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Use of magnetic and olfactory cues for orientation by a fossorial rodent, *Thomomys talpoides*

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**USE OF MAGNETIC AND OLFACTORY CUES FOR
ORIENTATION BY A FOSSORIAL RODENT, *THOMOMYS
TALPOIDES***

A Thesis
Presented to
Eastern Washington University
Cheney, Washington

In Partial Fulfillment of the Requirements
For the Degree
Master of Science

By
Dustin J. Cousins
Winter 2013

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MASTER'S THESIS

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Abstract

Fossorial, or below ground, living provides shelter from the elements and some predators, but comes at a cost with respect to metabolic requirements of movement and reduced, or altered, sensory cues. I examined the ability of the North American pocket gopher, *Thomomys talpoides*, to use magnetoreception and olfaction in navigation and foraging. Magnetoreception was tested using three manipulative experiments: 1) field homing of displaced animals, 2) nest location in an 8-arm maze, and 3) movement through a complex labyrinth. Homing results, analyzed by V-test, indicated that the gophers displaced from their burrow systems relied on magnetic cues for homing orientation. Although Rayleigh analysis of the 8-arm maze tests showed limited significance, gophers tended to nest in the conditioned direction, and nesting direction shifted with an altered field. Repeated Measures ANOVA results of performance in time and number of wrong turns in the complex labyrinth showed no significant differences between conditioned trials (unaltered-field) and test (field rotated 90°) trials. Use of olfaction was tested in T-maze trials with soils containing carrot kairomone versus control soil. Binomial probability analysis revealed in all tests comparing carrot soil vs. control that gophers disproportionately selected the carrot soils. Overall my study suggests *T. talpoides* can use both magnetic and olfactory cues while navigating, but the use of these cues is situation dependent. These results are similar to those found in other South American and Old World fossorial rodents.

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Introduction

Fossorial mammals spend most of their lives underground in self-excavated burrow systems that generally consist of foraging tunnels and chambers for nesting, food storage, and defecation. Living in a burrow system provides safety from some predators and buffering from some environmental variations such as temperature extremes (Begall et al. 2007). However, there are large metabolic costs associated with underground movement. Depending on soil conditions, digging tunnels can require 360-3,400 times more energy than above-ground movement (Vleck 1979). The high metabolic costs, in conjunction with reduced gas diffusion through soil, can result in burrow atmospheres that are hypercapnic and hypoxic (Darden 1972; Kennerly 1964; McNab 1966; Shams et al. 2005).

This high cost of fossorial exploration places a premium on efficient navigation. Animal movements are mediated through navigation, which requires orientation using internal and external cues. Although the mechanisms of animal navigation are not fully understood, two methods are generally described. The first, idiothetic navigation, relies on internal signals mainly from the proprioceptive and vestibular systems to calculate in which direction and how far the animal has moved to create a reference frame. The second, allothetic navigation, uses external cues collected during movement to create a reference frame (Whishaw 1998; Whishaw and Brooks 1999). Although it is likely animals use multiple modalities while navigating (Gould 2004), observations and mathematical modeling of above-ground animal navigation indicate idiothetic navigation alone is unable to provide enough feedback to allow for productive movement (Cheung et al. 2007). One of the largest hindrances is likely an inability to perceive small rotational errors which compound over time. However, the constraints to free movement in a burrow system might reduce this problem. Although idiothetic and allothetic navigation differ in the types of signals used, they both require distinct sensory input to operate.

Fossorial animals face the restriction of some sensory cues used by many above-ground animals during navigation and foraging, such as data-rich visual cues. Due to the differences between soil and air, these mammals might also encounter differences in the transmission of sound and chemical cues. Given the metabolic costs of underground excavation, efficient orientation would likely be of selective advantage to a fossorial mammal. Excavation of burrow systems suggests that the plains pocket gopher *Geomys bursarius* (Geomyidae) digs foraging tunnels as predicted by an area-restricted model (ARM; Benedix 1993). Under this model, an animal moves in one direction until

encountering a food source. When it finds a food source, the animal increases the search effort in that area, as evidenced by a greater number of lateral tunnel segments found around food clusters. The use of this foraging method suggests the gophers are able to 1) orient in a straight line between food clusters, and 2) detect food sources from a distance. Two sensory modalities that are not negated underground are magnetoreception, the ability to sense magnetic fields, and olfaction. Captive studies of the fossorial Zambian Ansell's mole rat (*Fukomys anselli*, Bathyergidae; Wegner et al. 2006) and Middle East blind mole rat (*Spalax ehrenbergi*, Spalacidae; Kimchi et al. 2001) provide evidence that some fossorial mammals use magnetoreception. Even though magnetoreception has been demonstrated in many taxa, its physiology is not completely understood. It is known that the physiological mechanisms behind magnetoreception are varied, suggesting that it has evolved multiple times. To add complexity, some vertebrates utilize more than one magnetoreceptive system (Gould 2008).

Although magnetoreception could aid a fossorial mammal in orienting foraging tunnels, it would be of no use when a food source is nearby but not in its direct path. While an above ground mammal would typically use vision and olfaction to locate a food source, the former would be of little use to a fossorial mammal. Olfaction is a conservative trait in vertebrates, as made evident by its shared physiological basis. Heth et al. (2002) showed the use of olfactory cues from plants (kairomones) influenced digging direction in four species of fossorial mammals.

Despite the potential constraints of underground living, the fossorial niche has been invaded by representatives of four orders of mammals: Rodentia (rodents), Afrosoricida (golden moles), Notoryctemorphia (marsupial moles), and Soricomorpha (moles). Within the rodents, fossorial species are known from four families from different continents: Geomyidae (North America), Ctenomyidae (South America), Bathyergidae (Africa), and Spalacidae (Africa and Asia). Given the constraints of living underground, these fossorial mammals have converged on similar morphologies including a tubular profile (often tapering toward the tail end), reduced eyes and pinnae, large and often external incisors and/or large front claws used in digging, short or no tails, and the ability to close their nares (Nevo 1979). Magnetoreception has been examined in fossorial representatives of three rodent families (Begall et al. 2007; Burda et al. 1990; Kimchi et al. 2001; Schleich and Antinuchi 2004) and olfaction in three (Heth et al. 2002). Neither sensory modality has been examined in the North American Geomyidae. The objectives of this study were to examine the ability of northern pocket gophers to use magnetoreception and olfaction

in navigation and foraging. This information provides a basis to compare convergence within fossorial rodents with respect to use of sensory modalities.

Materials and Methods

A description of materials used and their construction is provided in Table 1.

Collection of gophers

Gophers were collected in three alfalfa fields in Spokane County, Washington using live-traps constructed in a method similar to Baker and Williams (1972; Table 1) during October-November 2010, September-October 2011, and March-April 2012. Traps were set after 06:00 hr and checked every 1-1.5 hr until they were closed before 20:00 hr. All methods were approved by the EWU IACUC board. Collection was conducted under Washington Department of Fish and Wildlife Scientific Collections Permit # 11-348.

Housing

Gophers were housed separately to prevent possible aggressive interactions (Andersen 1978). Cages were constructed from two plastic cylinders (45 cm diameter x 30 cm high), connected by an opaque tube 8 cm diameter and 15 cm long. This caging style provided living conditions that partially mimic the compartmental living style of gophers, nesting in one area and foraging/defecating in others (Devries and Sikes 2009). Cages had a long axis between foraging and nesting chambers which allowed gophers to be conditioned to move along a specific magnetic axis. Nesting chambers were darkened and had ≈ 4 cm corn cob bedding with a handful of straw for striping and nest making. Foraging chambers were filled with ≈ 6 cm dirt and were on a 12 hr light/dark cycle. Gophers were held in the EWU Biology Department basement vivarium maintained at $12.5^{\circ} \text{C} \pm 1^{\circ} \text{C}$, and fed 12-15 g alfalfa hay, apple, carrot, rat chow, and sweet potato daily. No free water was provided because gophers obtain all their required water from food (Devries and Sikes 2009). To prevent incisor overgrowth, gophers were provided with apple tree branches for gnawing. Though most gophers kept their claws at a manageable length, in some cases claws were trimmed to maintain mobility.

Homing Experiment

The homing experiment was designed to test the impact of an altered magnetic field on a displaced gopher's ability to home toward its burrow. Upon capture, an animal was placed in a transport tube and then into the solenoid (Figure 1). When activated the solenoid shifts the horizontal magnetic field 180° . During transport the solenoid was pointed toward geomagnetic south. One half of the animals were moved 55 m to the east, and half of these were placed under a reversed field. The other half was moved 55 m to the west, with half of those under an altered field. The above methods were based on those used by August et al. (1989). The cylindrical testing arena (95 cm diameter) was enclosed in a canvas tent with PVC frame to minimize possible learned visual cues. Next, the animal was placed in the start tube of the arena and allowed to acclimate for 2 min before release. Upon release from the start tube, the animal's movements were monitored and recorded from the recording station (Table 1). To remove any east-west bias, the recording station was positioned ≈ 6 m away towards magnetic north. Once a gopher had moved 12 cm from center its position point was recorded every 30 s for 15 min, providing 31 instantaneous points for each individual (Altmann 1974). The distance from center and polar angle for each data point were measured (ImageJ software, NIH). To remove scent cues, the arena was cleaned between trials using Quatricide, water, and 90% ethanol. Heavy-weight red rosin paper was used to line the arena and was changed between each run to act as a scent barrier and to aid in infrared filming. Data from 19 individuals were obtained.

Data analysis - The hypothesis for the homing test was: Under a normal magnetic field gophers would orient movement in the direction of their burrow, whereas under a field shifted 180° they would orient movement in the direction away from their burrow. To test this hypothesis, each individual's mean activity vector was calculated from their 31 points using first-order vector calculations. The vectors of the normal and reversed groups moved west to east were rotated 180° to allow for all normal groups and all reversed groups to be compared. The group sizes for the gophers moved under the normal and shifted field were 10 and 9, respectively. Because each individual's vector was created using multiple samples, the final analysis used second-order circular statistics (Childs and Buchler 1982). Individual mean vectors were analyzed to see if they were from a binomial normal population. Next, movement for each group was described and analyzed by creating Hotelling's standard and confidence ellipses. After samples were shown to have direction, the V test (Durand and Greenwood 1958) was used to determine

if the groups' movements tended to aggregate around the previously hypothesized direction. The V test was selected, over the commonly used Rayleigh test, because a specific homing direction was hypothesized prior to testing. Also the V test is more powerful when testing for randomness (Batschelet 1981). All statistical methods used are outlined in Batschelet (1981).

Food Cache Experiment

The food cache experiment was designed to assess the gopher's ability to respond to magnetic cues when placing a food cache. To condition the animals to a specific axis when caching food, their cages were designed with a long axis between the foraging and nesting chamber. Gophers were housed individually in these cages for at least 8 wk before testing. Fourteen cages were aligned with the long axis on the 102-282° magnetic axis, with the nesting chamber at the 282° end. Fourteen others were aligned with the long axis on the 012-192° magnetic axis, with the nesting chamber at the 012° end (Figure 2). Gophers were conditioned in the basement vivarium, and moved to the testing facility no longer than 10 min before testing. The testing facility was located on the ground level of the EWU Science Building. To test for a learned response a cylindrical arena was placed inside a coil system that allowed for control of the horizontal factor of the magnetic field (Table 1). The gopher was placed in the start tube of the arena, and the opaque top was placed on the arena. Light only entered through the top of the start tube in the center of the arena, leaving the outer portions darkened. Gophers were held in the start tube for 15 min before being released into the arena. After 15 min of acclimation time, four food items (apple, carrot, sweet potato, and rat chow) were placed in the center of the arena through the start tube. The gopher was given 30 min to cache the food items before it was removed from the arena. The arena was then photographed from above on its central axis. This process was repeated the following day with the magnetic field shifted 180°. Food was considered cached if food items were moved from center and grouped within a 20 cm diameter circle. The arena was lined with a heavy-weight rosin construction paper, changed between trials, to act as a secondary scent barrier. The above methods were developed using pilot trials with four non-experimental gophers. Test trials using the general population showed the majority of experimental gophers did not cluster food in a cache, as the non-experimental gophers had done, and the test was canceled.

8-Arm Maze Experiment

The 8-arm maze experiment was designed to assess the gopher's ability to respond to magnetic cues when making a nest and choosing a latrine. Gophers were conditioned for this experiment using the same methods as the food cache experiment except the conditioning time increased from 8 to 16 wk. Ten animals were caged with the long axis aligned on the 102-282° magnetic axis, with the nesting chamber at the 282° end. Twelve others were aligned along the 012-192° magnetic axis, with nesting chamber at the 012° end (Figure 2). Gophers were conditioned in the basement vivarium, and moved to the magnetoreception testing facility no more than 10 min before testing. The field around the maze was controlled by the coil system. The gophers were placed in the start tube of the central chamber along with their daily apple, carrot, sweet potato, and rodent chow. After 2 min of acclimation, the start tube was actuated. Each test ran for 11 hr. After removing the gopher, the food cache, metabolic waste, and nest locations were recorded. Each gopher was tested once under a normal field and once under a field shifted 90° east. The gopher's second trial was conducted 36 hr after its first. Half of each group was first tested under a normal field and the other half was first tested under an altered field. Individual testing was conducted in a randomized order.

Data analysis - The hypothesis for the 8-arm maze test was: Under a normal field gophers would nest in the direction to which they were conditioned, and chose a latrine site in the bearing opposite (180°) from the nest bearing. When tested under an altered field their nesting and latrine locations would shift with the field. To test this hypothesis, data were analyzed using the first-order vector analysis Rayleigh test, corrected for the grouping factor, as described by Batschelet (1981). The Rayleigh test averages the vectors of each sample to form a mean vector. The more the samples are clustered around a given direction the greater the magnitude of the mean vector.

Complex Labyrinth Experiment

The complex labyrinth experiment was designed to assess the impact of an altered magnetic field on navigational performance. Two weeks prior to testing, gophers were placed on a restricted diet that reduced their body mass to 80 - 85% of their free feeding mass to provide motivation during trials (Mora et al. 2009). The maze was set up in the coil system to allow for magnetic field manipulation. Trials were conducted under I.R. light only, and video recorded for later analysis. During conditioning the coil current was left anti-parallel so the magnetic field of the coil system was left in line with the

geomagnetic field. A food reward of apple and sweet potato, ≈ 0.5 g each, was placed in the goal box. For each trial, the gopher was placed in the start box and given 2 min to acclimate before the start block was lifted. Once the gopher entered the end box and found the food reward the stop block was lowered to prevent the gopher from returning to the maze. After each trial the goal box, with the gopher still in it, was moved to the start location, while the old start box was moved to become the new goal box (Figure 3). Each gopher ran 5 consecutive trials/day. The maze was cleaned between each gopher (Table 1). Conditioning was carried out for 3 consecutive days. On day four, gophers ran 7 consecutive trials. Gophers were split into two randomly stratified groups to prevent any turn bias from the previous conditioning for the 8-arm maze experiment. Group A ($n = 7$) gophers were tested in a magnetic field shifted 90° east on their 4th trial run, while group B ($n = 7$) had the field shifted on their 6th trial run. Time to completion and number of wrong turns were recorded for each trial. Time to completion was defined by the gopher completely leaving the start box and then touching the food reward at the end. A turn was defined by the gopher moving $\geq 50\%$ of its body around a corner, or if in a straight area of the maze, when it backtracked an entire body length.

Data analysis - The hypothesis for complex labyrinth test was: Gopher performance in the maze would increase, measured by a decline in time taken and number of wrong turns, when the magnetic field was altered from the conditioned direction. To test this hypothesis results were analyzed using a One-Way Repeated Measure ANOVA on test trials (all trials run on the last day).

Olfaction Experiment

The olfaction experiment was designed to assess the ability of gophers to distinguish between control soil (kairomone free) and soil collected from around growing plants. Soil had been excavated a year prior to its use, during which time it had no vegetative growth on it. All soil was autoclaved before being sifted through a 0.5 cm screen to remove larger rocks. The soil composition had a clay component that was too high for good plant growth. To compensate, soil was amended with a small amount of sterile sand. After the soil was homogenized it was loaded into 1.8 l planting pots. These pots were put on two separate, but adjacent, growing tables. One table was planted with carrots (*Daucus carota sativus*) to create soil saturated with kairomones, while the other was left unplanted for control soil. Both tables were under the same grow light and had the same watering regimen. A week after sprouting, the pots were thinned to 5 plants/pot. Carrots were allowed to grow for 3 mo prior to using the soil. After removing carrots, the soil was

again sifted through a 0.5 cm screen to remove the majority of the root matter. Control dirt was also sifted, using a separate screen. Soil for each test was prepped within hours of use. Kairomone soil was mixed with control soil to create three different strengths; 100%, 50%, and 25%. Presence/absence experiments of 100%, 50%, and 25% vs. control, had sample sizes of 15, 16, and 15 respectively, while the gradient experiment, 100% vs. 50%, had a sample size of 18.

Olfaction testing used a transparent tubular T-maze with a 7 cm inside diameter. The runway was 40 cm long and each crossbar, A and B, was 20 cm. Since gophers close their nares when actively digging, the runway of the maze was left clear of dirt. This allowed the gophers to reach the decision point with open nares and provided a chance to sniff each choice prior to digging. Each crossbar was filled with 15 cm of soil, leaving 5 cm of space at the end of each arm. While filling each arm, a long plug was placed in the runway to prevent the soil types from mixing. Whether crossbar A or B was filled with control or kairomone soil was random. Trials were conducted under IR light only, and recorded for later analysis. After each trail, mazes were cleaned with unscented soap (Seventh Generation™), rinsed with water, cleaned with Quatricide, rinsed with water, rinsed with 90% ethanol, and allowed to dry.

Data analysis - The hypothesis for these olfaction experiments was: Gophers would disproportionately select the soil which had the greater kairomone soil concentration. Results for these tests were analyzed using binomial distributions. The binomial probabilities were calculated using VassarStats (VassarStats Software).

Results

Homing Results

Gopher movements were described using the 31 instantaneous positions collected from each video. Initially, gophers ($n = 19$) tended to move to the outer wall of the arena and walk along the perimeter, but then returned to the center before moving outward again. Using these instantaneous position points to represent a location in which they spent a given amount of effort, I observed that the gophers under normal magnetic field moved towards their burrows and those under altered fields moved in the opposite direction. Results of the Hotelling's confidence ellipse test show the axis origin (0, 0) is not located inside the confidence ellipse, indicating each group moved with directionality

(Figure 4C and D). The standard ellipse is used as a descriptive statistic and shows the amount of variability of the second-order sample (Figure 4A and B). Hotelling's confidence ellipse is used to describe the area in which the unknown population center is likely to be located (Batschelet 1981). The ellipse tests show oriented movement and give a general idea of direction. Analysis of the mean vector points using the V test provides statistical support that gophers oriented in the hypothesized directions (normal: $V = 0.168$, $p < 0.05$; reversed: $V = 0.254$, $p < 0.01$).

Food cache

The food cache experiment was originally planned to have a sample size of 20, but was canceled after 14 individuals were tested, only 7 of which created a cache within the predetermined requirements (all food items deposited within 20 cm of each other).

8-arm maze

Most nest placements were in the hypothesized quadrant, but generally spread within the quadrant. This led to nest site selection vectors which were generally directed toward the hypothesized bearing, but the Rayleigh results for each group failed to show significance in directionality of site selection (Figure 5; Table 2). However, when the groups were pooled, by rotating Group B's values 90° counter-clockwise, the Rayleigh test did show significance in nest selection when the coil field was in line with the geomagnetic field, but not in a field shifted 90°. The confidence interval for the pooled nesting vector also includes the predicted nesting direction of 12° (Figure 6). The graphs for latrine site selection show the vectors are not oriented in the hypothesized direction, but do appear to shift with the field.

Complex Labyrinth

Successful conditioning was shown by the decrease in the mean time to maze completion from > 400 to < 200 s and the mean number of incorrect turns from > 30 to ≈ 10 and a decrease in variance during the initial 15 trials (Figures 7A and 8A). The "plateau" in performance observed over the trials indicate that gophers had reached a relatively constant level of performance (Figures 7A and 8A). A Repeated Measures ANOVA, using the "plateau" trials, that compared the normal field to shifted trials showed no significant difference between or within groups for both time and number of wrong turns (Figures 7B and 9B; Table 3).

Olfaction testing

Pocket gophers selected the kairomone soils three times more often than the control soils (Figure 9A), indicating that kairomone presence affects directional selection of digging. However, there was no difference in the selection frequency between soils with 50% versus 100% kairomone soil (Figure 9B), suggesting that gophers could not discriminate between relatively high levels of kairomones.

Discussion

The magnetic experiments suggest that *T. talpoides* perceives magnetic fields, but its use in navigation is dependent upon the situation. The olfaction experiments indicate *T. talpoides* is able to detect cues from growing plants and use these cues in determining digging direction.

The open arena used in the homing experiment had less structure and provided fewer proprioceptive, vestibular, and tactile cues than the other tests and supports the hypothesis that gophers sense and use magnetoreception when navigating. The free movement afforded in the open field homing test best represents navigation above ground. Though gophers are usually described as spending most of their time below ground, they do move above ground under certain circumstances including dispersal, occasional above ground foraging, or when finding a mate in areas with low population levels or where soil conditions might restrict burrowing directly into their system, such as a mima mound habitat (Verts and Carraway 1999).

Although results of the 8-arm radial maze do not significantly support the use of magnetoreception while navigating underground, the group nesting and latrine vectors did point in the hypothesized direction and appeared to shift with the field change. In addition, the near 90° shift in the hypothesized direction suggests chamber selection was not completely random. Deutschlander et al. (2003) observed a similar problem in a nesting experiment which was explained with a likely cue conflict found between the trial and holding room, but no obvious cue conflicts were found in my study. The possibility of a lingering noise variable may exist as these trials were conducted in the EWU Science Building. The trials were stratified to try and equalize temporal effects on both groups, but it is possible that variability between daily activities produced auditory and seismic cues which were not equal between the groups. The discrepancy seen between the

hypothesized and observed latrine selection vectors is likely explained by the size of the conditioning nesting chambers. These chambers were relatively large, and it was observed that while gophers would occasionally use the dirt chamber as a latrine, it was more common for gophers to select a portion of their nesting chamber as a latrine. While these results do not allow rejection of the null hypothesis, they do tempt further testing.

The complex labyrinth test was used to present a more tunnel-like environment. However, no support for the use of magnetoreception was observed. These results suggest in this type of situation gophers do not use magnetoreception for orientation and might instead rely on spatial cues, proprioceptive cues, and motor response behavior. Aside from new tunnel creation, movement is largely determined by existing tunnels which may allow for idiothetic navigation to be used more accurately by removing the small rotational errors that compound in above-ground movement. It should also be noted that this experiment did not test for the use of magnetoreception while actively burrowing underground.

Support for the use of magnetoreception in other fossorial rodents is variable. Evidence supports the use of magnetoreception while navigating a complex labyrinth in the Old World fossorial *S. ehrenbergi* (Spalacidae; Kimchi et al. 2001). Of the Old World Bathyergidae, *F. anselli* has shown evidence of magnetoreception use in arena nesting experiments (Burda et al. 1990; Marhold et al. 1997; Wegner et al. 2006). Conversely, two Ctenomyidae New World species, *C. talarum* and *S. cyanus*, have not shown evidence of using magnetoreception when tested (Begall et al. 2007; Schleich and Antinuchi 2004). My study provides evidence supporting the use of magnetoreception when navigating in *T. talpoides*.

However, this study also indicates the northern pocket gopher will rely on cue types other than magnetic when available. This preference has been observed in other animals. For example, Mather and Baker (1981) conducted a homing experiment using the wood mouse, *Apodemus sylvaticus*, and found it will use visual cues over magnetic cues when homing. Kimchi et al. (2004) showed that the Middle East blind mole rat, *Spalax ehrenbergi*, will use idiothetic navigation for short distance trips with relatively low rotation, and fall back on magnetic cues when the trip increases in length and rotation. This indicates the animals were utilizing both idiothetic and allothetic navigation—likely mapping both cue types independently. These results raise the question of why idiothetic navigation is used when magnetic cues are present. Kimchi et al. (2004) suggest idiothetic cues may be less costly to gather and process. There could be

another explanation based on the instability of the magnetic field. Presently the Earth's magnetic field is relatively stable. However, geologic and solar influences do create both cyclic and random fluctuations which could possibly impact an organism's ability to use magnetic cues accurately. The magnetic field also changes with more long-term effects such as polar reversals. During these shifts the geomagnetic field becomes quite distorted with many more anomalies (Glatzmaier and Roberts 1995). Though these reversals occur on a geologic timescale, over the last 10 million years there have been over 30 reversals of the Earth's magnetic field (Berggren et al. 1995; Cande and Kent 1992) which may have had an impact on the evolution of magnetoreception and its low position in the cue hierarchy observed in some animals. This variability might account for the preference of other sensory cues over magnetic cues. For example, migrating birds will use sun and celestial cues over magnetic cues in many situations (Wiltschko and Wiltschko 1996)

The food cache experiment was modeled after tests conducted on *Phodopus sungorus* and *Fukomys spp.* (Burda et al. 1990; Deutschlander et al. 2003; Wegner et al. 2006). This test was not carried out to completion due to equipment failure and design flaws. The cylindrical arena had two seams in the wall that provided enough purchase that a gopher could begin to gnaw. During trials with the non-experimental animals, this behavior generally did not start until the animal was in the arena for about 1 hr. The gopher would also start tearing the lining paper around the same time. It was for these reasons the test was run for 45 min. Originally this was meant to be a nesting test, but when the restrictions of the equipment were realized, I decided a food cache experiment might be a viable alternative since the gophers would usually create a food cache in a shorter time period. Though the few gophers used in the trial runs generally cached their food items within 45 min, when the general population was tested, very few trials ended in the creation of a successful cache. This variation in behavior might be attributed to the trial gophers having been in captivity for over a year, while the testing gophers had been in captivity for only a few months. This serves as an example of how the behavioral testing environment must satisfy the animal's needs, and proper motivation must be supplied so the target behavior can be observed (Mora et al. 2009). If this test were to be run again, the arena should be seamless and composed of a material that is more resistant to scent absorption as scent was a difficult problem to deal with during the trials. Various cleaning methods were attempted that included wiping the arena with Quatricide, Dawn detergent, bleach, and ethanol (90%). The most effective method of blocking scent was to first clean the arena with a water rinse, then Quatricide, another water rinse, and an ethanol wipe; then line it with heavy weight rosin paper. It should be noted that the paper

only worked as a scent barrier if the trial was run within a couple hours of its application. If scents were able to be easily neutralized, and gnawable surfaces eliminated, the test could be conducted over a longer period, preferably 12 hrs, during which time the gophers would likely form a cache or nest. These data could then be analyzed using methods described in Batschelet (1982) and compared to other studies.

The olfaction trials suggest *T. talpoides* can detect the presence of plant kairomones in the soil and use olfaction when selecting a digging direction. Results for the kairomone vs. control tests are comparable to those found by Heth et al. (2002) for *S. ehrenbergi*. The lack of selection preference in gradient trial might suggest that gophers are not able to follow a gradient. However, the kairomone levels in these trials might have simply been too great and essentially overloaded the olfactory receptors. Conditions for transmitting odor were also optimized due to the high moisture content of the soil needed to pack it into the T-maze, and so it might be assumed that the cue level was about as high as it would be when in close proximity to a growing plant at which point the gopher might already be encountering rooting structure. Similar to this study, Heth et al. (2002) also conducted gradient trials and found that when presented with two relatively high levels of kairomone, no significance could be found in soil selection, but when the kairomone levels were reduced *S. ehrenbergi* preferentially selected soil with higher kairomone levels. This supports the suggestion that the soil used in my experiment had a large kairomone concentration compared to more natural settings.

Gophers commonly use an ARM while foraging (Benedix 1993), but cues used to determine branching direction within the system are unknown. Gopher might uses olfaction not only to guide it in the proper direction, but after reaching some olfactory threshold they might start increasing the burrow's fractal dimension, and thereby increase its likelihood of encountering a food source (Le Comber et al. 2006). To further investigate if gophers use gradients when foraging, gradient trials which test lower proportions of kairomones should be conducted. Also distance trials, similar to Lange et al. (2005), which use various forms of soil could be used to understand the situational use of olfaction. It would also be useful to incorporate an arena burrowing test utilizing varying levels of kairomone to analyze its effects on burrow fractal dimension. This might be accomplished using uniform burrowing chambers and watering them with water collected from hydroponically grown plants. Although olfaction plays a role in the subterranean foraging of the northern pocket gopher, it might not be the sole modality used in foraging. As in most navigation, an organism likely obtains cues from various

sensory modalities, and it is the cumulative input from these multiple modalities and higher order central nervous system processing that determines the motor output underlying behavior. For example, from observations and modeling it has also been suggested that the fossorial rodent *S. ehrenbergi* uses self-generated low frequency seismic waves to detect and effectively bypass underground obstacles (Kimche and Terkel 2003; Kimchi et al. 2005). *S. ehrenbergi* has also been shown to use olfaction while selecting burrow direction when foraging (Heth et al. 2002). It might be possible that kairomone cues guide a rodent close to a rooting mass, and the animal may then use somatosensory cues or “seismic echolocation” cues to gain the final location of the food item.

Combined with the morphological convergences seen across the fossorial mammals (Nevo 1979), my results allow comparisons to be made in the sensory ecology of magnetoreception and olfaction between *T. talpoides* and other fossorial rodents. Although Suprafamilial phylogeny within the rodent taxa is debated (Wilson and Reeder 2005), the relative distances in relations that I compare are usually agreed upon (Blanga-Kanfi et al. 2009; Montgelard et al. 2008; Fabre et al. 2012) and I focus on taxa that would be found at a roughly similar taxonomic level. Rodent species that I consider here are *Ctenomys talarum* and *Spalacopus cyanus* (Ctenomyidae, South America), *Cryptomys kafuensis* (Bathyerigidae, Africa) *F. anselli* (previously *Cryptomys hottentotus* of the Bathyerigidae, Africa), *Spalax ehrenbergi* (Spalacidae, Africa and Asia), and *T. talpoides* (Geomyidae, North America). Though split between Old and New World, the Ctenomyidae and Bathyerigidae are grouped as the Caviomorpha. A similar split is seen in the Neotominae and Spalacidae taxa which are grouped as the Myomorpha. The split that formed the Geomyidae taxa is found between these two groupings (Figure 10). Similar to the Old World fossorial rodents that have been studied (Burda et al. 1990; Kimchi et al. 2001; Wegner et al. 2006), *T. talpoides* of North America has the ability to perceive magnetic fields. In contrast, this ability has not been observed in South American fossorial rodents (Begall et al. 2007; Schleich and Antinuchi 2004). This apparent lack of convergence could be due to evolutionary differences or simply differences in situational use of magnetoreception. Olfaction is a conservative trait in vertebrates, therefore it is not surprising that the use of olfaction in directed digging has been observed all Old and New World fossorial rodents tested to date (Heth et al. 2002; Lang et al. 2005; Schleigh and Zenuto 2007).

Overall my study suggests *T. talpoides* uses both magnetic and olfactory cues while orienting, but use of these cues is dependent upon the situation. This situational use of cues suggests some hierarchy in cue processing. In addition to testing other sensory modalities, further research should investigate cue hierarchies and how sensory inputs are selectively integrated in fossorial rodents.

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Tables

Table 1. Materials used to collect gophers and conduct tests described above.

	Collection
Traps	<ul style="list-style-type: none"> • Traps used were similar to those described by Baker and Williams (1972) • The trap body was constructed from poly vinyl chloride electrical conduit pipe 45cm in length with an inside diameter of 6.1cm • The back of the trap was wired off to prevent gophers from escaping, while allowing airflow and light to penetrate • A Vector® rattrap was modified to allow a wire trigger to extend down into the tube to which it was attached • The trap was connected to the tube using two hex bolts • A door latch, 7cm, was attached to the front top of the tube so it could swing down • A wire was attached to the action bar, passed through the 45° hole to the inside of the tube, and attached to the free end of the door latch • To maintain pressure on the latch after the trap was triggered, the length of the wire was adjusted so when the door was fully closed the action bar was stopped 30-35° before reaching the trap base
	Homing Experiment
Solenoid	<ul style="list-style-type: none"> • Constructed of 10.16cm diameter section of PVC, 75cm in length and the back was capped • The middle 52cm section was wrapped 100 times with 20 gauge insulated copper wire • Wire connected to two 150Ω resistors in parallel then a 9v battery • Four sections of 1.27cm diameter PVC pipe attached to inner floor of solenoid to prop transport tube to center • Transport tube was a 5.08cm diameter PVC pipe with soled front cap and perforated rear cap
Cylindrical arena	

	<ul style="list-style-type: none"> • Cylindrical arena, 95cm in diameter with 25cm walls, was constructed of black Sentra® poly vinyl chloride • A pulley actuated poly vinyl chloride start tube, 10.16cm diameter 30cm long, was centered in the arena • Two lids, one of Plexiglas, one of black Sentra® poly vinyl chloride, were constructed with a hole for the start tube • The arena was also lined between each trial run with a heavy weight rosin paper
Recording equipment	<ul style="list-style-type: none"> • The web cam was connected to a laptop at the recording station using a USB extension cable of ≈ 6m • The web cam was modified to record Infrared light by removing the Infrared filter • An I.R. light source was constructed to run as a 9V system, and so could be powered with a 9V battery in the field, or a stable power source in lab
	Food Cache Experiment
Caging/husbandry	<ul style="list-style-type: none"> • The cages had two main chambers, 45cm x 30cm cylinder, connected by an opaque 15cm tube
Cylindrical arena	See Homing Experiment above
Coil system	<p>The coil system was composed of two perpendicular double-wrapped coils. Each coil was square 4 coil systems similar to the one described by Merritt (1983). This uses the magnetic field produced by current flowing through a wire to change the direction of the magnetic field inside the coil system. With two coils arranged horizontal and perpendicular to each other the horizontal component of the magnetic field could be manipulated leaving only the vertical component (inclination) which could not be altered. Each coil was double wrapped to allow current to be run parallel or anti-parallel. When run in parallel the field created by the two wires added together to create an alteration in the direction of the total field.</p>

	<p>When current was run anti-parallel the field created by the two wires effectively canceled each other, leaving the normal geomagnetic field. By running the normal conditions while the current was anti-parallel other variables are held constant, such as heat production and unfiltered radiofrequencies. Each coil was powered by an independent direct current power supply. The field in the coil was measured between each trial using a magnetometer (Applied Physics Systems, Model 539 high speed digital 3 axis fluxgate magnetometer), and adjusted if needed. Black plastic was draped from the ceiling down around the edge of the coil system to remove any variation in external visual stimuli. It also allowed for light control in the testing chamber to differ from the rest of the room. A single halogen light, IR light, and webcam were fixed 120cm above the center of the coil to provide lighting/recording when required.</p>
Recording Equipment	See Homing Experiment above
	8-Arm Maze Experiment
8-Arm Maze	<ul style="list-style-type: none"> • The central chamber of the maze was a 45cm x 30cm plastic cylinder with an open top • Maze arms were composed of a poly vinyl chloride tube, 20cm long, plastic nesting chamber 10cm x 15cm • The central chamber floor was covered with \approx 4cm corn cob bedding, and straw was uniformly spread over it • A poly vinyl chloride start tube, actuated by a pulley system, was set up in the center of this chamber • While nesting chambers were transparent, they were darkened using cardboard covers during trials
Coil System	See Food Cache Experiment above
Recording Equipment	See Homing Experiment above

	Complex Labyrinth Experiment
Complex Labyrinth Maze	<ul style="list-style-type: none"> • The support structure of this maze was constructed out of plywood • The walls were covered with black Sentra® poly vinyl chloride, while the floors were with white • The runways were 6.4cm wide, and 10.1cm tall • The maze was covered with and opaque acrylic • The start and end boxes were lined with heavy-weight red rosin paper to aid in scent suppression and filming • They were also covered with red tinted acrylic, to reduce stress of gophers when start and end boxes were switched between trials. This reduced the amount of direct handling and likely reduced anxiety levels of the animals • The maze was composed of removable parts, to allow for movement in and out of the coil to be cleaned • Between trials the maze was scrubbed with soapy water, Quatricide, rinsed with water, and wiped down with 90% ethanol
Coil System	See Food Cache Experiment above
Recording Equipment	See Homing Experiment above

Table 2. Rayleigh values for nest and latrine vectors of conditioned pocket gophers in an 8-arm radial maze under normal and altered fields. Significance is highlighted in grey.

	Normal Field				Altered Field			
	Nest		Latrine		Nest		Latrine	
	r value	p value	r value	p value	r value	p value	r value	p value
Group A (n = 10)	0.495	p >.079	0.199	p >.681	0.079	p >.900	0.251	p >.520
Group B (n = 12)	0.323	p >.255	0.113	p >.847	0.242	p >.454	0.317	p >.299
Pooled (n = 22)	0.400	p <.035	0.097	p >.806	0.165	p >.495	0.276	p >.179

Table 3. Time and turn performance of pocket gophers in a complex maze.

		F	p value
Time Performance	Between groups	0.23 (1, 6)	0.64
	Within groups	0.69 (6, 72)	0.57
	Within groups*trial	1.45 (6, 72)	0.24
Turn Performance	Between groups	0.86 (1, 6)	0.37
	Within groups	0.92 (6, 72)	0.46
	Within groups*trial	1.80 (6, 72)	0.14

Figures

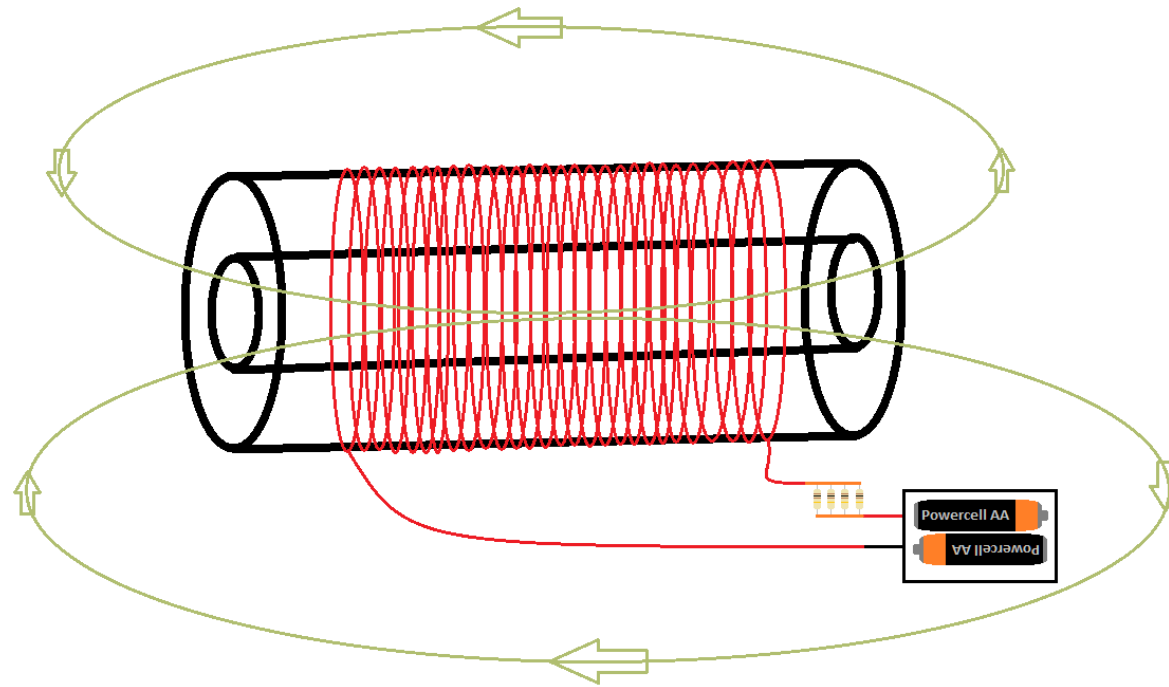


Figure 1. Diagram of the solenoid used to manipulate the magnetic field during transport in the homing experiment. The field was produced by allowing a controlled current to flow through the copper wire that was wound (≈ 2 wraps/cm) around the solenoid tube. The transport tube is located within the solenoid.

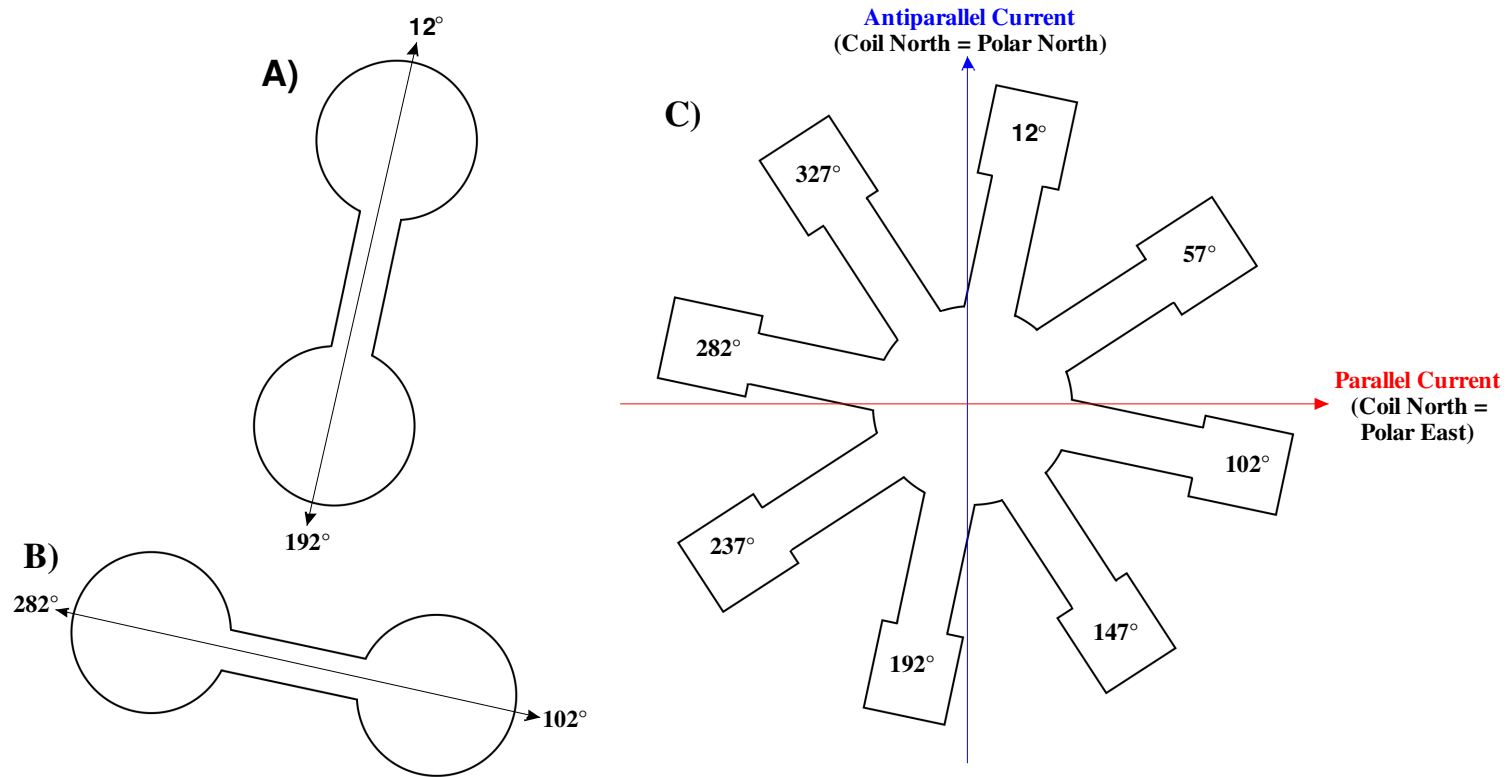


Figure 2. A) and B) diagram the caging and alignment used to condition gophers for the food cache and 8-arm radial maze experiments. C) Diagrams the 8-arm radial maze. The blue line indicates the direction of the magnetic field inside the coil is in-line with the earth's magnetic field when the current is antiparallel. The red line indicates the direction of the magnetic field inside the coil is shifted 90° , with respect to the Earth's, when the current is in parallel.

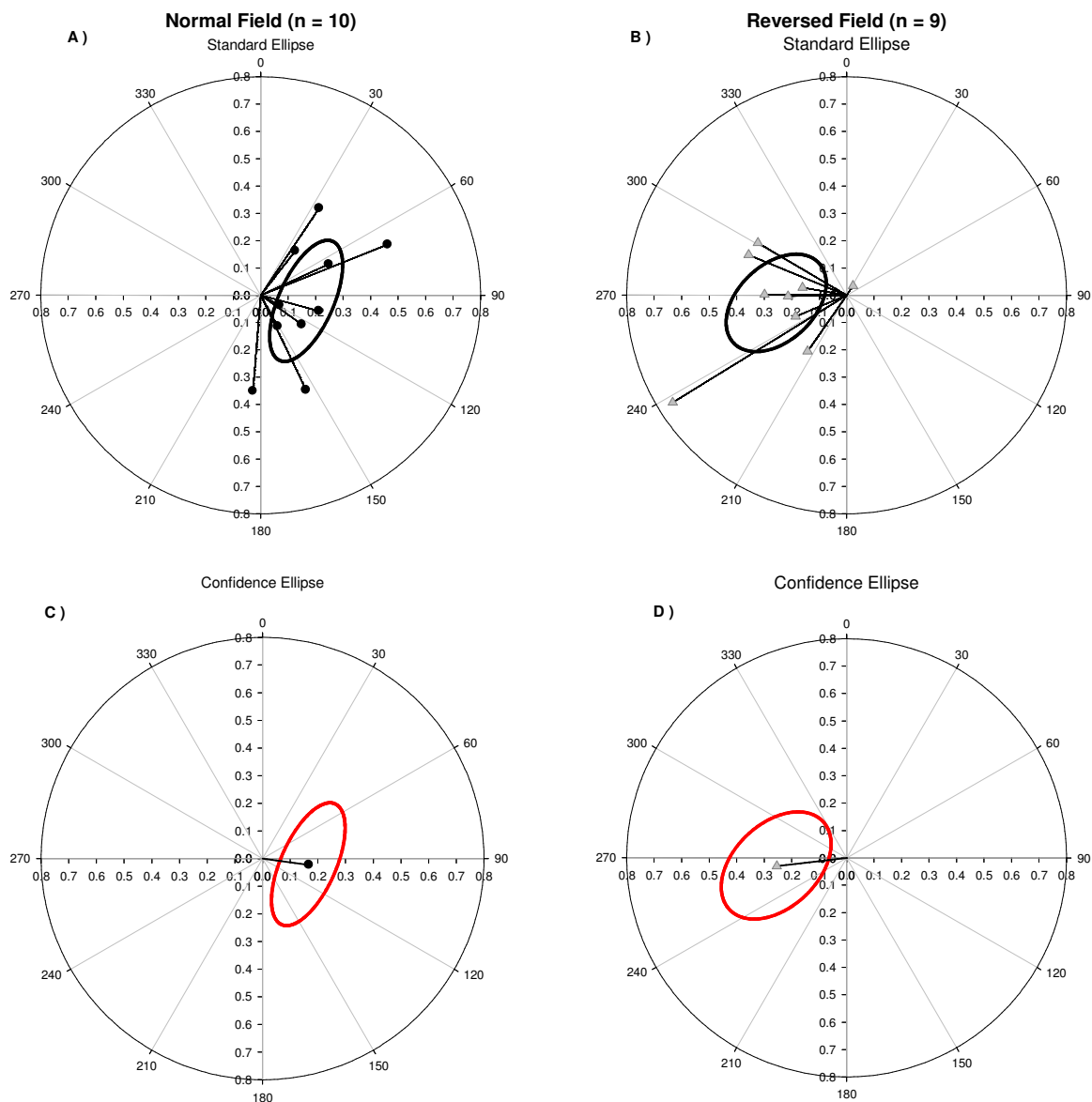
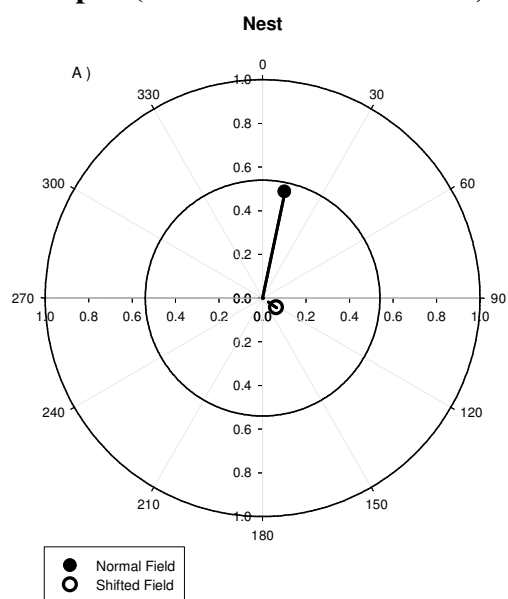


Figure 4. Magnetic orientation of displaced pocket gophers in an open field arena. Graphs A and B show the homing mean vector points of individual animals and their standard ellipses for the normal and reversed fields respectively. Graphs C and D show the homing mean vector and confidence ellipse for the normal and reversed fields respectively. The actual home direction is at 90°. All ellipses constructed at $\alpha = 0.05$.

Group A (conditioned axis 12-192°)



Group B (conditioned axis 102-282°)

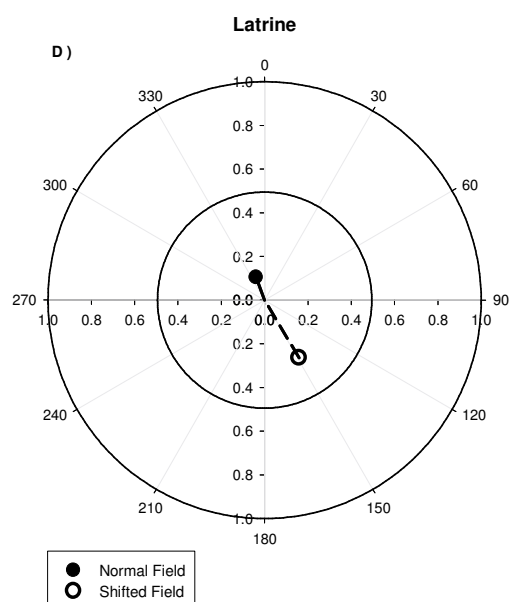
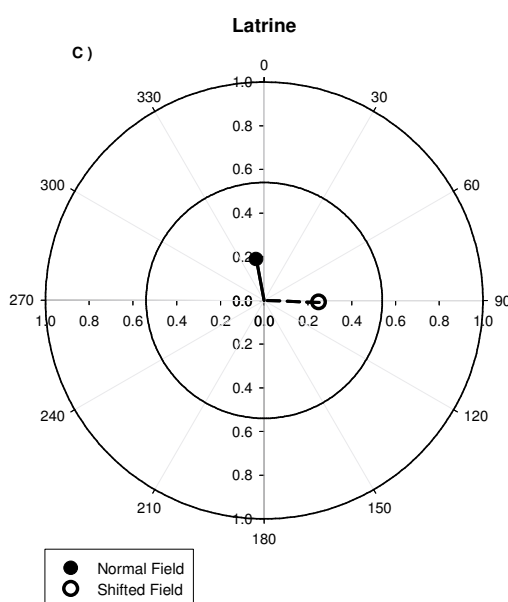
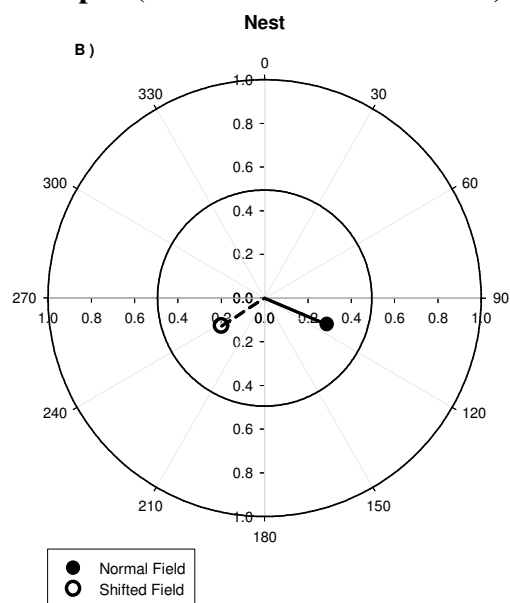


Figure 5. Nesting orientation of conditioned pocket gopher groups in an 8-arm radial maze. Group A ($n = 10$) was conditioned to nest toward 12° in the 8-arm maze. Group B ($n = 12$) was conditioned to nest toward 102° in the 8-arm maze. Individuals in each group were tested twice, once under a normal field and once under a field shifted 90° clockwise. The solid black inner circle marks the boundary a vector must reach to obtain significance when $\alpha = 0.05$.

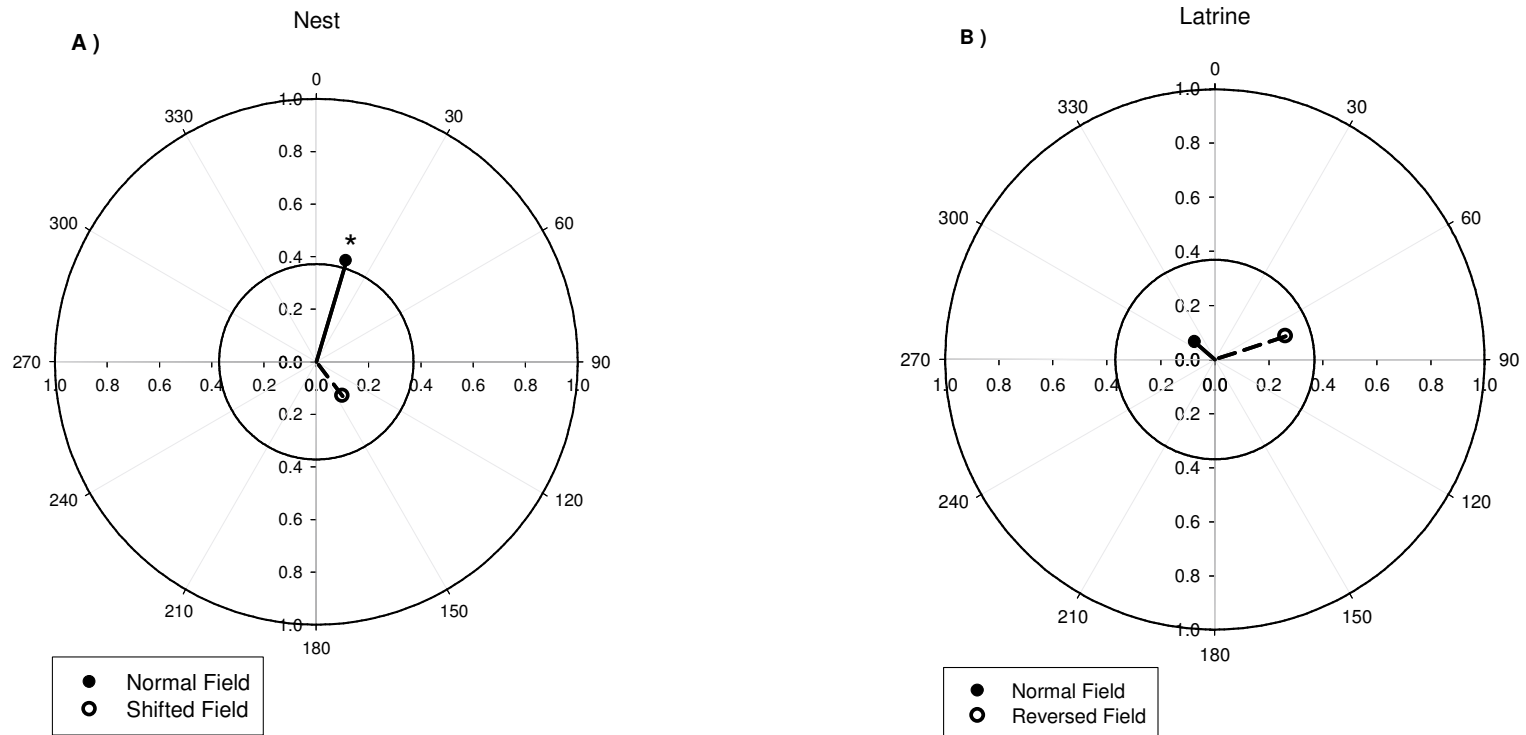


Figure 6. Pooled nesting orientation of conditioned pocket gophers in an 8-arm radial maze. Vectors from group B were standardized to 90° and averaged with group A. Individuals ($n = 22$) were tested twice, once under a normal field and once under a field rotated 90° clockwise. The solid black inner circle marks the boundary a vector must reach to obtain significance when $\alpha = 0.05$. Significance is indicated by an *.

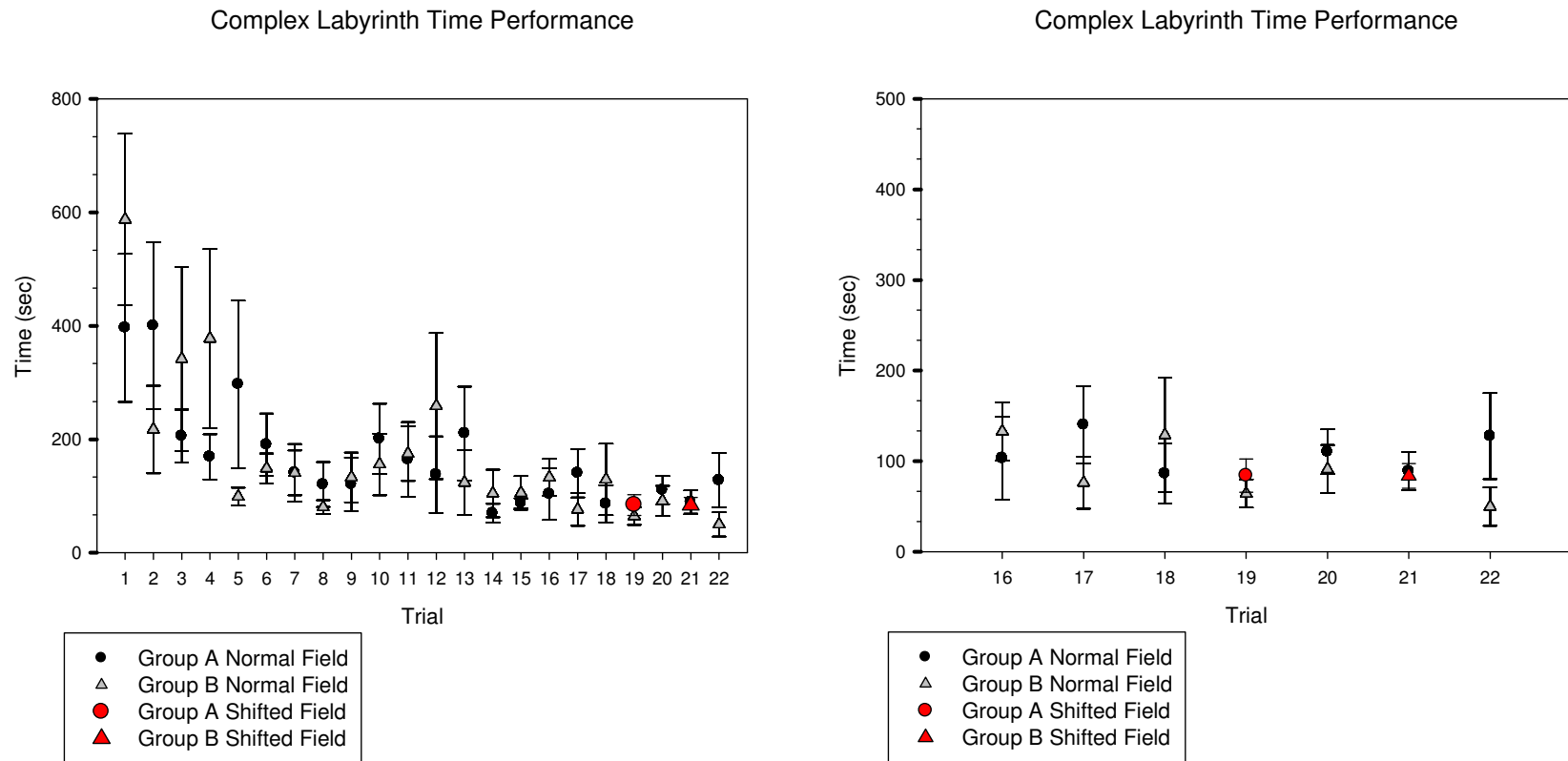
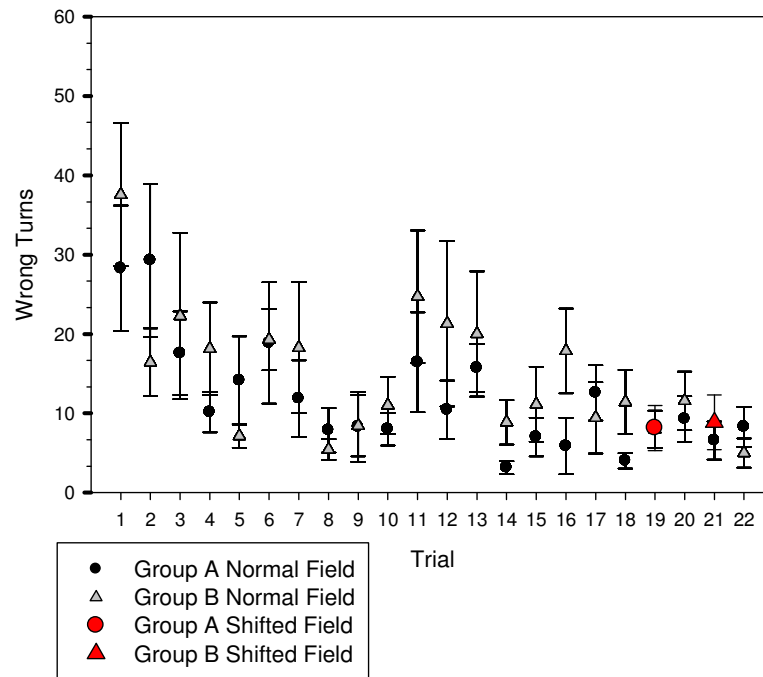


Figure 7. Mean time and standard error for each group over conditioning and testing trials. Graph A shows both the conditioning period trials (1-15) conducted over a three day period, and the testing trials (16-22) conducted on the fourth day. Graph B expands the testing trials. The field was shifted for Group A ($n = 7$) on the 19th and Group B ($n = 7$) on the 21st trial.

A) Complex Labyrinth Turn Performance



B) Complex Labyrinth Turn Performance

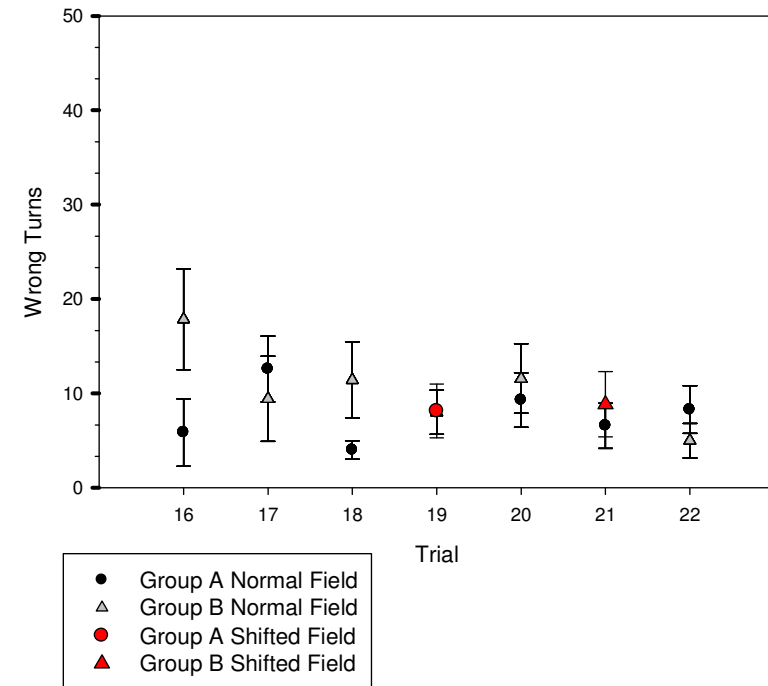


Figure 8. Mean number of wrong turns and standard error for each group over conditioning and testing trials. The conditioning period trials (1-15) occurred over three days, and the testing trials (16-22) occurred on the fourth day. The field was shifted for Group A ($n = 7$) on the 19th and Group B ($n = 7$) on the 21st trial.

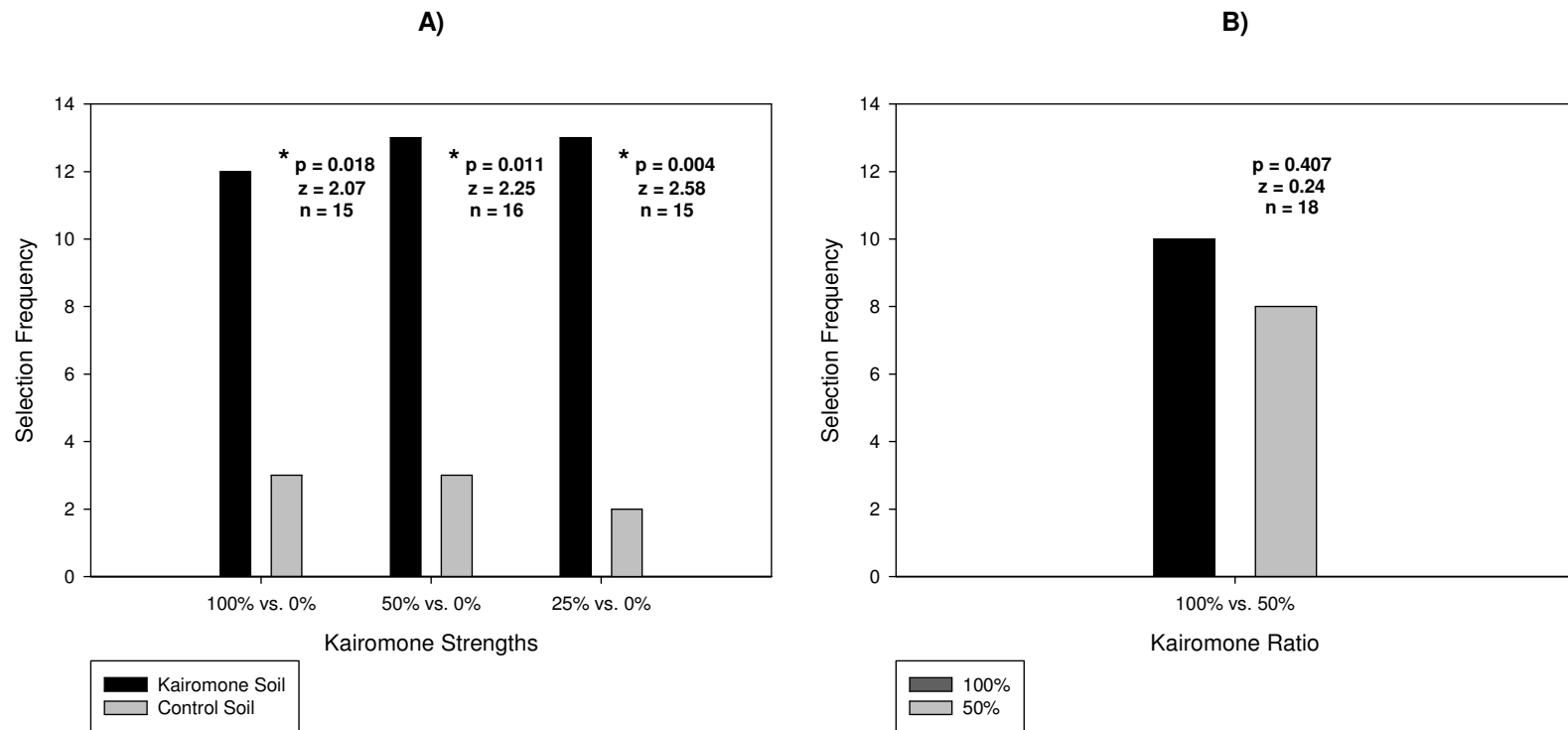


Figure 9. Soil selections of a foraging pocket gopher in a T-maze. Graph A) compares selection frequency of control versus three levels of kairomone soils. Graph B) compares selection frequency of two levels of kairomone soils. Significance is indicated by *.

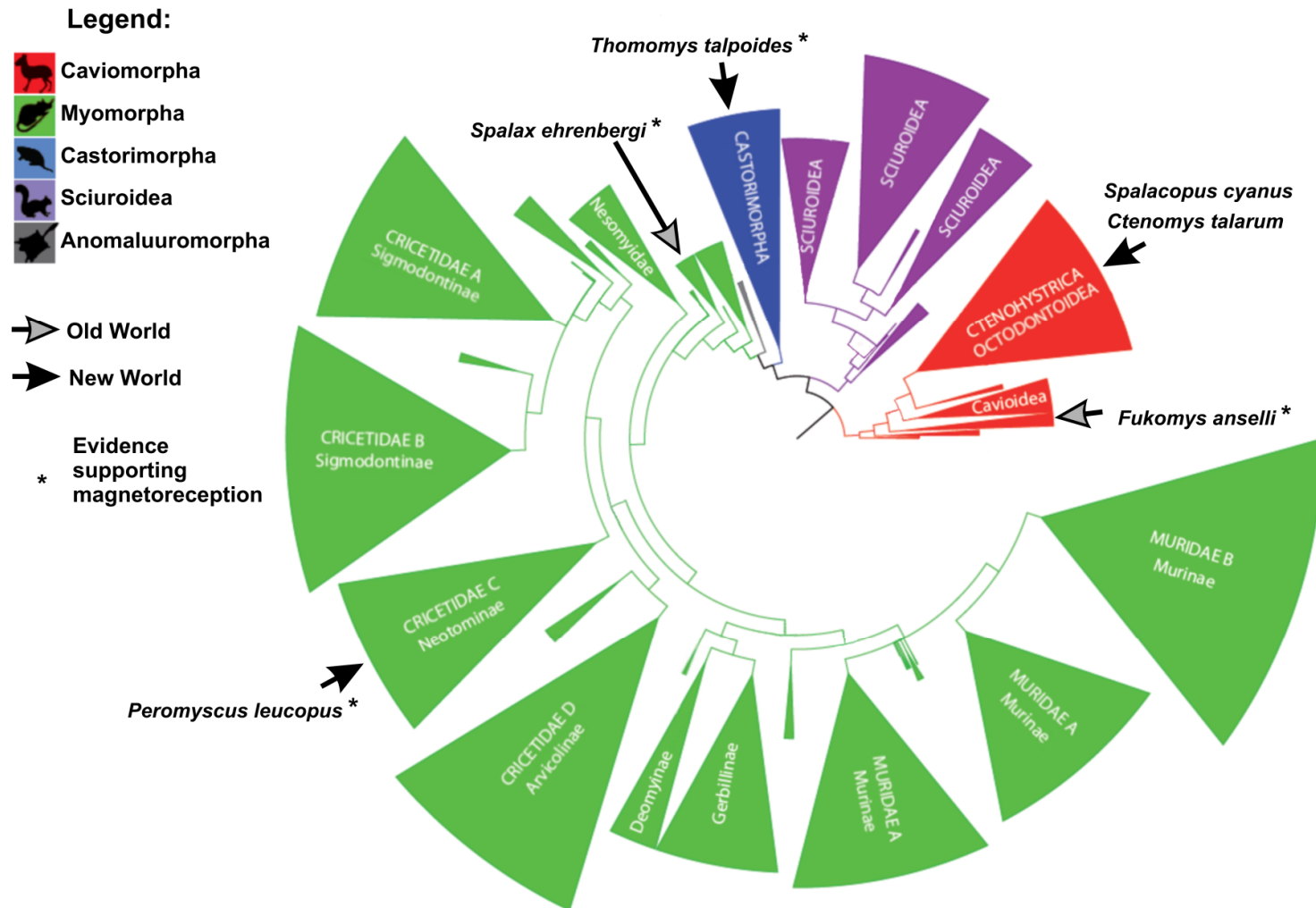


Figure 10. The phylogenetic relationship of the fossorial rodents discussed in this paper. The * indicates if previous studies have supported their ability to sense magnetoreception. This figure was modified from Fabre et al. (2012) to show specific relationships.

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