

species they observe, and there may be a bias to report primarily those species that show change. Even if there were such a bias, however, it would have no influence on our claim of a discernible impact of warming on plants and animals, because our metric of investigation is what fraction of those species that exhibit change has changed in the direction expected with local temperature trends, not what fraction of all species has exhibited change. The only way that observer bias could influence our metric would be if there were a systematic bias among the scores of studies we examine for researchers to select as study subjects only species showing changes in the direction preconceived by the authors to reflect temperature change. In addition, these many authors would have to have deliberately and systematically suppressed reporting on those species that changed in directions opposite to that expected. We find this possibility of widespread and systematic biases far-fetched, and thus believe that the metric we use is adequate for examining in an unbiased manner the existence of a discernible climatic signal in the traits of many plants and animals.

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## True navigation and magnetic maps in spiny lobsters

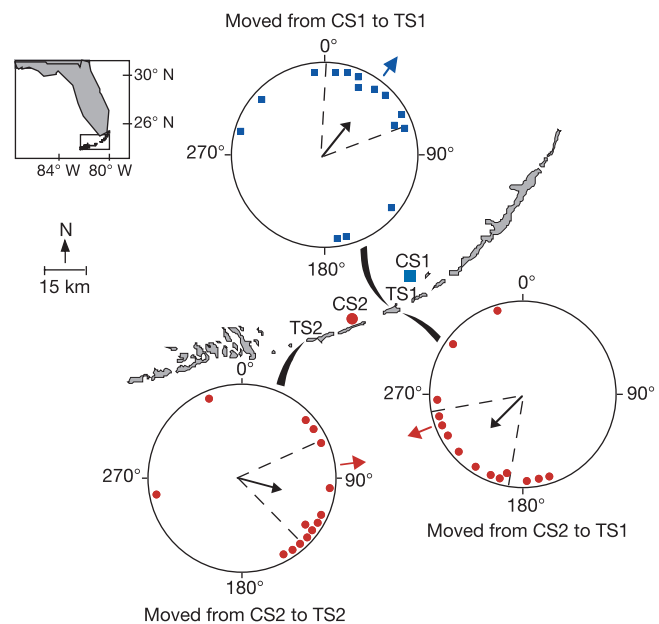
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Animals are capable of true navigation if, after displacement to a location where they have never been, they can determine their position relative to a goal without relying on familiar surroundings, cues that emanate from the destination, or information collected during the outward journey<sup>1,2</sup>. So far, only a few animals, all vertebrates, have been shown to possess true navigation<sup>3</sup>. Those few invertebrates that have been carefully studied

return to target areas using path integration, landmark recognition, compass orientation and other mechanisms that cannot compensate for displacements into unfamiliar territory<sup>4,5</sup>. Here we report, however, that the spiny lobster *Panulirus argus* oriented reliably towards a capture site when displaced 12–37 km to unfamiliar locations, even when deprived of all known orientation cues *en route*. Little is known about how lobsters and other animals determine position during true navigation. To test the hypothesis that lobsters derive positional information from the Earth's magnetic field, lobsters were exposed to fields replicating those that exist at specific locations in their environment. Lobsters tested in a field north of the capture site oriented themselves southwards, whereas those tested in a field south of the capture site oriented themselves northwards. These results imply that true navigation in spiny lobsters, and perhaps in other animals, is based on a magnetic map sense.

In the context of homing behaviour, an animal capable of true navigation must possess both a positional sense to determine its location and a directional or compass sense to orient in the appropriate homeward direction<sup>6,7</sup>. Many animals, both vertebrate and invertebrate, possess diverse compasses based on the Earth's magnetic field, the position of the Sun, patterns of skylight polarization and the positions of stars<sup>4,8</sup>. In contrast, few animals are known to possess the ability to determine position relative to a goal after being displaced to unfamiliar areas under conditions in which



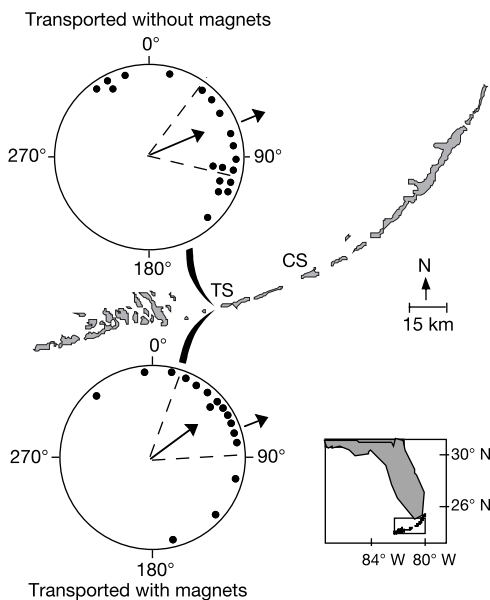
**Figure 1** Orientation of displaced lobsters. Lobsters were transported by boat from two capture sites (CS1, CS2) via circuitous routes (see the text) to one of two test sites (TS1, TS2). In the orientation diagrams, each small symbol represents the mean angle of a single lobster. Blue squares indicate lobsters captured at CS1, whereas red circles indicate lobsters captured at CS2. The arrow in the centre of each orientation diagram indicates the mean angle of each group; the arrow length is proportional to the mean vector  $r$ , with the radius of the circle corresponding to  $r = 1$ . Lobsters transported from CS1 to TS1 were significantly oriented ( $r = 0.51$ ,  $Z = 3.92$ ,  $P < 0.02$ , Rayleigh test) with a mean angle of  $38^\circ$ . Lobsters transported from CS2 to TS1 were significantly oriented ( $r = 0.65$ ,  $Z = 5.96$ ,  $P < 0.01$ ) with a mean angle of  $222^\circ$ . Lobsters displaced from CS2 to TS2 were also significantly oriented ( $r = 0.51$ ,  $Z = 3.89$ ,  $P < 0.02$ ) with a mean angle of  $105^\circ$ . In all orientation diagrams, the dashed lines represent the 95% confidence interval for the mean angle. Data are plotted relative to magnetic north. The blue or red arrow outside each orientation diagram indicates the direction from the test site to the capture site. In each case, the mean angle of orientation coincided closely with the direction towards the capture site (see the text) and the 95% confidence interval encompassed this 'homeward' direction.

they cannot monitor the outward journey to the test site. Until now, evidence for true navigation has been limited to birds and a few other specialized migrants, all of them vertebrates<sup>3</sup>.

Little is known about the sensory cue or cues that underlie true navigation. The navigational system of homing pigeons has been studied for decades, yet the nature of their position-finding system remains the subject of a long-standing and unresolved debate<sup>9,10</sup>. In principle, animals might derive positional information from one or more elements of the Earth's magnetic field<sup>2,11</sup>. However, little direct evidence exists that true navigation is based on magnetic cues, and whether magnetic maps exist at all has remained controversial<sup>12,13</sup>.

The Caribbean spiny lobster, *Panulirus argus*, is a migratory crustacean that is capable of homing<sup>14</sup>. Juvenile and adult lobsters spend daylight hours hidden inside coral reef crevices or holes, emerging at night to forage over a considerable area before returning in darkness to the same den or to one of several others nearby<sup>15</sup>. Tag-recapture studies have indicated that lobsters can return to a home area after being displaced to unfamiliar locations<sup>16</sup>. These considerations led us to investigate whether spiny lobsters are capable of true navigation.

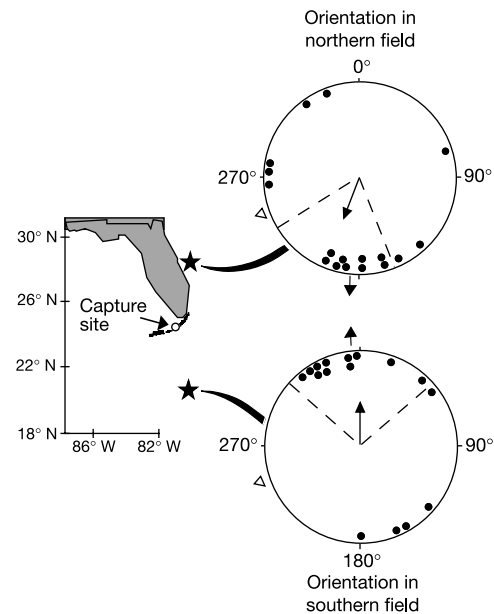
In an initial series of experiments, juvenile lobsters in Florida Bay, USA, were captured by divers and placed into opaque plastic containers partly filled with sea water. The containers were covered so that animals inside were deprived of visual cues. Lobsters were then transported by boat for 45–60 min along circuitous routes of up to 30 km, ending at one of two testing sites (Fig. 1). On the following morning, the eyestalks of the lobsters were covered with rubber caps to deprive them of visual cues during testing<sup>17</sup>, and each animal was tethered to a tracking system in the centre of a circular water-filled arena. The tracking system monitored the direction that each lobster walked.



**Figure 2** Orientation of lobsters transported overland by lorry in distorted magnetic fields. All lobsters in this experiment were collected from a single capture site (CS) near Long Key and transported to the test site (TS) at Pigeon Key. One group of lobsters (upper diagram) was subjected only to the magnetic field distortions produced by the metal body of the lorry. This group was significantly oriented ( $r = 0.62$ ,  $Z = 7.31$ ,  $P < 0.001$ , Rayleigh test) with a mean angle of  $68^\circ$ . The second group (lower diagram) was subjected to stronger, additional field distortions caused by stationary and moving magnets (see the text). This group was significantly oriented ( $r = 0.67$ ,  $Z = 7.31$ ,  $P < 0.001$ , Rayleigh test) with a mean angle of  $53^\circ$ . The arrows outside each orientation diagram indicate the direction from the test site to the capture site. Statistical conventions are as in Fig. 1. The two distributions were not significantly different ( $U^2 = 0.143$ , Watson test<sup>29</sup>); instead, both groups of lobsters oriented themselves approximately towards the capture site ( $71^\circ$ ).

Lobsters captured at a location (CS1 on Fig. 1) 12 km to the north/northeast of the first test site (TS1 on Fig. 1) were significantly oriented with a mean angle of  $38^\circ$ . This direction corresponded closely to the most direct route ( $36^\circ$ ) back to the area of capture (Fig. 1). Lobsters captured at a site (CS2 on Fig. 1) 14 km west-southwest of the first testing site also were significantly oriented but with a mean angle of  $222^\circ$ ; this direction also corresponded closely to the most direct path back ( $250^\circ$ ). An additional group of lobsters captured at this same location was transported to a second testing site 18 km away (TS2 on Fig. 1), where the most direct heading to the capture area was  $82^\circ$ . These lobsters were also significantly oriented with a mean angle of  $105^\circ$ . Thus, in each case, lobsters with their eyes covered walked in directions that would have led them back towards the area where they were captured.

The definition of true navigation requires that animals derive positional information from local cues available at the test site rather than by exploiting information gathered during the outward journey<sup>2,3</sup>. In our initial experiments, lobsters oriented towards the capture site despite being transported in sealed containers under conditions in which no useful visual and chemical cues were available *en route*. In addition, inertial cues were presumably obscured by the movement of the boat and constant sloshing of water within the container. However, magnetic cues were not disrupted and might have been perceptible during transport. An additional experiment was therefore conducted to determine whether lobsters could still orient towards the capture site even if all known sensory cues, including magnetic cues, were disrupted during displacement.



**Figure 3** Orientation of lobsters tested in magnetic fields replicating those that exist at two different geographic locations (marked by stars on the map). Lobsters were captured at Grassy Key (CS2 on Fig. 1), transported as before to the testing site (TS1 on Fig. 1), and held overnight in non-magnetic tanks in the local magnetic field. Lobsters tested in a field characteristic of a location north of the test site were significantly oriented ( $r = 0.51$ ,  $Z = 4.21$ ,  $P < 0.02$ , Rayleigh test) with a mean angle of  $199^\circ$  (upper diagram). Lobsters tested in a field characteristic of a location south of the test site were significantly oriented ( $r = 0.43$ ,  $Z = 3.0$ ,  $P < 0.05$ , Rayleigh test) but in approximately the opposite direction (a mean angle of  $1^\circ$ ; lower diagram). Other statistical conventions are as in Fig. 1. The arrow outside each orientation diagram indicates the direction in which lobsters would be expected to orient themselves if homing from the fictive locations. The open triangle outside each orientation diagram indicates the actual direction to the capture site from the test site. In each case, lobsters responded as if they had been displaced to the locations marked by the stars rather than by orienting in the direction that was actually towards the capture site.

Lobsters were captured near shore (location CS on Fig. 2), placed in a covered, opaque container and transported overland by lorry to the testing site. In half of the trips the container was lined with an array of magnets, some of which hung from strings and swung erratically, producing fields strong enough to continuously change the alignment of a compass placed anywhere in the container. In the other half of the trips, lobsters were transported in the same container but without magnets. In all trips, the container was suspended by ropes in the cargo section of a lorry so that it swung erratically as the vehicle moved. To disrupt inertial cues further, the lorry was manoeuvred through a series of erratic turns and circles before being driven to the test site 37 km away. All lobsters were then removed from the container and housed overnight in a holding tank in the natural local magnetic field.

In the morning the eyes of the lobsters were covered with rubber caps<sup>17</sup> and their orientation was tested as before. No differences in orientation were found between lobsters that had been transported with magnets and those that had not. Instead, both groups oriented significantly towards the direction of the capture site (Fig. 2). We therefore infer that lobsters deprived of all known orientation cues during transport are nevertheless capable of determining the direction to the capture site when released at unfamiliar locations, and that this homeward direction is apparently determined on the basis of information gathered at the test site. We conclude that lobsters fulfil the criteria of true navigation, as well as the definition of map-based navigation in the new terminology proposed by Able<sup>7</sup>.

How animals capable of true navigation determine their position relative to a goal after displacement into unfamiliar territory is not known. However, recent studies have shown that a few animals can detect elements of the Earth's magnetic field that might, in principle, provide positional information<sup>18,19</sup>.

Spiny lobsters possess magnetic material that might function in magnetoreception<sup>20</sup> and are also known to have a magnetic compass sense<sup>17</sup>, but whether they can derive positional information from the Earth's field has not previously been studied. To investigate whether true navigation in lobsters is based on magnetic positional information, lobsters were tested in magnetic fields replicating those that exist at different geographic locations.

Lobsters were collected (location CS2 on Fig. 1) and transported by boat to the first test site (TS1 on Fig. 1) as described for the initial displacement experiments. They were then randomly assigned to two groups: one was tested in a magnetic field that exists at a location ~400 km north of the test site; the other was tested in a field replicating one found at a location ~400 km to the south. Simulated displacements were of greater distance than the actual displacements (Figs 1 and 2) because it is difficult to reproduce consistently the small field differences experienced by lobsters in the initial experiments. However, these simulated displacements are within the range of distances that spiny lobsters are known to move<sup>21,22</sup>.

Lobsters exposed to the field of the northern site walked south-southwest (Fig. 3). Those exposed to the field of the southern site walked approximately north (Fig. 3). The two distributions are significantly different ( $U^2 = 0.269$ ,  $P < 0.01$ , Watson test), indicating that lobsters can distinguish between magnetic fields that mark different geographic locations within their environment. Moreover, they responded to each field by orienting in a direction that would have led them towards the capture site had they actually been at the location where each field naturally occurs. These results provide strong evidence that spiny lobsters have a magnetic map sense that is used in navigation.

The precise magnetic feature or features that lobsters detect, and the exact way in which the map is organized, cannot be determined from these initial experiments. The responses to magnetically simulated displacements (Fig. 3) might be explained by proposing that lobsters determine whether they are north or south of a goal by perceiving a single magnetic element (such as inclination or

intensity) that varies in the north–south direction. Such a ‘univariate map’<sup>18</sup>, however, cannot easily account for the ability to orient towards the capture site from locations that are not along the north–south axis (Figs 1 and 2). Among several alternative possibilities, it might be that lobsters rely on bicoordinate navigation by detecting two different magnetic field elements that vary in different directions across the region<sup>2</sup>, that an unknown non-magnetic cue provides the second coordinate, or that lobsters learn the local magnetic topography and exploit features of the magnetic relief as magnetic ‘landmarks’<sup>11</sup>. Thus, in concluding that lobsters possess a magnetic map, we use the phrase in its most general sense<sup>9,23</sup>, intending it only as a convenient shorthand to indicate that displaced lobsters can somehow derive sufficient positional information from the Earth's magnetic field to determine the direction towards home. Precisely how they do so remains to be determined.

To use magnetic map navigation over relatively short distances, an animal must overcome several potential problems<sup>2,10,11</sup>. One requirement is an acute sensitivity to small differences in magnetic fields. A second is an ability to filter out or otherwise compensate for the regular daily variations in the Earth's field, which are caused in part by ionospheric currents<sup>11,24</sup>. A third is that the magnetic topography in the area must provide a pattern of variation that can be exploited in position-finding.

The degree of magnetic sensitivity in lobsters is not known. However, theoretical considerations suggest that biological receptors can indeed achieve the sensitivity required to use magnetic maps over distances as small as ~10 km (ref. 24). Lobsters are likely to encounter minimal problems with temporal variation in the Earth's field because they normally leave their dens only at night, when the field is most stable<sup>11</sup>. Analysis of the fine-scale magnetic topography of the study area is not yet possible because detailed magnetic surveys have apparently not been done in this location. However, if magnetic anomalies exist, they do not necessarily impede magnetic navigation because local gradient contours are often aligned in such a way that useful positional information can be extracted from them<sup>2,11</sup>. Maps of the regional magnetic isolines<sup>11,24</sup> indicate that, on a larger scale, several magnetic elements vary regularly and predictably across the Florida region and might therefore provide reliable positional information to lobsters or other animals able to detect them.

Regardless of these considerations, our results demonstrate for the first time that an invertebrate animal is capable of true navigation. Moreover, lobsters exposed to magnetic fields replicating those that exist at different geographic locations responded as if homing from each fictive site. These results provide the most direct evidence yet that animals possess and use magnetic maps. Similar mechanisms might function not only in lobsters, but in various animals that migrate or home, including certain fishes<sup>25</sup>, amphibians<sup>18</sup>, reptiles<sup>26</sup> and birds<sup>27</sup>. □

## Methods

### Animals and study area

Juvenile lobsters (carapace length 47–82 mm) were captured by divers in Florida Bay, USA, a shallow area north and west of the Florida Keys (see map inset and larger map, Fig. 1). Capture site 1 (CS1) was located at Peterson Key (latitude 24.92° N, longitude 80.75° W). Capture site 2 (CS2) was located at Grassy Key (latitude 24.79° N, longitude 80.96° W). Test site 1 (TS1) was located at Long Key (latitude 24.83° N, longitude 80.82° W) and test site 2 (TS2) was located at Pigeon Key (latitude 24.70° N, longitude 81.15° W).

### Experimental protocol

The procedure for tethering lobsters has been described previously<sup>17</sup>. Each lobster was temporarily blinded with rubber eyecaps, attached by monofilament line to a tracking system modified from one used previously<sup>28</sup>, and placed into the orientation arena facing in a randomized direction. After a 5-min acclimation period, the data acquisition computer recorded the orientation of the lobster once every 30 s for 30 min. The data were used to calculate a mean angle of orientation for each lobster by using standard procedures for circular statistics<sup>29</sup>. Those few lobsters that remained motionless for 5 min or longer after being placed into the arena were replaced with other, more active individuals. All trials were conducted during the morning hours after sunrise.

**Magnetically simulated displacements**

In the experiments described in Fig. 3, the orientation arena was surrounded by a magnetic coil system that was used to control the field in which each lobster walked. The coil system consisted of two different independent four-coil systems arranged orthogonally<sup>28</sup>. Each coil measured 2.3 m on a side. Lobsters were restricted by a tether to an area in the centre of the coil defined by a horizontal circle of radius 25 cm. In this region, calculated<sup>30</sup> and measured deviations from perfect field uniformity were less than 0.5%. Each lobster was then tethered as before and tested in one of two magnetic fields. One field replicated magnetic conditions that exist at a location approximately 400 km to the north, whereas the other replicated a field at a location approximately 400 km to the south. The field used to approximate magnetic conditions at the location north of the test site had an inclination of 59.3° and a total intensity of 47.9 μT. The field simulating the location south of the test site had an inclination of 51.4° and total intensity of 42.8 μT. All magnetic field values were verified by three independent measurements with an Applied Physics Fluxgate Magnetometer (model 520A). The experimental fields were based on estimates provided by the International Geomagnetic Reference Field (IGRF) model, 2000 revision, for August 2001 (when the data were collected) using latitude 28.5° N, longitude 80.5° W for the northern site, and latitude 20.5° N, longitude 80.5° W for the southern site. Experiments were conducted in Long Key, Florida (latitude 24.8° N, longitude 80.8° W) where the measured inclination angle was 55.8° and the total field intensity was 45.3 μT.

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**Role of duplicate genes in genetic robustness against null mutations**

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Deleting a gene in an organism often has little phenotypic effect<sup>1–5</sup>, owing to two mechanisms of compensation<sup>4–10</sup>. The first is the existence of duplicate genes: that is, the loss of function in one copy can be compensated by the other copy or copies. The second mechanism of compensation stems from alternative metabolic pathways, regulatory networks, and so on. The relative importance of the two mechanisms has not been investigated except for a limited study, which suggested that the role of duplicate genes in compensation is negligible<sup>10</sup>. The availability of fitness data for a nearly complete set of single-gene-deletion mutants of the *Saccharomyces cerevisiae* genome<sup>11</sup> has enabled us to carry out a genome-wide evaluation of the role of duplicate genes in genetic robustness against null mutations. Here we show that there is a significantly higher probability of functional compensation for a duplicate gene than for a singleton, a high correlation between the frequency of compensation and the sequence similarity of two duplicates, and a higher probability of a severe fitness effect when the duplicate copy that is more highly expressed is deleted. We estimate that in *S. cerevisiae* at least a quarter of those gene deletions that have no phenotype are compensated by duplicate genes.

No correlation was found between the sequence similarity of duplicate genes and the fitness effect of a null mutation in one of the two duplicates when functional data from the yeast *S. cerevisiae* was analysed previously<sup>10</sup>. It was therefore concluded that gene duplications contribute little to the ability of an organism to withstand mutations (genetic robustness), although they may be responsible for a small fraction of weak, null-mutation phenotypes<sup>12</sup>. Because this conclusion was based on only 45 duplicate genes, however, the issue deserves further investigation. Indeed, this conclusion is not supported by a limited analysis of a third of the genes in the yeast genome<sup>1</sup> and is contrary to the general observation of relaxed selective constraints after gene duplication<sup>13,14</sup>.

From 5,766 yeast open reading frames (ORFs) for which we had a fitness measure of strains with a corresponding single-gene deletion<sup>11</sup>, we found 1,509 duplicate (paralogous) genes. To avoid including pseudogenes and erroneously predicted genes, we subsequently analysed only genes that had been studied previously (that is, each had a gene name in the *Saccharomyces* Genome Database (SGD) in addition to its ORF name). This yielded 1,275 singleton genes, and 1,147 duplicate genes that had at least one paralogue elsewhere in the genome. We compared the frequency distribution of fitness for duplicate genes with that for singletons (Fig. 1a). We classified genes into four groups on the basis of the minimum fitness value for a strain across the five different growth conditions tested (Methods) including both fermentation and respiration, the main growth conditions of yeast.

The two distributions were significantly different ( $P \ll 0.001$ ): duplicate genes had a significantly lower proportion of genes with a lethal effect of deletion (12.4% versus 29.0%) and a significantly higher proportion of genes with a weak or no effect of gene deletion