268
15122*	2001	12 June	45	2.5	270
21914*	2001	10 July	37	2.3	279
25476	2002	24 April	37	2.7	266
94593	2009	06 July	41	2.8	254
67769*	2009	05 May	32	2.8	270
67770*	2009	06 May	36	2.6	268

Figure legends

Fig.1 Heat map for postnesting simulations. Colours of different cells represent the percentage of routes successfully reaching the Brazilian target area for each starting date in the 13 years considered (actual values are shown in each cell).

Fig.2 Simulated trajectories with different strategies and actual routes of the 11 tracked turtles (black dashed line). The target area around each turtle's landfall (LF) is represented by the red area. In the 6 cases where the location of the foraging ground (FG) of the tracked turtle was assessed, the foraging ground target area (green area) is also shown. Various vector navigation strategies were modelled, each with a different heading: V.LF = heading corresponding to the beeline angle between the starting point and landfall; V.270° = heading 270°; V.275° = heading 275°; V.280° = heading 280°. Two true navigation strategy were modelled: true.LF = navigation towards the turtle's landfall location; true.FG = navigation towards the turtle's foraging ground location.

Fig.3 Arrival dates for the different navigational strategies in relation to the arrival date of the real turtle. The white cells represent the cases where foraging ground location is unknown.

Fig.4 Route diversity values for each simulated navigational strategy. Higher values indicate lower similarity between real and modelled routes. Asterisks indicate significance level of the comparison between each strategy and V.LF one (***: $P<0.001$; *: $P<0.05$; ns: $P>0.05$). Red dots show mean values.

Fig.5 Heat maps for simulations of pre-breeding migrations with an heading of a) 80° and b) 85°. Other explanations as in Fig.1.

Fig.6 Examples of modelled pre-breeding simulations with heading 85° starting on the same day (1 January 2005) from different locations (top panel) and from the same location (7.5°S) in different dates (lower panel).

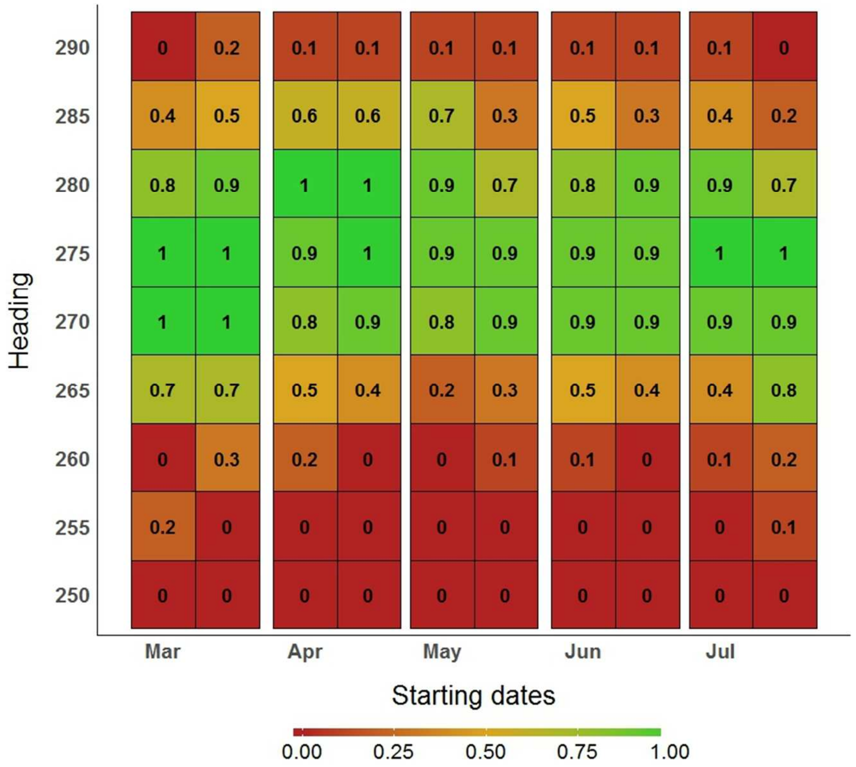

Fig.1 Heat map for postnesting simulations. Colours of different cells represent the percentage of routes successfully reaching the Brazilian target area for each starting date in the 13 years considered (actual values are shown in each cell).

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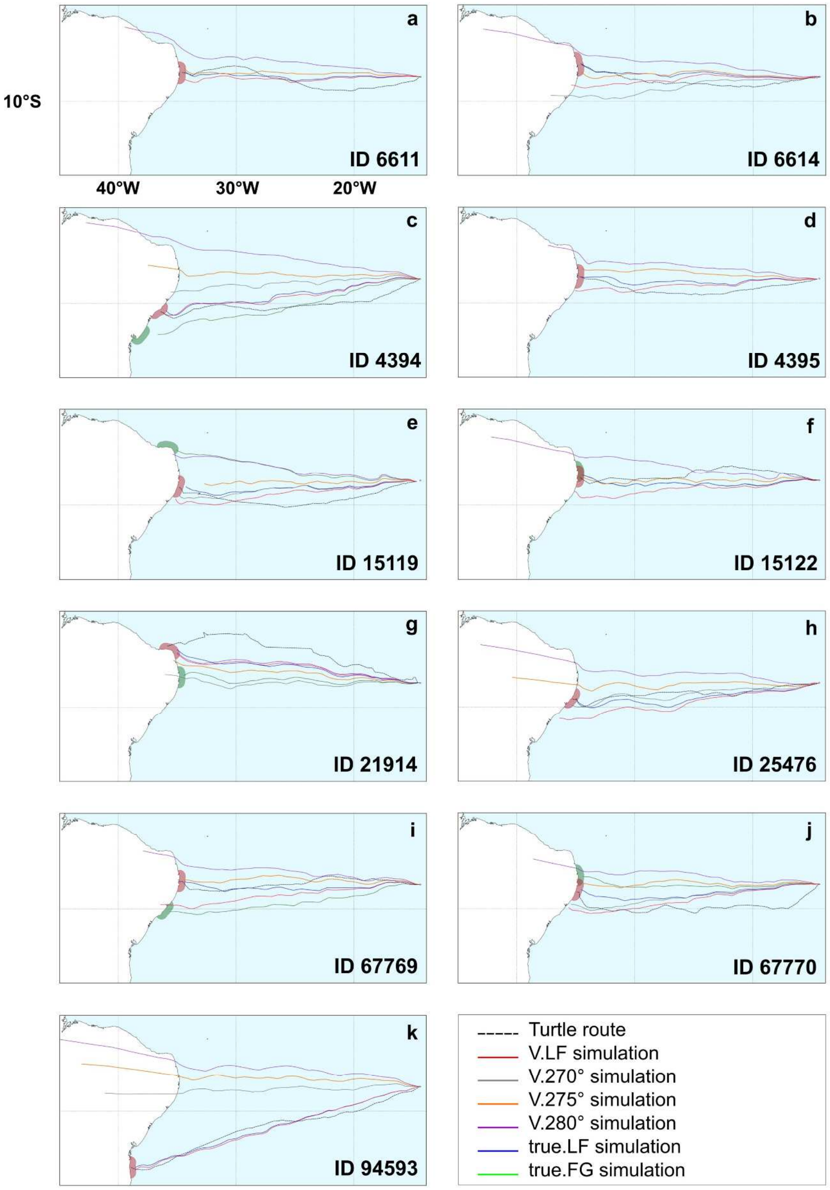

Fig.2 Simulated trajectories with different strategies and actual routes of the 11 tracked turtles (black dashed line). The target area around each turtle's landfall (LF) is represented by the red area. In the 6 cases where the location of the foraging ground (FG) of the tracked turtle was assessed, the foraging ground target area (green area) is also shown. Various vector navigation strategies were modelled, each with a different heading: V.LF = heading corresponding to the beeline angle between the starting point and landfall; V.270° = heading 270°; V.275° = heading 275°; V.280° = heading 280°. Two true navigation strategy were modelled: true.LF = navigation towards the turtle's landfall location; true.FG = navigation towards the turtle's foraging ground location.

201x286mm (300 x 300 DPI)

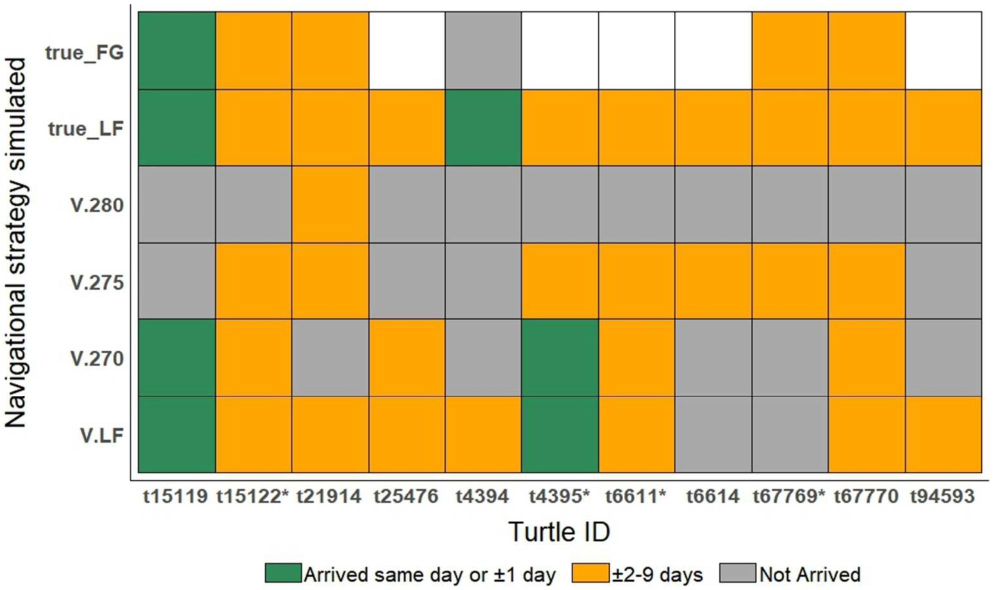

Fig.3 Arrival dates for the different navigational strategies in relation to the arrival date of the real turtle. The white cells represent the cases where foraging ground location is unknown.

270x210mm (96 x 96 DPI)

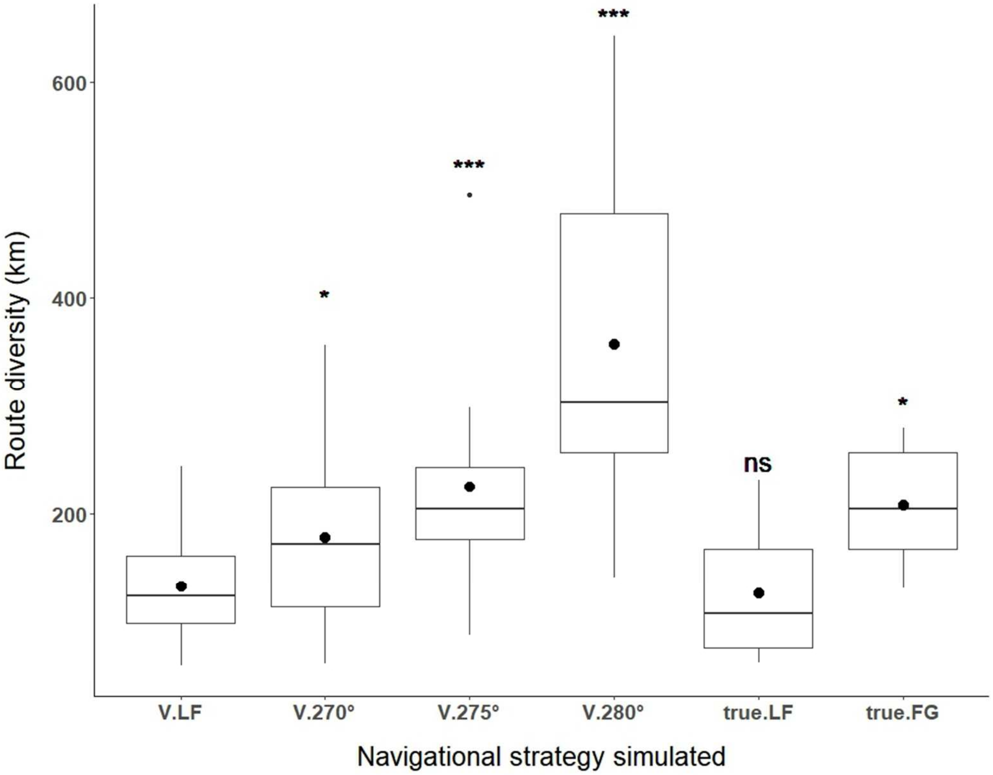

Fig.4 Route diversity values for each simulated navigational strategy. Higher values indicate lower similarity between real and modelled routes. Asterisks indicate significance level of the comparison between each strategy and V.LF one (***: P<0.001; *: P<0.05; ns: P>0.05). Red dots show mean values.

270x210mm (96 x 96 DPI)

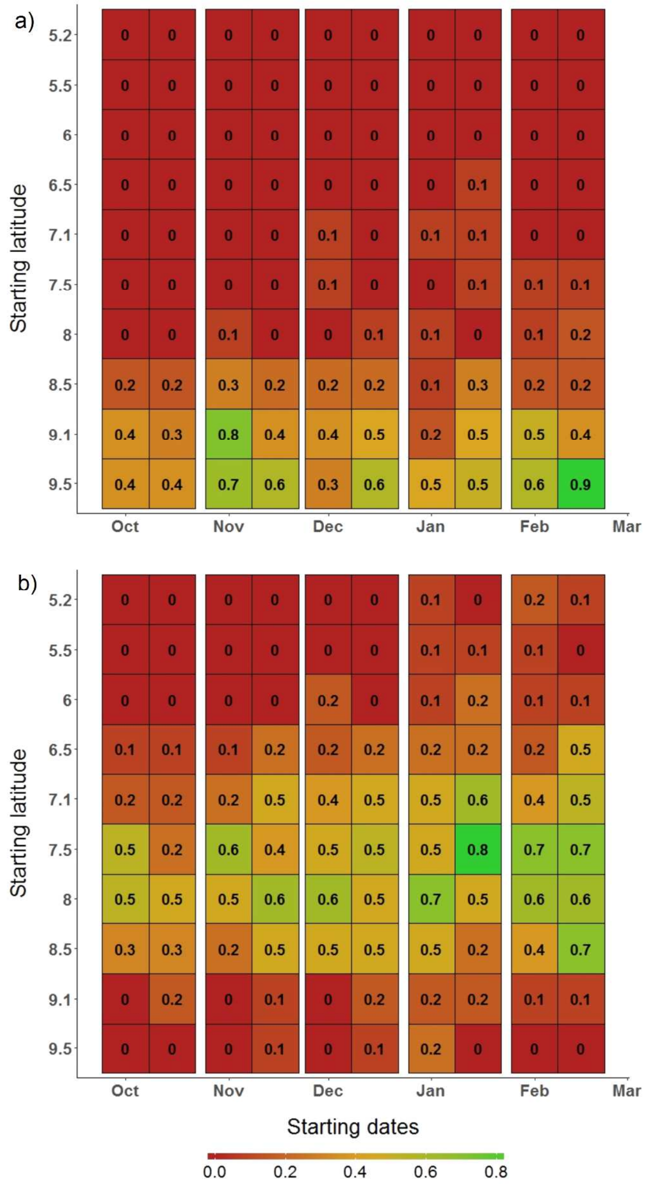

Fig.5 Heat maps for simulations of pre-breeding migrations with an heading of a) 80° and b) 85°. Other explanations as in Fig.1.

163x293mm (300 x 300 DPI)

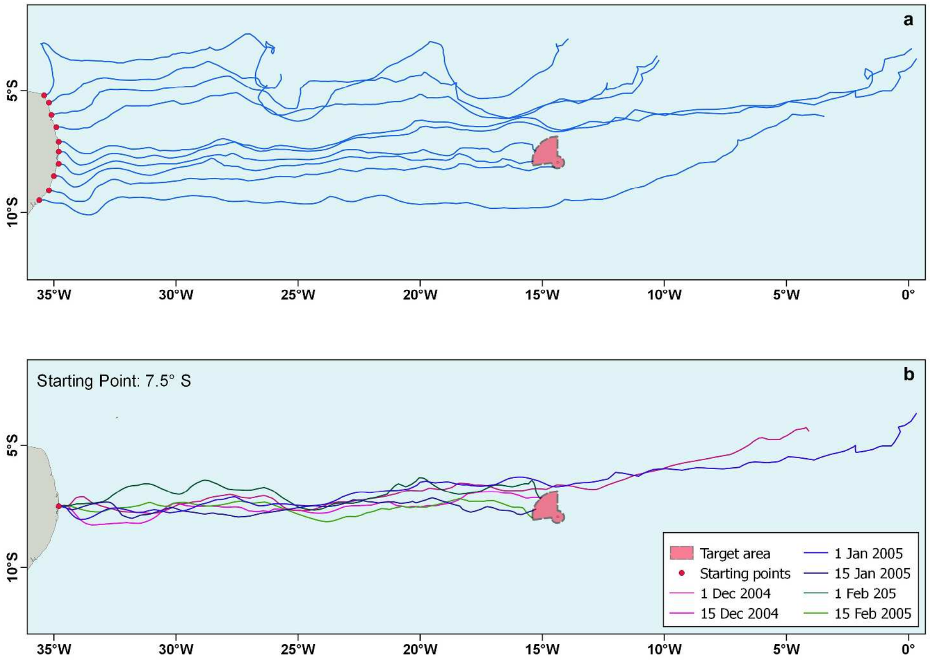

Fig.6 Examples of modelled pre-breeding simulations with heading 85° starting on the same day (1 January 2005) from different locations (top panel) and from the same location (7.5°S) in different dates (lower panel).

297x210mm (299 x 299 DPI)