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Size-dependent avoidance of a strong magnetic anomaly in Caribbean spiny lobsters

Key words: magnet, magnetoreception, lobster, orientation, *Panulirus argus*

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Summary statement: Lobsters avoid artificial dens below strong magnets, suggesting that magnetic anomalies might affect lobster orientation and movement.

Abstract:

On a global scale, the geomagnetic field varies predictably across Earth's surface, providing animals that migrate long distances with a reliable source of directional and positional information that can be used to guide their movements. In some locations, however, magnetic minerals in Earth's crust generate an additional field that enhances or diminishes the overall field, resulting in unusually steep gradients of field intensity within a limited area. How animals respond to such magnetic anomalies is unclear. The Caribbean spiny lobster, *Panulirus argus*, is a benthic marine invertebrate that possesses a magnetic sense and is likely to encounter magnetic anomalies during migratory movements and homing. As a first step toward investigating whether such anomalies affect the behavior of lobsters, a two-choice preference experiment was conducted in which lobsters were allowed to select one of two artificial dens, one beneath a neodymium magnet and the other beneath a non-magnetic weight of similar size and mass (control). Significantly more lobsters selected the control den, demonstrating avoidance of the magnetic anomaly. In addition, lobster size was found to be a significant predictor of den choice; lobsters that selected the anomaly den were significantly smaller as a group than those that chose the control den. Taken together, these findings provide additional evidence for magnetoreception in spiny lobsters, raise the possibility of an ontogenetic shift in how lobsters respond to magnetic fields, and suggest that magnetic anomalies might influence lobster movement in the natural environment.

Introduction:

Animals rely on numerous sources of information for guidance while migrating, homing, and moving around their habitats. Among these, Earth's magnetic field is a particularly pervasive environmental feature, one that exists virtually everywhere on the planet. It is thus not surprising that diverse organisms, ranging from bacteria to vertebrate animals, have evolved ways to exploit the geomagnetic field to guide their movements (Wiltschko and Wiltschko, 1995; Johnsen and Lohmann, 2005).

Most studies on magnetoreception have focused on animals that derive directional or compass information from Earth's field. A magnetic compass sense enables animals to maintain a consistent bearing, such as north or south. In addition, some animals can derive positional or 'map' information by detecting magnetic parameters such as intensity and inclination angle (the angle at which field lines intersect Earth's surface), both of which vary predictably across the globe (Lohmann and Lohmann, 1994; 1996; Phillips et al., 2002; Lohmann et al., 2007).

For long-distance marine migrants such as sea turtles, salmon, and eels, the variation in Earth's magnetic field across the surface of the planet is sufficiently predictable that different oceanic regions and coastal locations can be identified by animals on the basis of distinctive magnetic signatures (Lohmann et al., 2001; 2012; Putman et al., 2013; Brothers and Lohmann, 2015; Naisbett-Jones et al., 2017). Nevertheless, local irregularities in the global pattern of geomagnetic variation exist. For example, in some locations, iron-containing rocks in the earth's crust result in steep intensity gradients relative to the overarching regional magnetic field (Parkinson, 1983; Skiles, 1985; Lanza and Meloni, 2006). These gradients can be significantly stronger than the geomagnetic field; moreover, the direction of these local field gradients often differs from the overall pattern of Earth's main dipole field (Lohmann et al., 2007).

Relatively little is known about how such magnetic anomalies affect animals. One possibility is that such anomalies interfere with the normal functioning of magnetic compasses or maps and thus lead to disruptions in orientation and navigation. Consistent with this hypothesis, homing pigeons and migratory birds released at magnetic anomalies show signs of impaired orientation under some conditions (Walcott, 1978, 1992; Wiltschko et al., 2009, 2010; Schiffner et al., 2011). Alternatively or additionally, such anomalies might be exploited by animals as landmarks (Walker et al., 2002) or otherwise incorporated into navigational strategies. Several methods of navigation that rely at least partly on detecting naturally occurring magnetic intensity anomalies have been proposed for hammerhead sharks (Klimley, 1993), pigeons (Walker, 1998; Dennis et al., 2007), and whales (Klinowska, 1985; Kirschvink et al., 1986).

The Caribbean spiny lobster, *Panulirus argus* (Latreille 1804), is a benthic marine invertebrate that undertakes mass migrations (Kanciruk and Herrnkind, 1978; Herrnkind, 1980), is capable of homing (Creaser and Travis, 1950), and is known to exploit Earth's magnetic field for navigation (Lohmann et al., 1995; Boles and Lohmann, 2003; Ernst and Lohmann, 2016). Although numerous invertebrates extract directional information from the geomagnetic field, the spiny lobster is the only invertebrate known to also possess a magnetic map sense (Lohmann and Ernst, 2014). Because of their mobile lifestyle and regular migrations, spiny lobsters are likely to encounter magnetic anomalies in their environment, some resulting from natural geological formations and others from anthropogenic sources (e.g., submerged iron boat wreckage, oil platforms, and underwater cables).

As a first step toward determining if lobster behavior is influenced by magnetic anomalies, we conducted a simple laboratory experiment in which lobsters were allowed to choose between sheltering in artificial dens that were either: (1) below sealed capsules containing neodymium magnets; or (2) below identical capsules containing non-magnetic weights. Results indicated that lobsters spontaneously avoided strong magnetic anomalies and that avoidance behavior varied with size, inasmuch as lobsters that selected dens without magnets were significantly larger than those that occupied the magnet dens.

Materials and Methods:

Animal collection and holding tanks

All experiments were conducted in Layton, Florida, U.S.A., at the Keys Marine Laboratory (24.83°N, 80.81°W) in July and August 2014. Lobsters with carapace lengths ranging from 42 to 88 mm were captured in Florida Bay within 350 m of the lab by swimmers using hand-held nets. Each animal was visually inspected for symptoms of *Panulirus argus* Virus 1 (PaV1), a viral infection that is prevalent in the Florida Keys and is known to affect lobster behavior. Animals that exhibited obvious signs of infection were not used in experiments.

After capture, lobsters were transported to the lab where they were housed in rectangular, outdoor fiberglass holding tanks (122×67×39 cm) filled with flow-through sea water from Florida Bay. The ambient magnetic field within both holding tanks was measured with a triaxial fluxgate magnetometer (model 520A, Applied Physics Systems, Sunnyvale, CA, USA). The field had an inclination angle of 55.5^0 and an intensity of 43.7 µT. Each tank was shaded from the sun and contained a cement block that the lobsters used as a refuge. All lobsters were tested within 48 hours of capture. The collection of lobsters was authorized by the Florida Fish and Wildlife Conservation Commission (permit SAL-11-1333D-SR).

Experimental arena

Lobsters were tested within a circular fiberglass tank (164 cm in diameter) filled with seawater to a depth of 23 cm. Measurements with the fluxgate magnetometer indicated that the ambient magnetic field in the arena had an inclination angle of 55.5^0 and an intensity of 43.7 µT, the same as in the holding tanks. Within the arena, concrete blocks (19×19×39.5 cm) were positioned to restrict lobsters to a rectangular channel (39.5×109.25 cm) oriented along the east-west axis within the center of the tank (Fig. 1). An additional concrete block was positioned at each end of the channel and against the wall of the tank, with the block openings (12×12 cm) oriented toward the center of the tank. This provided two artificial 'dens' at each end of the channel. A PVC capsule (2.54 cm diameter × 7 cm length) containing either a cylindrical neodymium magnet (1.27 cm diameter × 2.54 cm length; grade=N50; surface field = 703.1 mT; Applied Magnets; Plano, Texas, USA) or a non-magnetic weight of similar size (control) was then centered on top of each concrete block so that the capsules were flush with the edge of the block faces (Fig. 1). The capsules were sealed to prevent olfactory cues from the magnet or weight from entering the water.

Preference test

Lobsters were chosen at random and carefully placed in the center of the arena facing toward north and away from the person releasing the lobster. Thus, each lobster began its trial aligned perpendicular to the long axis of the arena and den openings. Lobsters were left alone in the arena for 15 minutes, after which time an observer returned to note the den that the lobster occupied.

After each trial, the water in the arena was thoroughly mixed so that residual odorants from lobsters tested previously were evenly dispersed throughout the tank. The water in the tank was completely changed at least once per day. In addition, the locations of the magnet and weight capsules were alternated between trials, and the north and south pole of the magnet were randomly oriented toward or away from the center of the channel (see Fig. 2 for magnet field intensity vs. distance).

Each lobster was tested a single time. Prior to release, individuals were measured and sexed, and a semicircular notch was removed from one of the uropods. The notch permitted identification of lobsters that had been tested previously so that none were recaptured and tested multiple times.

All statistical analyses were conducted using R (Version 3.3.3, R Development Core Team, 2017). Only lobsters that were within a den at the end of the 15-min trial (49 of 51) were included in the analysis. To investigate the relationship between size and den preference, we built a logistic regression model with carapace length as a predictor of den choice.

Results:

Of the 49 lobsters that occupied a den by the end of the 15-min trial period, 33 (67%) occupied the control den and 16 (33%) occupied the magnet den (Fig. 3). Thus, lobsters showed a significant preference for the control den ($p=0.021$, exact binomial test). No relationship existed between sex and den preference ($\chi^2=0.085$, $df=1$, $p=0.77$, χ^2 test). In addition, male and female carapace length was not significantly different ($U=227$, $p=0.2$, Mann-Whitney U test).

Lobsters that chose the magnet den were significantly smaller than those that chose the control den (Fig. 4; U=142.5, p=0.0095, Mann-Whitney U test). Smaller lobsters had no apparent preference for either type of den, but as carapace length increased, the proportion of lobsters that chose the control den increased (Fig. 5). Moreover, a logistic regression model showed that carapace length is a significant predictor of den choice (Fig. 6; Table 1; p=0.019).

Discussion:

In a two-choice preference test, significantly more lobsters selected the control den than selected the den associated with the neodymium magnet (Fig. 3). The overall aversion to dens with magnets was driven primarily by the behavior of the larger lobsters, which showed a strong preference for control dens (Fig. 4; Fig. 5; Table 1); by contrast, smaller lobsters as a group lacked a preference for den type. Although previous studies have revealed that spiny lobsters detect and respond to Earth-strength magnetic fields, these findings are the first to demonstrate that they also detect and respond to a localized magnetic anomaly produced by a magnet.

What field component(s) do lobsters detect?

The results demonstrate that lobsters detect and avoid the magnetic fields produced by magnets, but they do not reveal the precise element(s) of the magnetic field that lobsters detect. The magnetic field that naturally exists at any location on Earth can be described in terms of total field intensity and inclination angle (Lohmann et al., 1999). The same is true for the field produced by a magnet, with the caveat that the magnet's field, unlike the natural geomagnetic field, has a strong gradient (i.e., both field strength and inclination vary greatly over a short distance). Thus, in principle, lobsters might detect one or more of the following: (1) the total intensity of the field produced by the magnet; (2) the inclination angle; (3) the intensity gradient; (4) the inclination gradient; (5) the range of field directions within the horizontal plane when close to the magnet. Additional changes in field components such as horizontal and vertical intensity also occur close to a magnet, but whether any animal can resolve the total field into vector components is not known.

Why avoid dens with magnets?

The reason why lobsters avoided dens with magnets is not known, but several explanations are plausible. Given that lobsters are known to possess 'magnetic maps' and can thus assess their geographic location relative to 'home' (Boles and Lohmann, 2003), one possibility is that lobsters preferred dens with ambient magnetic fields similar to those in their home area. Because the test arena was located within 350 m of the capture site, the control den had a magnetic field nearly identical to that of the capture location. As lobsters approached the magnet den, they might have interpreted the anomalous field to mean that they were far from home, resulting in exploration that led eventually to the discovery of the control den and the more familiar magnetic field.

Another possibility is that lobsters avoided dens with magnets because the anomalous field represented an unnatural and unfamiliar magnetic environment. For example, some of the inclination and intensity values near the magnet were presumably outside the range that a lobster in Florida would normally encounter; moreover, the magnet created steep gradients in magnetic parameters, so that as a lobster approached a den with a magnet, the intensity, inclination, and direction of the field all changed rapidly. Lobsters might thus have found the magnet's field to be confusing or disturbing. In addition, the magnetic gradient produced by the magnet might conceivably have generated unusual or uncomfortable sensations through effects on the lobster magnetoreceptor system. Magnetic material has been detected in spiny lobsters (Lohmann, 1984), and experiments with magnetic pulses suggest that this material might provide the physical basis for magnetoreception (Ernst and Lohmann, 2016). Because magnetic particles experience a force in a magnetic gradient (Oldenburg et al., 2005), an interesting speculation is that lobsters approaching magnets experienced unusual or uncomfortable sensations resulting from forces exerted on magnetite-based magnetoreceptors, and therefore moved away.

Size-dependent magnetic field avoidance

Interestingly, the behavioral response of lobsters to a strong magnetic anomaly was size-dependent; larger lobsters avoided dens with magnets whereas smaller lobsters appeared indifferent to magnets when choosing a den. These findings are consistent with the hypothesis that lobsters undergo a size-dependent shift in the behavioral response to magnetic fields, although additional studies are needed to confirm or refute this possibility.

The reason for the size-dependent aversion to magnets remains unknown, but an interesting possibility is that larger lobsters might be more sensitive to magnetic stimuli than smaller lobsters. Consistent with this idea, the magnetic remanence (a measure of the quantity of magnetic material present) of the lobster cephalothorax and abdomen increased with carapace length (Lohmann, 1984), as might be expected if larger, more mature lobsters have a more developed magnetite-based magnetoreceptor system. An alternative explanation for the present results, however, is that smaller lobsters are under greater risk of predation than larger lobsters (Andree, 1981; Eggleston & Lipcius, 1992; Smith & Herrnkind, 1992) and might therefore be more strongly motivated to take cover, even in suboptimal dens. By contrast, larger lobsters less vulnerable to predation might be more willing to explore further until encountering a den with more favorable magnetic conditions. Regardless, further studies will be needed to investigate the cause of the observed size effect.

Natural anomalies vs magnet anomalies

Although our results provide the first evidence that spiny lobsters detect and respond to a strong magnetic anomaly, the anomalies used in this study were greater in intensity, and had stronger gradients, than naturally occurring anomalies caused by geological formations. For this reason, and because strong fields might hypothetically affect physiological processes that are unaffected by weaker fields, caution is needed in extrapolating the results to the natural behavior of lobsters. Nevertheless, if lobsters do indeed generally avoid magnetic anomalies, then an interesting speculation is that the animals might avoid geographic areas where the ambient field varies irregularly, perhaps because such conditions make it difficult for the animals to guide themselves using their magnetic compasses (Lohmann et al., 1995) and magnetic maps (Boles and Lohmann, 2003). Further studies will be needed to investigate how lobsters respond to more natural magnetic anomalies and whether they attempt to circumvent them when possible.

Responses of animals to magnets

Most studies on animal magnetoreception have involved magnetic fields that closely resemble the natural field of the earth. Indeed, an increased emphasis in recent years has been on developing coil systems that generate highly uniform fields and minimize anomalies (Kirschvink, 1992), a trend fueled by the belief that animals will not spontaneously respond to magnetic fields unlike those that exist in nature. A growing body of literature, however, suggests that at least some animals can detect the fields of magnets and respond to them either spontaneously (Brown et al., 1960a,b; Kremers et al., 2014; O'Connell et al., 2015; Vidal-Gadea et al., 2015) or after being conditioned to do so (Thalau et al., 2007; Denzau et al., 2011; Freire et al., 2012). If spontaneous responses similar to those we have observed in lobsters turn out to be widespread phylogenetically, then exposing animals to the fields of magnets might provide a new and useful assay of magnetic sensitivity.

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Competing Interests:

No competing interests declared.

Author Contributions:

D.A.E. and K.J.L. conceived the study, drafted the manuscript, and designed the experiments. D.A.E. carried out the experiments and data analysis. Both authors read and approved the final manuscript.

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References

1. **Andree, S. W.** (1981). Locomotory activity patterns and food items of benthic postlarval spiny lobsters, *Panulirus argus*. Florida State University, Tallahassee, FL.
2. **Boles, L. C. and Lohmann, K. J.** (2003). True navigation and magnetic maps in spiny lobsters. *Nature* **421**, 60-63.
3. **Brothers, J. R. and Lohmann, K. J.** (2015). Evidence for geomagnetic imprinting and magnetic navigation in the natal homing of sea turtles. *Curr. Biol.* **25**, 392-396.
4. **Brown, F. A., Brett, W. J., Bennett, M. F. and Barnwell, F. H.** (1960a). Magnetic response of an organism and its solar relationships. *Biol. Bull.* **118**, 367-381.
5. **Brown, F. A., Webb, H. M. and Brett, W. J.** (1960b). Magnetic response of an organism and its lunar relationships. *Biol. Bull.* **118**, 382-392.
6. **Creaser, E. P. and Travis, D.** (1950). Evidence of a homing instinct in the Bermuda spiny lobster. *Science* **112**, 169-170.
7. **Dennis, T. E., Rayner, M. J. and Walker, M. M.** (2007). Evidence that pigeons orient to geomagnetic intensity during homing. *Proc. R. Soc. B* **274**, 1153-1158.
8. **Denzau, S. and Kuriakose, D.** (2011). Conditioning domestic chickens to a magnetic anomaly. *J. Comp. Physiol. A* **197**, 1137-1141.
9. **Eggleston, D. B. and Lipcius, R. N.** (1992). Shelter selection by spiny lobster under variable predation risk, social conditions, and shelter size. *Ecology* **73**, 992-1011.
10. **Ernst, D. A. and Lohmann, K. J.** (2016). Effect of magnetic pulses on Caribbean spiny lobsters: implications for magnetoreception. *J. Exp. Biol.* **219**, 1827-1832.
11. **Freire, R., Dunston, E., Fowler, E. M., McKenzie, G. L., Quinn, C. T. and Michelsen, J.** (2012). Conditioned response to a magnetic anomaly in the Pekin duck (*Anas platyrhynchos domestica*) involves the trigeminal nerve. *J. Exp. Biol.* **215**, 2399-2404.
12. **Herrnkind, W. F.** (1980). Spiny lobsters: patterns of movement. In *Biology and Management of Lobsters, Vol. 1* (ed. J. S. Cobb and B. J. Phillips), pp. 349-407. New York: Academic Press.
13. **Johnsen, S. and Lohmann, K. J.** (2005). The physics and neurobiology of magnetoreception. *Nature Rev. Neurosci.* **6**, 703-712.

14. **Johnsen, S. and Lohmann, K. J.** (2008). Magnetoreception in animals. *Physics Today* **61**, 29-35.

15. **Kanciruk, P. and Herrnkind, W.** (1978). Mass migration of spiny lobster, *Panulirus argus* (Crustacea: Palinuridae): behavior and environmental correlates. Bull. Mar. Sci. **28**, 601-623.

16. **Kirshvink, J.** (1992). Uniform magnetic fields and double-wrapped coil systems: Improved techniques for the design of bioelectromagnetic experiments. *Bioelectromagnetics* **13**, 401-411.

17. **Kirschvink, J. L., Dizon, A. E. and Westphal, J. A.** (1986). Evidence from strandings for geomagnetic sensitivity in cetaceans. *J. Exp. Biol.***120**, 1-24.

18. **Klimley, A. P.** (1993). Highly directional swimming by scalloped hammerhead sharks, *Sphyrna lewini*, and subsurface irradiance, temperature, bathymetry, and geomagnetic field. *Mar. Biol.* **117**, 1-22.

19. **Klinowska, M.** (1985). Cetacean live stranding sites relate to geomagnetic topography. *Aquat. Mamm.* **1**, 27-32.

20. **Kremers, D., Marulanda, J. L., Hausberger, M. and Lemasson, A.** (2014). Behavioural evidence of magnetoreception in dolphins: detection of experimental magnetic fields. *Naturwissenschaften* **101**, 907-911.

21. **Lanza, R. and Meloni, A.** (2006). *The Earth's Magnetism: An Introduction for Geologists*. New York: Springer Berlin Heidelberg.

22. **Lohmann, K. J.** (1984). Magnetic remanence in the western Atlantic spiny lobster, *Panulirus argus*. *J. Exp. Biol.* **113**, 29-41.

23. **Lohmann, K. J. and Lohmann, C. M. F.** (1994). Detection of magnetic inclination angle by sea turtles: a possible mechanism for determining latitude. *J. Exp. Biol.* **194**, 23-32.

24. **Lohmann, K. and Lohmann, C.** (1996). Orientation and open-sea navigation in sea turtles. *J. Exp. Biol.* **199**, 73-81.

25. **Lohmann, K. J. and Ernst, D. A.** (2014). The geomagnetic sense of crustaceans and its use in orientation and navigation. In *Crustacean Nervous Systems and Control of Behavior* (ed. C. D. Derby and M. Thiel), pp. 321-336. New York: Oxford University Press.

26. **Lohmann, K. J., Pentcheff, N. D., Nevitt, G. A., Stetten, G. D., Zimmer-Faust, R. K., Jarrard, H. E. and Boles, L. C.** (1995). Magnetic orientation of spiny lobsters in the ocean: experiments with undersea coil systems. *J. Exp. Biol.* **198**, 2041-2048.
27. **Lohmann, K. J., Hester, J. T. and Lohmann, C. M. F.** (1999). Long-distance navigation in sea turtles. *Ethol. Ecol. Evol.* **11**, 1-23.
28. **Lohmann, K. J., Cain, S. D., Dodge, S. A. and Lohmann, C. M. F.** (2001). Regional magnetic fields as navigational markers for sea turtles. *Science* **294**, 364-366.
29. **Lohmann, K. J., Lohmann, C. M. F. and Putman, N. F.** (2007). Magnetic maps in animals: nature's GPS. *J. Exp. Biol.* **210**, 3697-3705.
30. **Lohmann, K. J., Putman, N. F. and Lohmann, C. M. F.** (2012). The magnetic map of hatchling loggerhead sea turtles. *Curr. Opin. Neurobiol.* **22**: 336-342.
31. **Naisbett-Jones, L. C., Putman, N. F., Stephenson, J. F., Ladak, S. and Young, K. A.** (2017). A magnetic map leads juvenile European eels to the Gulf Stream. *Curr. Biol.* **27**, 1236-1240.
32. **O'Connell, C. P., Hyun, S. Y., Gruber, S. H. and He, P.** (2015). Effects of barium-ferrite permanent magnets on great hammerhead shark *Sphyrna mokarran* behavior and implications for future conservation technologies. *Endang. Species Res.* **26**, 243-256.
33. **Oldenburg, A., Toublan, F., Suslick, K., Wei, A. and Boppart, S.** (2005). Magnetomotive contrast for *in vivo* optical coherence tomography. *Opt. Express* **13**, 6597-6614.
34. **Parkinson, W. D.** (1983). *Introduction to Geomagnetism*. Edinbergh: Scottish Academic Press. Ltd.
35. **Phillips, J. B., Freake, M. J., Fischer, J. H. and Borland, C. S.** (2002). Behavioral titration of a magnetic map coordinate. *J. Comp. Phys. A* **188**, 157-160.
36. **Putman, N. F., Lohmann, K. J., Putman, E. M., Quinn, T. P., Klimley, A. P. and Noakes, D. L. G.** (2013). Evidence for geomagnetic imprinting as a homing mechanism in Pacific salmon. *Curr. Biol.* **23**, 312-316.
37. **Schiffner, I., Fuhrmann, P. and Wiltschko, R.** (2011). Tracking pigeons in a magnetic anomaly and in magnetically "quiet" terrain. *Naturwissenschaften* **98**, 575-581.
38. **Skiles, D. D.** (1985). The geomagnetic field: Its nature, history and biological relevance. In *Magnetite Biomineralization and Magnetoreception in Organisms* (ed. J. L.

Kirschvink, D. S. Jones, and B. J. MacFadden), pp. 43-102. London, New York: Plenum Press.

39. **Smith, K. N. and Herrnkind, W. F.** (1992). Predation on juvenile spiny lobsters, *Panulirus argus*: influence of size, shelter, and activity period. *J. Exp. Mar. Biol. Ecol.* **157**, 3-18.
40. **Thalau, P., Holtkamp-Rözler, E., Gleissner, G. and Wiltschko, W.** (2007). Homing pigeons (*Columba livia* f. *domestica*) can use magnetic cues for locating food. *Naturwissenschaften* **94**, 813-819.
41. **Vidal-Gadea, A., Ward, K., Beron, C., Ghorashian, N., Gokce, S., Russell, J., Truong, N., Parikh, A., Gadea, O., Ben-Yakar, A. and Pierce-Shimomura, J.** (2015). Magnetosensitive neurons mediate geomagnetic orientation in *Caenorhabditis elegans*. *eLife* **4**, e07493.
42. **Walcott, C.** (1978) Anomalies in the earth's magnetic field increase the scatter of pigeons' vanishing bearings. In *Animal Migration, Navigation and Homing* (ed. K.Schmidt-Koenig and W. T. Keeton), pp 143–151. Springer, Heidelberg.
43. **Walcott, C.** (1992). Pigeons at magnetic anomalies: the effects of loft location. *J. Exp. Biol.***170**, 127-141.
44. **Walker, M. M.** (1998). On a wing and a vector: a model for magnetic navigation by homing pigeons. *J. Theor. Biol.* **192**, 341-349.
45. **Walker, M. M.** (2002). The magnetic sense and its use in long-distance navigation by animals. *Curr. Opin. Neurobiol.* **12**, 735-744.
46. **Wiltschko, R. and Wiltschko, W.** (1995). *Magnetic Orientation in Animals.* Berlin: Springer.
47. **Wiltschko, R., Schiffner, I. and Wiltschko, W.** (2009). A strong magnetic anomaly affects pigeon navigation. *J. Exp. Biol.* **212**, 2983-2990.
48. **Wiltschko, R., Schiffner, I., Fuhrmann, P. and Wiltschko, W.** (2010). The role of the magnetite-based receptors in the beak in pigeon homing. *Curr. Biol.* **20**, 1534-1538.

Figures

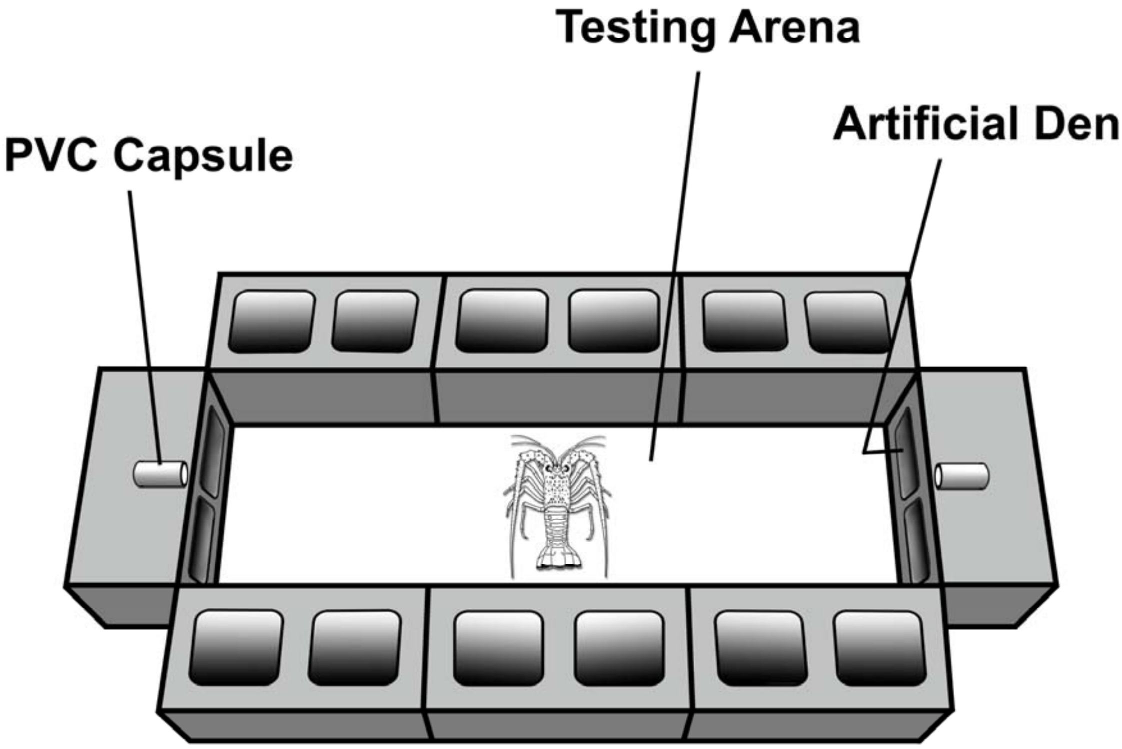

Figure 1: Schematic of the experimental arena. Each sealed PVC capsule contained either a neodymium magnet or a non-magnetic weight of similar size.

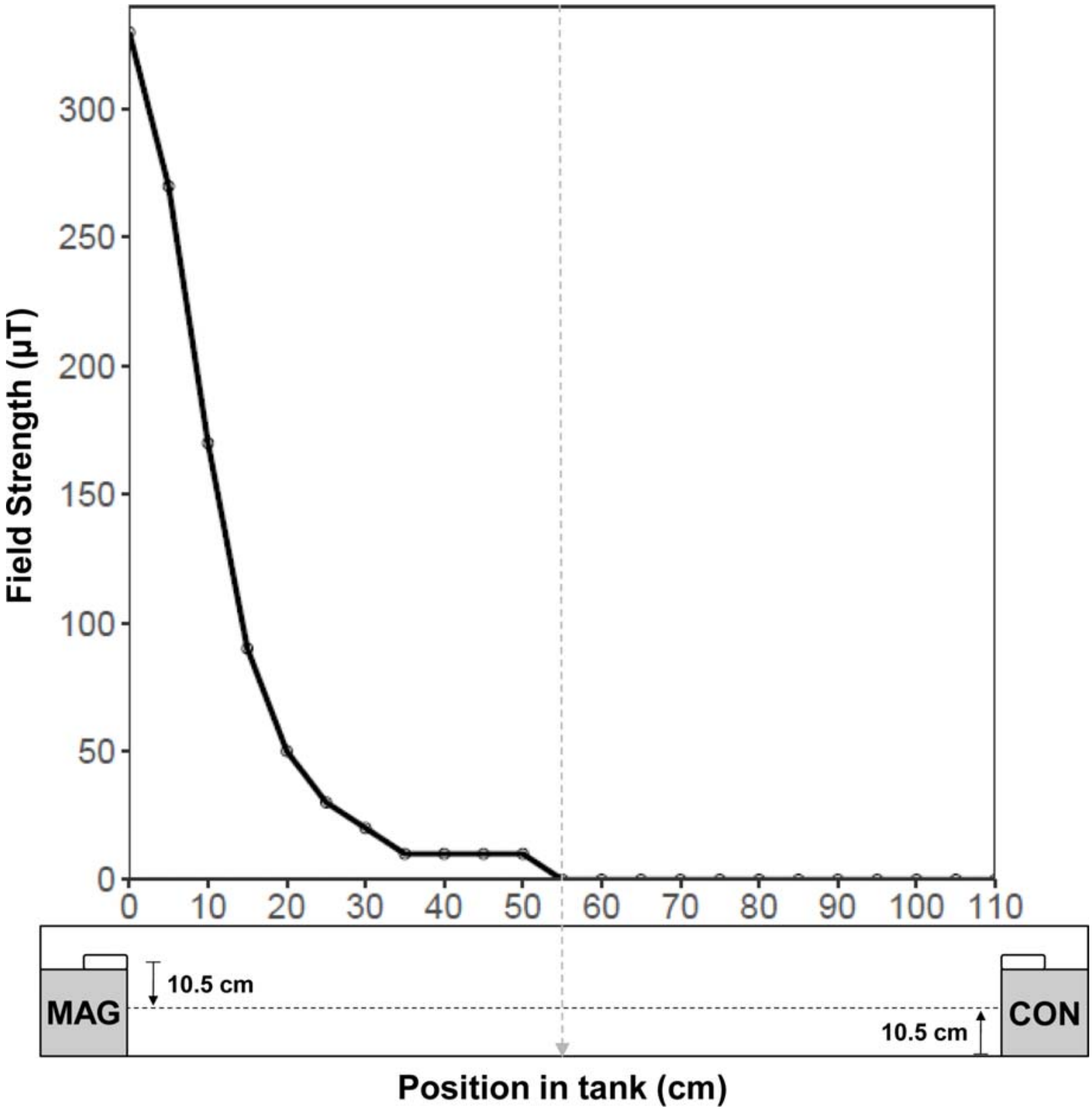

Figure 2: Approximate magnetic field strength experienced by lobsters as a function of distance from the magnet's surface. All values were calculated for positions on a horizontal plane that approximated the height of a walking lobster; the plane was 10.5 cm above the floor of the arena and 10.5 cm below the midway point of the magnet positioned on top of the concrete block (see diagram at bottom of figure). "0" on the x-axis indicates a position 10.5 cm directly below the magnet surface. The grey vertical dashed line at "55" indicates the midpoint of the arena (i.e., the lobster release location). Measurements taken with a DC magnetometer (AlphaLab, Inc.; West Salt Lake City, UT, USA) at various distances from the magnet showed

good agreement with the calculated values and were used to spot-check the general accuracy of the graph. Both calculations and measurements indicated that, at the level where the lobsters walked, the field produced by the magnet was essentially zero beyond the midpoint of the arena. MAG = den with magnet; CON = den with non-magnetic weight; white rectangles on dens = PVC capsules).

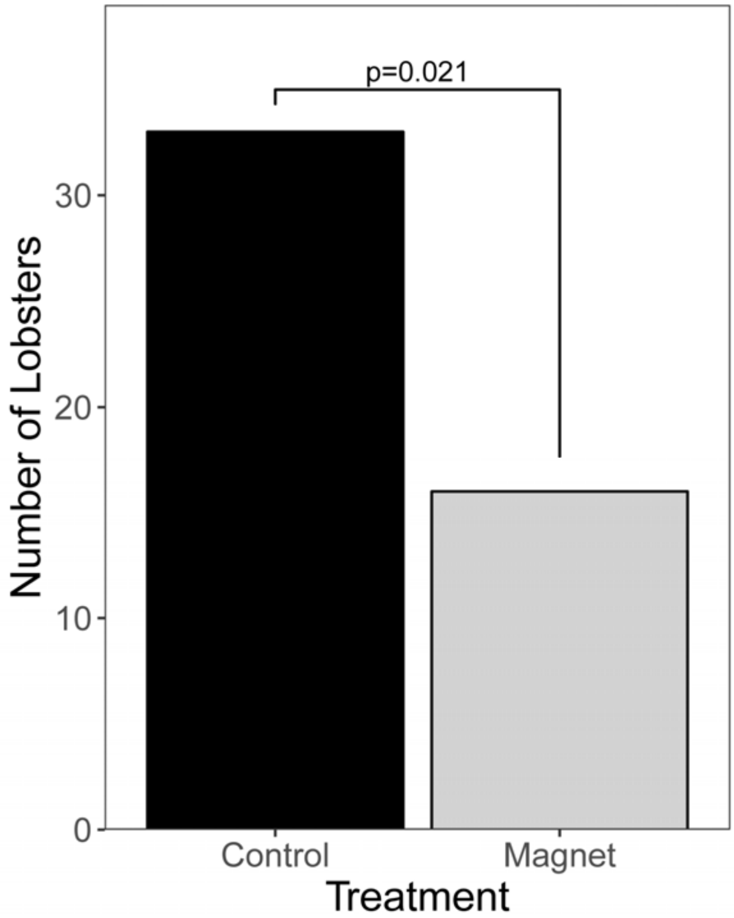

Figure 3: Total numbers of lobsters that occupied each den type. More lobsters took refuge in control dens (n=33) than in dens below a magnet (n=16); the difference is significant (p=0.021, exact binomial test). Control = non-magnetic weight; Magnet = neodymium magnet.

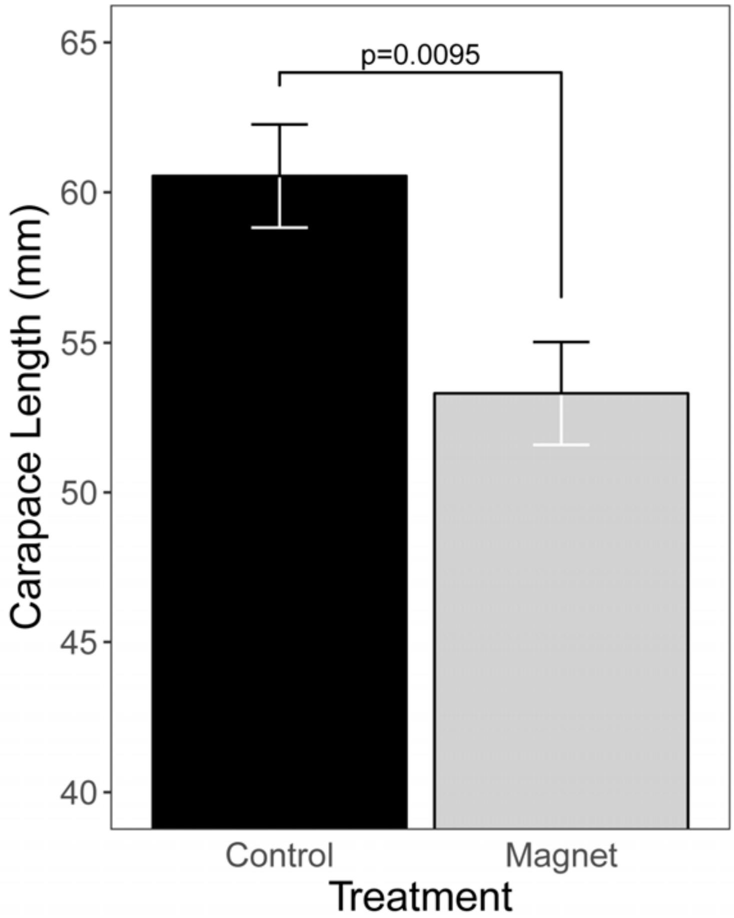

Figure 4: Mean carapace length of lobsters that occupied each den type. Lobsters that selected control dens (n=33) were significantly larger on average than those (n=16) that selected magnet dens (p=0.0095, Mann-Whitney U test). Error bars indicate standard error of the mean.

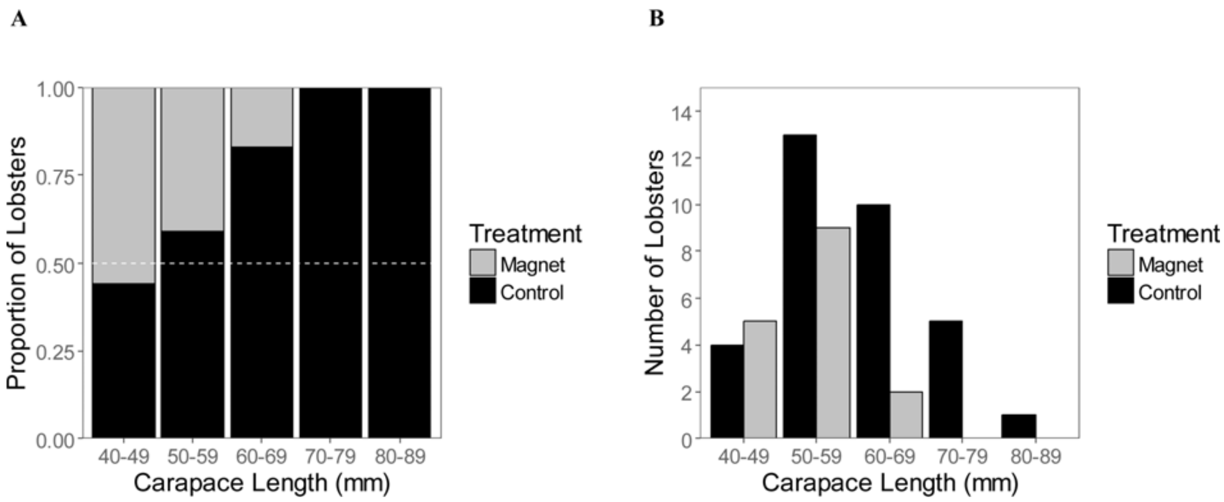

Figure 5: Den choice across 10 mm carapace length bins. (A) Proportion of lobsters that occupied each den type. (B) Total number of lobsters that chose each den type (n=49).

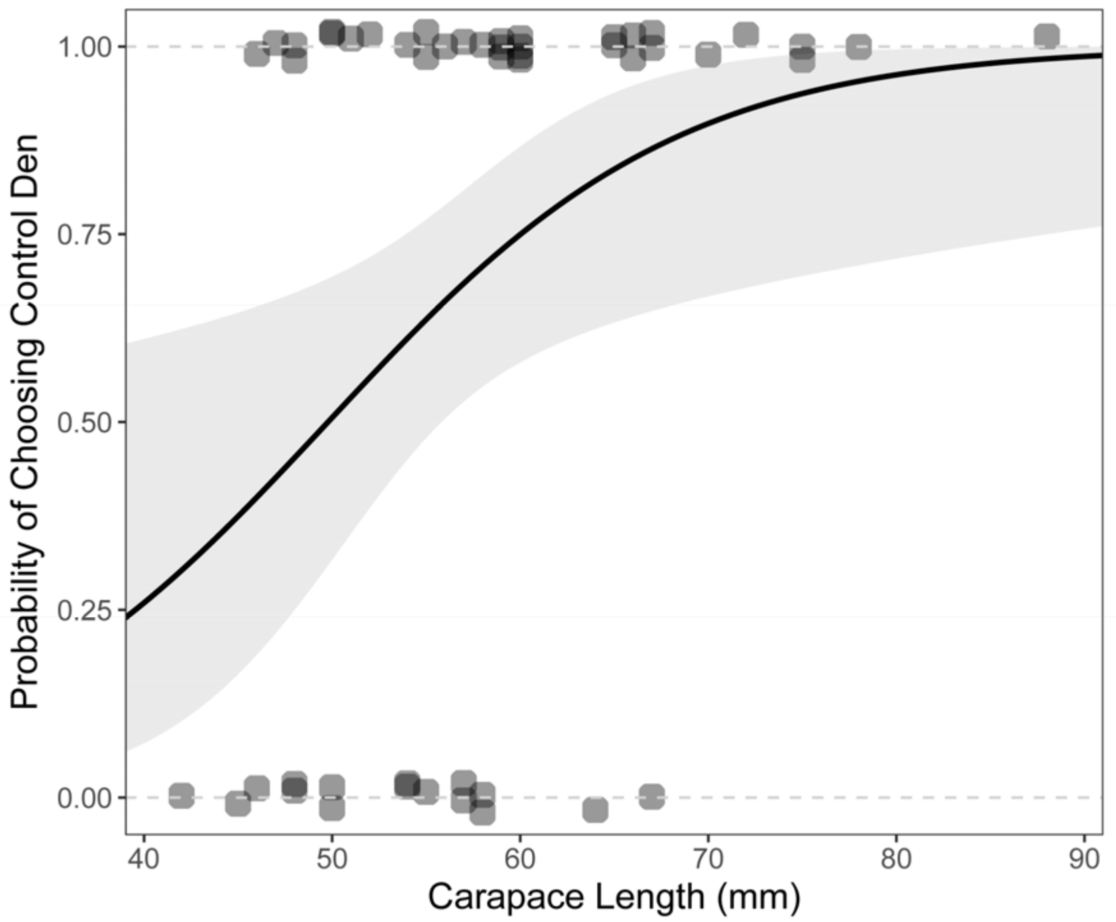

Figure 6: Logistic regression curve showing the relationship between carapace length and den choice. Carapace length is a significant predictor of den choice (p=0.019). Each circle represents an individual lobster, with circles along the "1.00" line representing lobsters that chose the control den (n=33) and points along the "0.00" line denoting lobsters that chose the den with the magnet (n=16). Circles are offset and transparent for clarity. The shaded area represents the 95% confidence interval.

Variable	Coefficient	SEM	Odds Ratio	2.5% CI	97.5% CI	z	P-value
Intercept	-5.34	2.53	0.005	1.93×10^{-5}	0.45	-2.11	0.035*
Carapace Length	0.11	0.05	1.11	1.03	1.23	2.36	0.019*

CI = confidence interval; SEM = standard error of the mean; * = p<0.05

Table 1: Logistic regression model statistics, with carapace length as a predictor of den choice.