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Rare-Earth Magnets Influence Movement Patterns of the Magnetically Sensitive Nudibranch *Tritonia exsulans* in Its Natural Habitat

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Abstract. The nudibranch *Tritonia exsulans* (previously *Tritonia diomedea*) is known to have behaviors and neurons that can be modified by perturbations of the Earth's magnetic field. There is no definitive evidence for how this magnetic sense is used in nature. Using an exploratory approach, we tested for possible effects of magnetic perturbations based on underwater video of crawling patterns in the slugs' natural habitat, with magnets of varying strength deployed on the substrate. For analysis, we used a paired comparison of tracks of animals between segments 25–50 cm distant from the magnets and segments of the same tracks 0–25 cm from the magnets, to determine whether any differences depended on the strength of the magnet. Most track measurements (length, displacement, velocity, and tortuosity) showed no such differences. However, effects were observed for the changes in track headings between successive points. These results showed that tracks had relatively higher heading variability when they moved closer to stronger magnets. We suggest that this supports a hypothesis that *T. exsulans* continuously uses a magnetic sense to help maintain straight-line navigation. Further specific testing of the hypothesis is now needed to verify this new possibility for how animals can benefit from a compass sense.

Introduction

Many animals use the geomagnetic field to guide long-distance navigation toward fixed goals. Birds, fish, turtles, and a range of other species rely on magnetoreception to find habitats critical for their reproduction and survival (Wiltschko and Wiltschko, 2005; Lohmann *et al.*, 2007; Lohmann and Lohmann, 2019). One of the magnetic senses commonly understood for these and other animals is a compass, which allows relatively straight movement over very long distances, distances over which other guidance cues are absent or unreliable. However, a geomagnetic compass can also be used to maintain a fixed heading over much shorter distances (Narazaki *et al.*, 2009; Vasey *et al.*, 2015; Painter and Plochocka, 2019). Indeed, evidence for such a possibility has been found in a number of different animals, including mealworm beetles, cockroaches, fruit fly larvae, amphipods, and mole rats (Arendse, 1978; Vácha and Soukopová, 2004; Dommer *et al.*, 2008; Vácha *et al.*, 2008; Tomanova and Vacha, 2016; Malewski *et al.*, 2018a, b).

The nudibranch mollusc *Tritonia exsulans* Bergh, 1894 (previously classified as *Tritonia diomedea*; Korshunova and Martynov, 2020) has a magnetic sense. Magnetic sensory input has been recorded from a number of peripheral nerves (Popescu and Willows, 1999; Pavlova *et al.*, 2011). Neurophysiological experiments have shown that several different neurons in the brain respond to changes in the Earth's magnetic field (Lohmann *et al.*, 1991; Wang *et al.*, 2003, 2004; Cain *et al.*, 2006). Laboratory behavioral experiments have also shown that movement patterns can be manipulated by changing magnetic fields (Lohmann and Willows, 1987). Three hypotheses have been proposed for how the slugs might use a magnetic sense. All three hypotheses are linked to navigating with respect to their prey, pennatulacean soft corals (sea pens or sea whips) that form beds in subtidal soft sediments. (1) A lunar-modulated preference for different magnetic headings could lead to a spiral search pattern if the animals are swept out of their sea pen or sea whip bed habitat (Lohmann and Willows, 1987). (2) Learning a shoreward geomagnetic heading could similarly be beneficial in returning to sea pen beds (Willows, 1999). (3) Maintaining a constant geomagnetic heading

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toward an attractive odor source would be beneficial when first navigating inside a turbulent odor plume but then losing contact with the plume due to a change in bulk flow direction (Wyeth, 2010; Vasey *et al.*, 2015; Endres *et al.*, 2016). We now additionally propose a more generalized version of the third hypothesis. Navigation in *T. exsulans* is primarily controlled by odors and flow (Murray and Willows, 1996; Wyeth and Willows, 2006a, b; Wyeth *et al.*, 2006; Murray *et al.*, 2011; McCullagh *et al.*, 2014), but a geomagnetic sense could help the slugs maintain crawling in straight lines in a number of circumstances. The slugs lack visual capabilities (Chase, 1974a, b) that could help generate efficient straight-line navigation toward or away from navigational targets. Thus, whether crawling upstream or downstream relative to odor sources, or searching for odor plumes, the slugs could benefit from a magnetic sense that helps maintain straight headings, particularly if odor sources or plumes are only intermittently detected. None of these hypotheses have been tested with magnetic manipulations in the natural habitat.

Field tests of whether magnetic fields influence behavior are constrained by the options available for magnetic manipulations. Creating realistic Earth-strength magnetic field changes requires coil systems (Kirschvink, 1992; Lohmann *et al.*, 1995; Gottardi *et al.*, 2003), which are difficult to deploy underwater. Thus, we chose to use rare-earth magnets, which are simple to deploy but create a highly heterogeneous perturbation of the magnetic field, depending on how far and in what direction an animal is relative to the position and orientation of the magnet. This approach, or a similar alternative involving attaching rare-earth magnets directly to the animal, has been used with a number of different animals (Brown *et al.*, 1964; Mora and Walker, 2012; Weijers *et al.*, 2018; Bainbridge *et al.*, 2020). In either case, the massive local disruption of the Earth's magnetic field can provide an assessment of whether a magnetic sense plays a role in guiding movement. However, this approach lacks the precision necessary to predict the exact behavioral consequences of the perturbation, and it is not able to decisively determine how the magnetic sense is used.

Given these constraints, we chose an exploratory approach to recording and analyzing the consequences of magnetic perturbations on the navigation behavior of *T. exsulans*. We tracked movement paths of the slugs in their natural habitat, where normal navigation behaviors relative to prey, predators, and conspecifics will occur. By using a series of magnets with increasing strengths, we created magnetic perturbations at different distances from the magnets. If the slugs do indeed use a magnetic sense as a secondary cue to augment navigation, as has been suggested for various other animals (Johnsen *et al.*, 2020), then we would expect changes in navigation dependent on the strength of the magnets. Because the nature of those changes and their exact distance from magnets are not predictable, we used a variety of navigational metrics calculated from the tracks to characterize whether changes in navigation occur closer to magnets (where a magnetic sense might be influenced) *versus* farther from the magnets (where there is little or no chance that a magnetic sense might be influenced). Any differential effects on navigation (close to the magnets *vs.* far from the magnets) that depend on the strength of the magnet would then be consistent with the magnetic perturbation causing a change in navigation behavior by *T. exsulans*.

Materials and Methods

Location and animals

Behavioral experiments were conducted in May of 2013 at MacIntosh Rocks (49°12.60′ N, 125°57.45′ W), north of Vargas Island, British Columbia, Canada. This site contained *Ptilosarcus gurneyi* beds where *Tritonia exsulans* Bergh, 1894 had previously been known to occur (Wyeth and Willows, 2006a), though none were observed during this trip. Therefore, 48 slugs were imported from Yellow Bank (48°14.07′ N, 122°25.22′ W, 3.2 km northeast), which had an abundant population of *T. exsulans* but was too exposed to wind to be suitable for our camera system. Therefore, our observations are primarily of the 48 transplanted slugs, although additional slugs from the surrounding area may have been included in the study.

Video methods

We recorded time-lapse videos of the behavior of *T. exsulans* in its natural habitat, using methods similar to Wyeth and Willows (2006). Sets of three underwater cameras (Speco Technologies CVC321WP, Amityville, NY) were attached to steel conduit poles pushed into the sediment (small magnetic perturbations from the poles were far removed from the area recorded by cameras). Poles were arranged in an equilateral triangle, with cameras angled down at the substrate so that all three camera views overlapped at the center of the triangle while still retaining a mostly unique field of view (Fig. 1A). A marker indicating magnetic north was placed on the substrate, visible in all three cameras. Two of these 3-camera setups were deployed each day, at least 5 m apart. All cameras were cabled directly to a PC computer digital video recording system (Novex 2000, North York, Ontario, Canada) onboard a research vessel anchored at least 6 m away from both camera setups. Videos were recorded straight to hard disk at 2.5 frames per second, with a resolution of 352 × 240 pixels. At both the start and end of each day, divers placed a meter stick marked at 25-cm intervals atop the substrate, to give scale for the camera (and also position the magnets; see *Magnetic manipulations*, below). Two or three times per day, nearby slugs were collected and placed in view of the camera if there were few in the recorded area, allowing recordings of slug movements 7 to 10 hours per day.

Magnetic manipulations

The experimental treatments consisted of neodymium rare-earth magnets glued to steel spikes that were marked with flagging tape for identification in the videos. Three sizes of

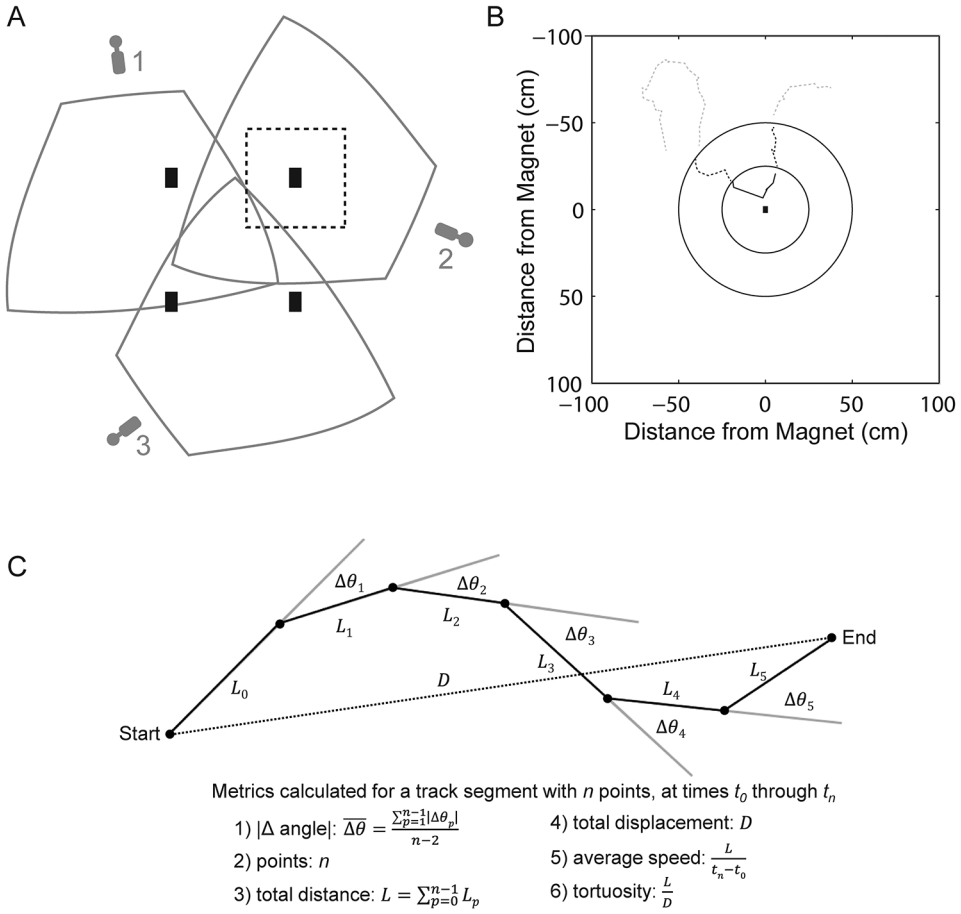

Figure 1. Camera setup and track analysis approach. (A) Three cameras (gray, numbered 1–3) with slightly overlapping fields of view on the substrate (gray outlines) recorded *Tritonia exsulans* movements around a set of four magnets (black rectangles). Not to scale; dashed outline around one magnet shows approximate region shown in (B). (B) Analysis of tracks was conducted relative to single magnets (small black rectangle). Tracks were divided into segments close to the magnet (<25 cm; inside the inner circle; solid line) and far from the magnet (25–50 cm; between the inner and outer circles; dashed line); segments beyond 50 cm from the magnet (gray dashed line) were excluded from analysis. (C) For all track segments, six track metrics (listed 1–6) were calculated from the lengths and angles between points. To test for the effect of each magnet type, tracks with segments both close to and far from magnets were chosen, and the six metrics were calculated for both the close and far segments. For each magnet type, this created six paired data sets for statistical testing of whether the average differences between metrics close to *versus* far from magnets were significantly different from zero.

magnets from Indigo Instruments (Waterloo, Ontario, Canada) were used: weak (5 × 15 mm [diameter × length]; catalog no. 44201-15), medium (15 × 12.5 mm; 44205-12.5), and strong (25 × 20 mm; 44209-20). A fourth control treatment consisted of steel spikes without magnets. For each 3-camera setup on each day, 4 spikes with magnets of the same strength (or controls) were driven into the sediment in a 1 × 1-m square (Fig. 1A) surrounding the north marker. All magnets were deployed with their south pole oriented toward magnetic north and vertically flush with the sediment surface, such that they would have little or no influence on water flow patterns over the substrate. On 5 days, from May 20 to May 25, weak magnets were deployed in one 3-camera setup; and medium magnets were deployed in the other 3-camera setup. On 5 other days, May 26 to May 31, the strong magnets and controls were deployed in the 2 respective 3-camera setups.

The magnetic field perturbation of the strong magnets was measured with a DC Milligauss Meter 3 Axis (model no. 3AMG, AlphaLab, Salt Lake City, UT) by placing the magnets in the same orientation as when deployed in the field (south pole oriented toward magnetic north). The measurements were completed in Hayward, California (37°39.422′ N, 122°3.183′ W), in a grassy area that was at least 15 m away from any buried electric cables or pipes (thus that ensuring no such structures biased our measurements). The sensor was held parallel to the horizontal plane and moved by 20-cm intervals out to 140 cm away in both horizontal directions, measuring the magnetic field vector at each location. This two-dimensional

grid of measurements was then interpolated using Matlab software (MathWorks, Natick, MA) to generate a map of magnetic field strengths around the magnet (Fig. 2). Notably, the perturbations to ambient field strengths that were created by the magnet fell steeply between 25 and 50 cm distant from the magnet.

Analysis

Tracking. All behavioral videos were analyzed to track slugs relative to the position of the magnets (Fig. 1B). Videos were imported into FIJI (Schindelin *et al.*, 2012), and slugs were tracked at 30-s intervals, using the MTrackJ plug-in (Meijering *et al.*, 2012). Tracking consisted of marking each slug's location (specifically, the point between the rhinophores) in each video frame. Tracking was completed blind to the strength of magnets in the video (the schedule of deployments was unknown, and the magnets are sufficiently small as to not be readily distinguishable). Every tracked slug in each video was identified separately, except when it was possible to determine when a slug moved between multiple camera views (in which case two separate tracks would be associated with the same slug, and both tracks would be used separately for analysis). If a slug was tracked simultaneously in two or more cameras, only one track (in which the slug was closer to the camera) was used in analyses. In the relatively rare situation when a slug was first visible in one camera and then subsequently moved into the view of a second camera, the two successive tracks (one in each camera) were used for analysis. We chose to include both tracks because some animals undoubtedly moved between cameras without our knowledge; thus, ensuring that we acquired only single tracks from each slug during a given camera deployment was not possible. Movements when divers were present in the videos, as well as in the five minutes following any diver activity, were omitted from the analyses. Periods where the slugs were not crawling were also excluded from analyses. Finally, magnet locations in all cameras' videos were also marked using MTrackJ, to establish relative slug and magnet positions in a common coordinate system for each video.

Metrics. Five different movement metrics were calculated from the series of point locations that comprised each track segment included in analyses (Fig. 1C). (1) The absolute change in angle ($|\Delta \text{ angle}|$) was calculated for every set of three successive points: the absolute value of the difference in direction between the vector formed by points 1 and 2 and the vector formed by points 2 and 3, and then the average across all triplets of points in the track segment. Because this measure of variability in direction is not circular, but rather a linear measure on the interval [0, 180], subsequent analyses treat the metric as linear data. (2) The total distance of the track segment was the summed distances between successive points. (3) The total displacement of a track segment was the distance between the start and end points of a track segment. (4) The average speed of movement over the track segment was the distance divided by the time interval between the first and last points

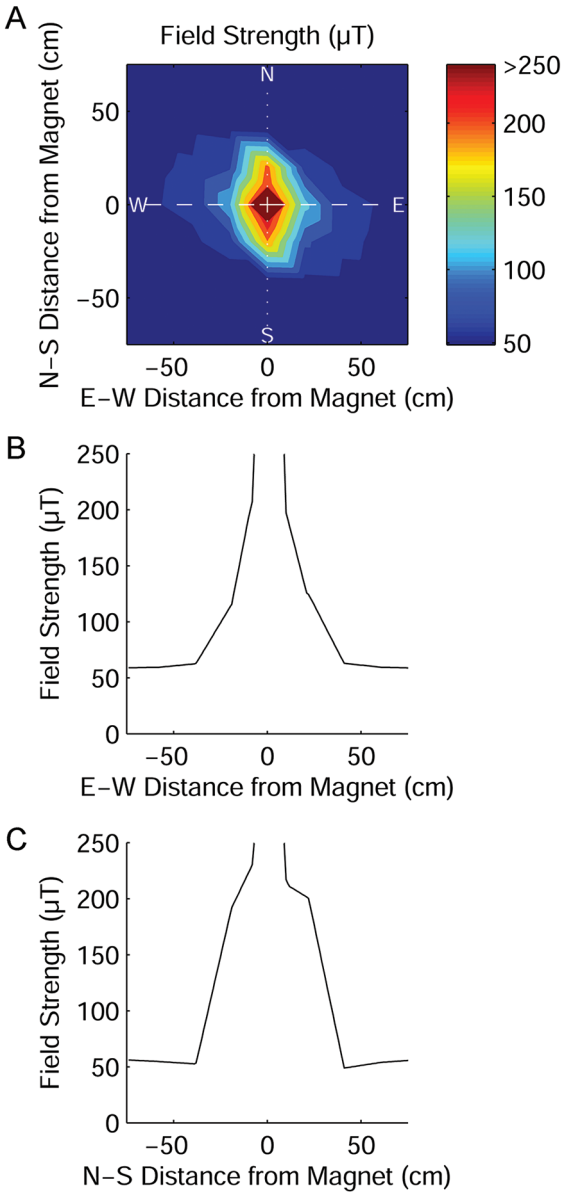

Figure 2. Magnetic field strengths surrounding one of the strong magnets used to perturb magnetic fields experienced by *Tritonia exsulans*. The magnet was aligned with the Earth's magnetic field as deployed in the field, with south pole pointing magnetic north. Total field strength was measured, combining both the Earth's magnetic field and any perturbations from the magnet. All data were interpolated from a rectangular grid of measurements (every 20 cm) centered on the magnet and were made at the same height of the magnet. Field strengths between 250 and 5×10^5 μT (found between 10 and 0 cm from the magnet) are not plotted so as to avoid obscuring the effects of the magnets at greater distances, where they diminish to negligible, relative to the Earth's magnetic field (~50 μT). (A) Heatmap showing the magnetic field strength in the two-dimensional plane surrounding the magnet. Position of the magnet indicated by + at the origin of the *x*- and *y*-axes, both of which measure distance from the magnet in centimeters. The magnetic field strength (μT) at each location in the heatmap is scaled according to the color bar to the right of the heatmap. Cardinal directions, east (E), west (W), north (N), and south (S), are indicated at the margins for orientation. (B) and (C) show the magnetic field strength profiles along two orthogonal lines that intersect the center of the magnet: west to east in (B) (corresponding to the profile along the dashed line in A) and south to north in (C) (corresponding to the profile along the dotted line in A).

of the track segment. (5) Tortuosity was defined as the distance divided by the displacement of a track segment, ranging from 1 (a straight line) to infinity (maximum tortuosity). All metrics involving length (distance, displacement, speed) were adjusted for the varying scale that resulted from the different heights and the angled view of the cameras with respect to the substrate. Scales were thus determined using a linear function of the Y pixel value that was empirically derived from the 1-m distances between magnets in each day's recordings. In addition to these movement metrics, we also verified that the number of points included in track segments was similar (across different magnet strengths for segments both close to and far from magnets), to ensure that such a difference could not be a source of bias in our analysis.

Effects of the magnets. Extensive preliminary analyses of crawling patterns identified substantial differences in metrics when comparing segments of tracks of slugs recorded by different cameras and on different days (relative to arbitrary points rather than magnets). We attribute these differences to the differences in camera heights and angles with respect to the substrate. Camera position had to be set each day by iterative communication between divers and someone observing the camera videos, adjusting for water turbidity (which varied substantially over the 10 days of video recording). Thus, we abandoned our original plan of comparing tracks directly between the treatments because these were confounded by the effects of camera angle, turbidity, or both.

Instead, to eliminate the effects of these confounds, we proceeded with paired track segment comparisons within tracks (any one track comes from a single camera on a single day, thus removing the potential for these to differentially affect the metrics). We then assessed the difference in the metrics between segments of tracks that occurred closer to and farther from the magnets (Fig. 1B). Thus, any effects of the magnets should be revealed as changes in the differences between segment metrics closer to *versus* farther from the magnets. For example, we measured whether there was a greater difference in speed close *versus* far, relative to a strong magnet, than the difference in speed close *versus* far, relative to a weak magnet. Track segments within 25 cm of a magnet were designated as "close" (to a magnet), while track segments between 25 and 50 cm from a magnet were designated as "far" (from a magnet). These distance thresholds were chosen in part because the magnetic perturbations around the strong magnets decline steeply after about 25 cm (Fig. 2) and because the 1-m spacing of the magnets resulted in the possibility of another magnet having a greater influence on tracks >50 cm from a given magnet.

To complete the comparison of metrics for paired segments close to and far from magnets for all treatments, we used two analysis options: normalized and paired. For each metric in each treatment, we normalized the data to the average metric for the segment far from the magnet. Thus, the metrics for the segment far from the magnet (and which should be unaffected by the magnet) will have an average of 1 in each treatment; and if there is any effect of the magnet on the metrics for the segment close to the magnet, it will be revealed as a deviation from 1. As noted above, these data were influenced by confounding factors that we decided precluded further analysis. To fully account for the pairing of segments close to and far from magnets (and completely remove the effects of the confounds), we then determined arithmetic differences between paired metrics for close and far track segments, followed by Wilcoxon signed rank tests of these paired data when the data showed an increasing effect in correspondence with increasing magnet strength. Two-tailed tests were used because we could not predict, *a priori*, how each metric might change as slugs moved closer to or farther from magnets.

We chose this simplified statistical approach as the best means available to minimize the possibility of pseudoreplication affecting our results (Colegrave and Ruxton, 2018). Because tracking the identity of slugs is not possible either across days or if slugs left the combined fields of view of the cameras and then returned, we could not use statistical methods that account for the effect of individuals (*e.g.*, linear mixed-effects models). Instead, as in the original field behavioral studies of *T. exsulans* (Wyeth and Willows, 2006a; Wyeth *et al.*, 2006), we rely on the haphazard introduction of animals beneath the cameras to produce effectively random samples (with repetition) of the 48 animals used in the study. The probability of any bias being introduced into the data is low, given that we collected and distributed most of the animals in the study twice or more every day. The routes taken by divers during collection were haphazard, and the order in which slugs were released in the study area was also haphazard; thus, there is little or no chance that a particular group of slugs was consistently moving close to magnets of a particular strength in the videos. Thus, we used the paired tests, with the assumption that any non-independence between segment pairs created by recording paths from the same slug more than once would have had little effect on our estimates of population variance (and, thus, little effect on our tests of significance), given the relatively large group of animals from which the samples were drawn. We chose not to use the Bonferroni correction to correct for multiple comparisons because it is not supported either for exploratory analyses such as ours (focused on identifying hypotheses for future testing) or for experiments with so few tests: four, one for each treatment (Streiner and Norman, 2011; Armstrong, 2014).

Flow variability

Fluorescein dye plumes were used to assess flow variability in the videos. Fluorescein dye emitters were prepared by mixing fluorescein, plaster of paris, and water. Once dried and then placed underwater at each magnet, these slowly dissolved, releasing a continuous dye plume for about three hours. Divers replenished the dye emitters once or twice per day.

To assess flow variability, we used the dye plumes and other indicators of flow at the substrate (sea pens; drift algae) to count the frequency of large changes in flow direction. These were defined as flow direction changes of 45° or more. Data from all 6 cameras deployed at a time were used to establish flow direction change frequencies in 15-minute intervals spanning all times during which slug movements were recorded. Low-variability intervals were designated when the frequency of >45° flow direction changes was 1 or less, while high variability was designated for intervals with 2 or more 45° direction changes. This categorization was chosen because 45° changes were predicted to hamper navigation by the slugs toward odor sources (Wyeth *et al.*, 2006). These data were then used to filter our track data, limiting some analyses of tracks to only periods of high flow variability.

Results

Numerous tracks were recorded as slugs crawled below the cameras. Based on a population of about 50 slugs, a total of 876 tracks were recorded over the 10 days. For each of the magnet types, more than 175 tracks, comprising an average of 24 points, were measured relative to a magnet visible in the same video (Fig. A1). Among these, a subset could be partitioned into paired segments (each with four points, on average) both near and far from a magnet (near: within 25 cm; far: between 25 and 50 cm; Fig. 1B; see Table 1 for sample sizes). Careful examination of these suggests a subtle change in the difference between close *versus* far tracks when comparing those near controls and those near strong magnets (Fig. 3). The tracks are relatively less straight close to strong magnets *versus* far from strong magnets when compared against the difference in tracks close to *versus* far from controls. Quantitative analysis of the metrics supports this observation. To facilitate comparisons between all treatments, metrics for paired segments close to and far from magnets were normalized to the average segments far from magnets. Any effects of the magnets would thus be revealed as a dependency on magnet strength for any deviations from a normalized measure of 1 for the segments close to the magnet. One metric, $|\Delta \text{ angle}|$, shows such an effect, with substantially different results for medium and strong magnets in comparison to the results for controls and weak magnets (Fig. 4). Indeed, the average pairwise differences in the $|\Delta \text{ angle}|$ between tracks close to and far from the magnets increased in a stepwise fashion as magnet strength increased (Fig. 5). Thus, the data show that the slugs had a greater increase in how much their tracks wandered (as measured by track $|\Delta \text{ angle}|$) as they moved nearer to magnets of greater strength than when they moved near controls or magnets of weaker strength. Pairwise statistical comparison of the track segments close to and far from the magnets showed no significant difference for controls and weak magnets but a significant difference in the $|\Delta \text{ angle}|$ for both medium and strong magnets (Table 1). This same pattern held true, regardless of whether tracks were filtered to only include slugs moving during periods of higher flow direction variability (Table 1). No other differences in track segment metrics were observed across different magnet strengths (including data for distance, displacement, speed, and tortuosity; Fig. 5; also see Table A1 for summary statistics for each of the metrics).

Table 1

Wilcoxon signed rank test statistics for the difference in mean $|\Delta \text{ angle}|$ for track segments of Tritonia exsulans *crawling close to and far from magnets of varying strength*

Flow conditions	Magnet	*n*	*W*-statistic	*P*-value
Low and high variability	Control	25	96	0.074
	Weak	27	149	0.337
	Medium	19	45	**0.044**
	Strong	46	318	**0.015**
High variability only	Control	17	72	0.831
	Weak	20	75	0.263
	Medium	13	11	**0.013**
	Strong	32	117	**0.006**

Tests performed on tracks recorded in all flow conditions (low and high variability) and also on a subset of tracks recorded only during periods of high variability in flow direction. Significant *P*-values are shown in bold.

Discussion

We demonstrate that magnetic perturbations cause a significant change in navigation behavior by *Tritonia exsulans.* To remove the influence of extraneous factors (particularly, camera heights and angles), we used a paired analysis of tracks divided into segments closer to and farther from magnets. For magnets of all strengths, those segments closer to the magnets would have been subject to greater magnetic perturbations than the segments farther from the magnets. If magnetic perturbations do affect crawling by the slugs, then one prediction would be increasing differences between track segments closer to *versus* farther from the magnets as the strength of the perturbing magnet increases. We found such a pattern for a measurement of how much the direction slugs are crawling wanders in track segments. The mean absolute value of the Δ angle measures how much the slug movement directions change from point to point along a track segment. The difference in $|\Delta \text{ angle}|$ between segments close to and farther from magnets increased as magnet strength increased, with significant differences for the medium and strong magnets.

The significant effects of medium and strong magnets on $|\Delta \text{ angle}|$ differences are consistent with the hypothesis that the blind slugs have a magnetic sense to help move in straight lines. The increased $|\Delta \text{ angle}|$ differences indicate that the slugs were diminished in their ability to follow straight paths while crawling close to stronger magnets. For track segments of slugs crawling within 25 cm of strong magnets, the mean $|\Delta \text{ angle}|$ was 10° higher than the mean $|\Delta \text{ angle}|$ for those same slugs crawling between 25 and 50 cm distant from the

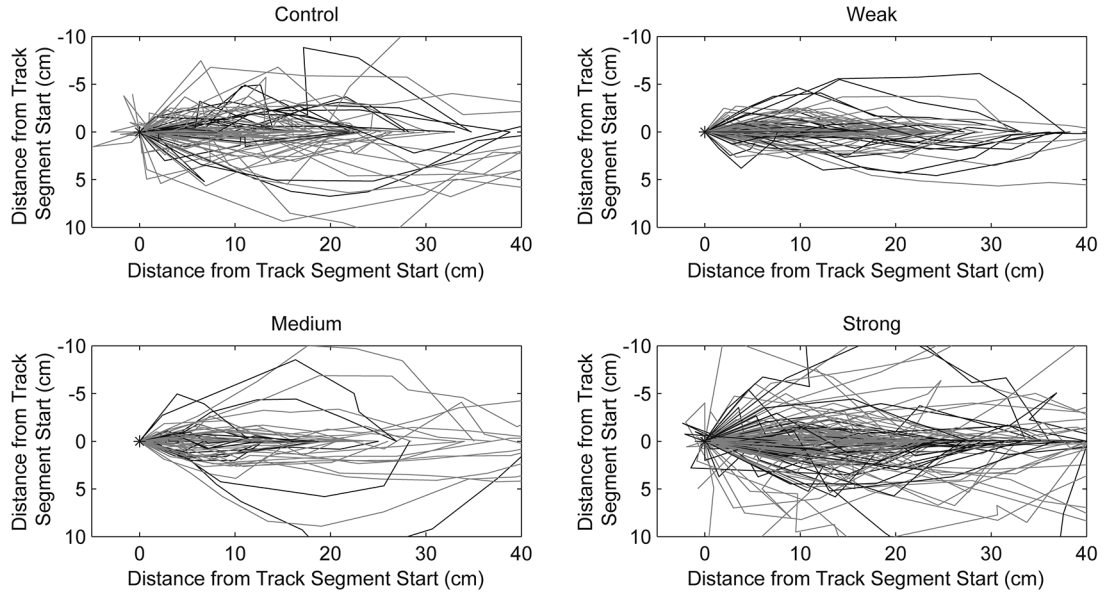

Figure 3. Paired track segments close to and far from magnets, affine transformed and superimposed to demonstrate potential differences in path patterns for *Tritonia exsulans* crawling relative to magnets of varying strengths (control, weak, medium, and strong). Track segments close to the magnets (gray) include all points <25 cm from a magnet, and track segments far from the magnets (black) include all points between 25 and 50 cm from a magnet. Note the greater relative variability in headings (*i.e.*, jaggedness) of the track segments close to strong magnets (gray tracks). Affine transformation: all tracks translated to a common starting point ($x = 0$, $y = 0$) and rotated to end on a common line ($y = 0$). Axes units are shown in centimeters.

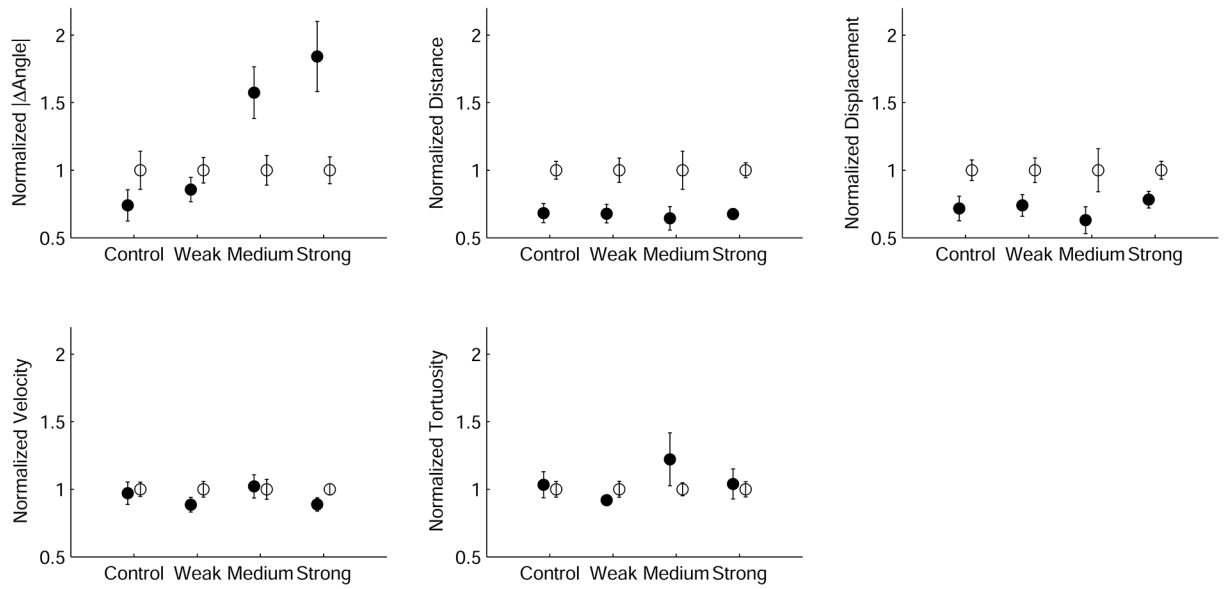

Figure 4. Normalized metrics ($|\Delta \text{ angle}|$, distance, displacement, velocity, and tortuosity) for paired segments of tracks of *Tritonia exsulans* crawling close to (filled circles) and far from (open circles) magnets of varying strengths (control, weak, medium, and strong). Data are presented as means with standard errors, with the normalization step fixing the average metrics at 1 for the segments far from the magnet. Only the difference in $|\Delta \text{ angle}|$ showed any consistent pattern of differences across the different magnet strengths. Three outliers (points that are greater than 1.5 times the interquartile range above the 75th percentile) are excluded from the tortuosity data to confirm that they had no effect on tests of significance.

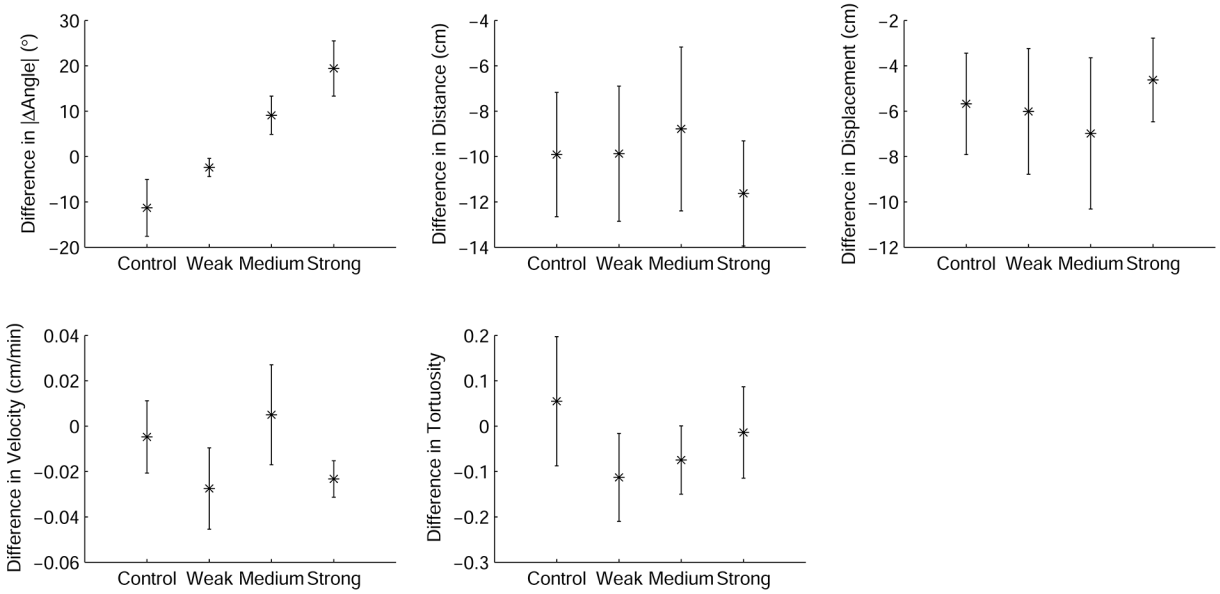

Figure 5. Difference in metrics (|Δ angle|, distance, displacement, velocity, and tortuosity) between paired segments of tracks of *Tritonia exsulans* close to and far from magnets of varying strengths (control, weak, medium, and strong). Data are presented as means with standard errors. Only the difference in |Δ angle| showed any consistent pattern of differences across the different magnet strengths. Three outliers (points that are greater than 1.5 times the interquartile range above the 75th percentile) are excluded from the tortuosity data to confirm that they had no effect on tests of significance.

magnet. Given the effect of the magnets on this measurement of how headings change, differences may be expected in track segment tortuosity as well. However, we found no significant difference in tortuosity between track segments close to and far from the magnets (for all magnet strengths). The relatively small number of points (~4) comprising the track segments likely account for this, because correspondences between mean |Δ angle| and tortuosity will be reinforced for tracks with more points. This could be especially true if the animals only intermittently use magnetic fields (which would still be measured as intermittent changes in |Δ angle| but not necessarily tortuosity, which was calculated over the full length of track segments). Although further subdivision of our tracks based on number of points was not a feasible option, analysis across the entire data set showed an increasing correlation between mean |Δ angle| and tortuosity with longer tracks (data not shown). Thus, we suggest that the absence of any effect on tortuosity is a consequence of our paired analysis approach, with relatively small regions designated as close to or far from magnets, and that the slug's ability to navigate in straight lines was probably indeed differentially affected by magnets of different strengths, as shown by the |Δ angle| data. In addition, finer-grained spatial and temporal analyses of tracks, made feasible by higher-resolution cameras and automated tracking (augmented with machine learning), should be considered for future work (Geuther *et al.*, 2019; Bonneau *et al.*, 2020; Francisco *et al.*, 2020).

Our results suggest that *T. exsulans* may use the Earth's magnetic field for navigation differently from what has been suggested for many other animals. Rather than act as a compass to maintain consistent orientation toward a distant migratory target, the slugs could be using the magnetic field to maintain constant headings while crawling, with no particular preference for direction. The visual system in *T. exsulans* consists of five photoreceptors in two bilaterally symmetric eyes located beneath the skin (Chase, 1974a); thus, the slugs have little or no ability to use visual references to counteract heading deviations potentially induced by topography or buffeting by flow. Similarly, the other primary senses (chemosensation, rheosensation, mechanosensation) are not likely to provide reliable cues for maintaining a constant heading. Odors shift as the currents change, and substrates provide no straight lines for thigmotaxis; and there is no evidence, as yet, that *T. exsulans* follows mucus trails or odors embedded in the substrate (Schwarz *et al.*, 2016). Yet, from an energetic point of view, optimal navigation behavior will require some ability to move in straight lines so as to both avoid wasting energy following a longer path to a target and reach intermittently detected targets (Cheung *et al.*, 2007). Thus, it is possible that *T. exsulans*, and perhaps other effectively blind animals, exploit a magnetic sense solely to improve the efficiency of navigation involving other senses as the primary cue driving short-distance movement as well as long-distance movement. An analogous use of a different cue for navigation behavior would be the use of celestial cues by dung beetles to maintain straight lines as they move away from dung (Dacke *et al.*, 2019). Moreover, a related hypothesis has been proposed for how magnetic orientation

could benefit cockroaches (Vácha *et al.*, 2010), and other animals can also apparently learn and use magnetic fields to guide short-distance movement patterns (Vácha and Soukopová, 2004; Dommer *et al.*, 2008; Vácha *et al.*, 2008; Tomanova and Vacha, 2016; Malewski *et al.*, 2018a). Slugs could benefit from this maintenance of straight-line movement during upstream navigation toward attractive odor sources, downstream movement away from predators, and potentially cross-stream or downstream movements when searching for attractive odor plumes.

Another possibility for how the slugs might use the magnetic field could be to improve success rates during odor-based navigation toward attractive odor sources in variable flow (Wyeth, 2010; Vasey *et al.*, 2015). A magnetic sense could be used to maintain consistent orientation while moving toward an odor source that can no longer be detected due to a shift in flow direction. In this case, we might expect a clearer relationship between magnetic strength and differences in the $|\Delta \text{ angle}|$ metric as slugs approach magnets. This was not the case, because filtering the data to include only track segments recorded during periods of high flow variability did not change the patterns of our results. Thus, either the slugs are not using the magnetic orientation preferentially during variable flow or our measurements of movement or flow variability lacked the precision to detect such a pattern.

Two further alternatives could also explain the changes in movement patterns that we observed. Rather than disruption of a natural orientation system that relies on magnetic fields, the changes in behavior could be a direct response to the magnets, presumably based on their substantial perturbations in the Earth's magnetic field. Previous studies have shown that it is possible for animals to show apparently innate attraction or aversion to magnets (Ernst and Lohmann, 2018; Malewski *et al.*, 2018b), as well as exhibiting associative learning of magnetic stimuli, without any apparent link to magnetic orientation or navigation (*e.g.*, Malewski *et al.*, 2018b; Martini *et al.*, 2018). In our results, then, it could be that the slugs were responding directly to the magnetic perturbations with increased variation in their headings, without necessarily any use of magnetic fields during normal navigation farther from the magnets. A second possibility could be that the behavioral changes were a purely artifactual consequence of the movement of the slugs through the strong magnetic fields surrounding the magnets. Electromagnetic induction could act on electroreceptors (for which there is no evidence in *T. exsulans*) or directly on components of the nervous system, in such a way as to affect neural activity patterns and, thus, perturb the crawling patterns as the animals near the stronger magnets. Neither of these two alternative explanations for how the magnets could have affected the slug behaviors can be discounted with methods used in our study; thus, some caution should be exercised in attributing our results to an effect on a magnetic-based orientation system used during navigation by *T. exsulans.*

Further testing is clearly needed to fully establish the effects of magnetic fields on the movement *T. exsulans* and the role a magnetic sense may play in the species' navigation behavior. Rare-earth magnets provide a crude, spatially heterogeneous disruption of the Earth's magnetic field, impeding any precise predictions of behavioral effects or ability to distinguish effects on magnetically guided navigation *versus* direct responses to a magnetic perturbation. Thus, our methods were designed to capture a broad range of movement patterns at varying distances from a number of magnets. In addition, the exploratory design also precluded direct control of which individuals were recorded next to the different magnets, forcing us to use paired statistical tests without guaranteed independence between all pairs in the samples. Although our methods were unlikely to have introduced bias based on the individuals tested (*i.e.*, our methods effectively randomized the slugs measured in each treatment), we have no ability to test whether slug responses changed over the course of repeated exposures to the magnets. Taking these caveats with regard to magnetic manipulations and statistical analyses together, we suggest that our data serve primarily as a foundation for more precise hypotheses for future lab and field experiments with *T. exsulans*. In the lab, a three-coil system surrounding a flow tank could be used to create small incremental changes in Earth-strength fields to determine whether this could influence crawling directions toward attractive odor sources. In the field, higher-precision measurement of slug tracks (*via* video or perhaps acoustic tags) over distances of only 0.5 m could generate far greater detail on how slug movements change as they approach the strong magnets shown to have an effect here. At the same time, these measurements could be combined with high-resolution flow detection to both better document flow variability and control for the effects of flow on slug movements. Finally, subjecting slugs to these more precisely controlled manipulations and measurements could be matched with controlling which slugs receive the different treatments, thereby avoiding any risks of violated statistical assumptions during analyses.

Additional efforts are also needed to determine the underlying nervous system components that could continuously exert an influence on crawling headings. The nature and location of magnetoreceptive sensory neurons remain elusive in *T. exsulans* (Pavlova *et al.*, 2011). Our data provide no further insight into the issue, nor into which of the hypothesized mechanisms for magnetoreception might underlie magnetic responses in *T. exsulans* (Johnsen and Lohmann, 2005; Nordmann *et al.*, 2017). Moreover, although motor neurons known to be involved in locomotion can have their activity changed by magnetic manipulations (Wang *et al.*, 2003, 2004; Cain *et al.*, 2006), those changes occur with latencies between 2 and 10 minutes and in response to large step changes in Earth-strength magnetic field orientation. Yet the effects we observed involved changes in behavior in the 30-second intervals during which slugs were tracked, suggesting that a shorter time course for neural responses might be expected. The longer latency responses were recorded in neurons that have been hypothesized to control cilia on the surface of the foot (Willows *et al.*, 1997);

thus, they would not necessarily be involved in maintaining consistent headings while crawling. The cilia provide the propulsion for crawling, while current understanding suggests that turns are controlled by muscular contractions that create lateralized bending of the foot (Murray *et al.*, 1992; Redondo and Murray, 2005). Thus, magnetically induced heading corrections to maintain a constant heading might be expected to converge on the motor neurons involved in turning; future work could test whether those neurons have shorter latency responses to more subtle rotations of Earth-strength magnetic fields than do the ciliary motor neurons.

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Appendix

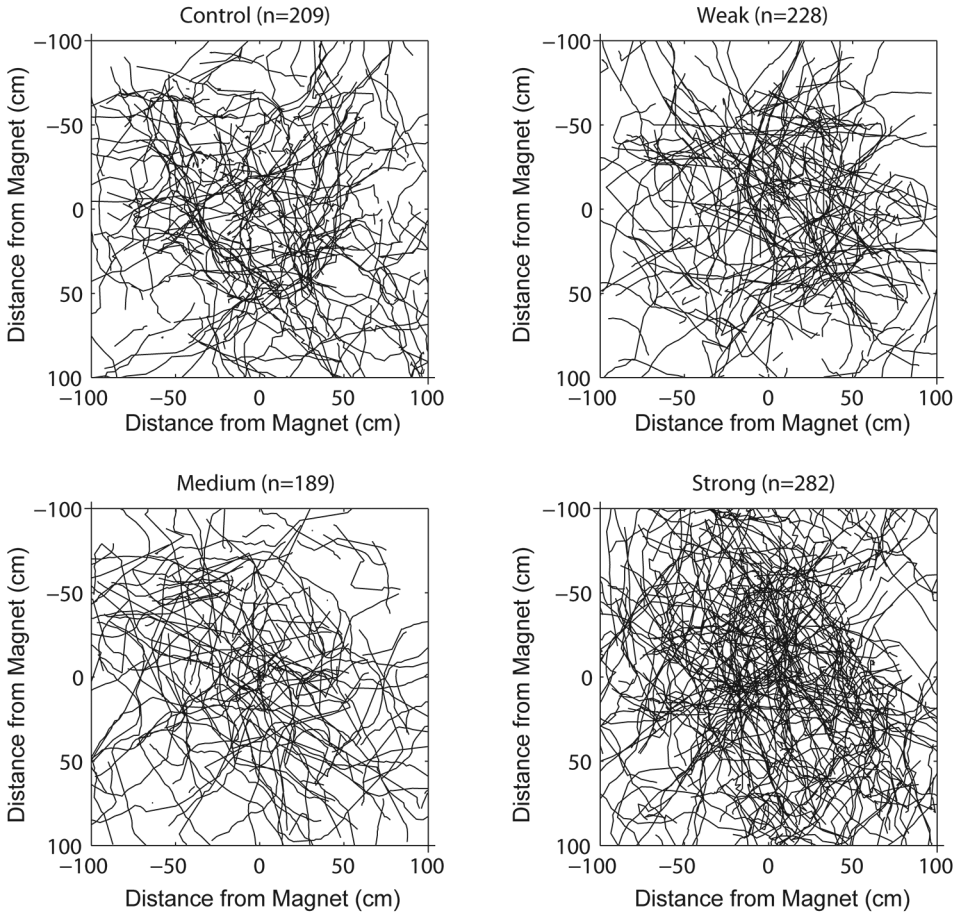

Figure A1. All tracks of *Tritonia exsulans* recorded within a 2-m square surrounding the 4 types of magnets. Tracks measured in all cameras and days relative to each magnet type are superimposed after affine transformation to a common location of the magnet (centered at the origin in each panel) and a common magnetic north heading (upward in each panel). Axes units are shown in centimeters.

Table A1

*Descriptive statistics (sample sizes [*n*], mean, and standard error of the mean [SEM]) for all six metrics for each magnet type (control, weak, medium, and strong)*

		Paired track segments only				
Magnet	Metric	*n*	Close mean	Close SEM	Far mean	Far SEM
Control	|Δ angle|	25	32.26	5.05	43.58	6.12
Control	*n* points	26	3.50	0.37	2.65	0.30
Control	Distance	26	21.39	2.23	31.30	2.04
Control	Displacement	26	14.42	1.83	20.10	1.54
Control	Velocity	31	0.16	0.01	0.17	0.01
Control	Tortuosity	25	1.70	0.16	1.64	0.09
Weak	|Δ angle|	27	14.56	1.53	16.99	1.61
Weak	*n* points	27	4.59	0.47	3.67	0.32
Weak	Distance	27	20.86	2.12	30.73	2.75
Weak	Displacement	27	17.11	1.86	23.12	2.11
Weak	Velocity	33	0.21	0.01	0.24	0.01
Weak	Tortuosity	26	1.29	0.05	1.40	0.08
Medium	|Δ angle|	19	24.92	3.03	15.83	1.73
Medium	*n* points	20	3.75	0.46	3.00	0.47
Medium	Distance	20	15.91	2.14	24.69	3.48
Medium	Displacement	20	11.92	1.87	18.90	3.01
Medium	Velocity	21	0.24	0.02	0.23	0.02
Medium	Tortuosity	19	1.69	0.27	1.38	0.07
Strong	|Δ angle|	46	42.48	5.97	23.06	2.29
Strong	*n* points	47	3.49	0.28	2.45	0.22
Strong	Distance	47	24.23	1.49	35.86	1.97
Strong	Displacement	47	16.64	1.31	21.26	1.40
Strong	Velocity	50	0.18	0.01	0.21	0.01
Strong	Tortuosity	44	1.85	0.20	1.78	0.10

Only tracks of *Tritonia exsulans* with segments both close to and far from magnets were used in the analysis, creating a paired data set of close and far segments. Here, the summary statistics are calculated separately for "Close" and "Far" segments. Note that these non-paired data were not used in the primary analysis. Instead, the primary analysis tested for significant differences between metrics calculated for the paired segments close to and far from each of the magnet types.