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Experimental approaches comparing the magnetoreception capabilities of two sister storage mite species *Tyrophagus putrescentiae* (Schrank) and *Tyrophagus longior* (Gervais) (Acari: Acaridae)

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Key Words: *Tyrophagus*, Mites, Magnetoreception, Orientation, Alignment, Compass

Contents

Abstract

Animal magnetoreception is a biological mystery that has maintained its intrigue and complication from the very first study. Evidence from the literature suggests that various species of birds, mammals, reptiles, invertebrates and fish have been able to detect and utilise magnetic fields to gain directional information to navigate their respective environments. Regarding the literature focussing on animal magnetoreception, it is evident that the class Arachnida has been considerably overlooked. Acariformes are some of the most diverse organisms within Arachnida, however their magnetoreception capabilities have not yet been investigated. This study focusses on two specific species of storage mites *Tyrophagus putrescentiae* and *Tyrophagus longior*, both of which can be pests found in anthropogenic habitats. These two species were selected as they are sister species and of the two of them, only *Tyrophagus putrescentiae* possesses eyes. The mites were put through several experiments which were slightly altered each time using trial and error to perfect the experimental design each time. The mites were introduced to petri dishes atop a dyed filter paper base dipped in a whole wheat flour solution to keep the mites interested in remaining within the experimental arena. These arenas were placed in a blackened box with an artificial light to ensure that the light was as homogenous as possible (see Figure 1). The mites were allowed approximately 24 hours to move around freely within the petri dishes before they were dispatched using a freezer. These mites were individually counted in their directional groups using a microscope and fine paint brush so that there could be no miscounts. The data that was yielded was analysed using the Rayleigh *z* test for uniformity from 10 observations per species (n = 10). Results suggest that *Tyrophagus longior* is capable of orientating using the Earth's magnetic field as they predominantly gravitate towards the South-South West compass points ($p = 0.02$). However, results gathered from *Tyrophagus putrescentiae* suggest that their directional behaviour is predominantly uniform, suggesting randomness and an inability to follow the Earth's magnetic field ($p = 0.414$). These results indicate that *T. longior* relies on magnetoreception to compensate for its inability to visually perceive its environment to maintain sporadic colony structure. *T. putrescentiae* on the other hand, may still use visual cues to sense larger or more desirable items of food, whilst still being able to maintain a compact, unpredictable colonial structure. This study indicates that these mite species can be used as cheap and effective model species in future magnetoreception studies involving

invertebrates. The mechanism(s) that this species uses to sense these magnetic fields, however, is still unknown and yet unstudied.

Figure 1: Photograph taken using a digital camera of the blackened cardboard box atop the illuminated drawing table (within a Helmholtz Coil) used during experiment 2.4.

Introduction

Animal magnetoreception is a phenomenon that has fascinated biologists and zoologists for many years, instigating debates and a plethora of scientific articles as a result. Both field and experimental studies have suggested that species across many different genera possess the ability to sense and orientate with the Earth's magnetic field (Johnsen & Lohmann, 2008). Many of the studies which focus on magnetoreception focus on avian species. This is mostly due to the vast interest in the impressive navigational capabilities of many migratory birds. Evidence suggests that many migratory birds are capable of true navigation, meaning that they are able to orientate themselves in a particular direction so that they can reach their nesting or feeding grounds, primarily using a 'map and compass' (Kramer, 1961, p. 341-369). The 'map' aspect is the animal's ability to judge their own position in relation to a specific goal, whereas the 'compass' aspect describes the course setting in order to reach that goal (Walker, *et al*. 2002). Studies carried out on European starlings (*Sturnus vulgaris*) provided evidence for true navigation by translocating adult and juvenile birds from the Netherlands for release in three different areas of Switzerland to observe whether they were still capable of orienting themselves in the direction of their wintering grounds (Perdeck, 1958). Juveniles were found to be incapable of realignment and appeared to travel in the original compass direction that they were moving towards before they were captured, whereas the adult birds showed the ability to realign themselves in the direction of their wintering grounds without learning any landmarks or routes (Perdeck, 1958). This study also indicates the importance of life history in an animal's magnetoreception and orientation capabilities. In 1972 European robins (*Erithacus rubecula*) were extensively studied in both laboratory and field conditions to determine whether they possess a magnetic compass to reach their intended goal. It was suggested that this particular species does not use a polarity based magnetic compass but utilises the smallest angle between the magnetic field lines and gravity vector on the magnetic north-south axis to distinguish the northern direction (Wiltschko & Wiltschko, 1972). In 2005, Mouritsen & Ritz highlighted the importance of magnetic fields in bird navigation. Birds are capable of effectively using magnetic field lines as a reference point to function as a magnetic compass (Mouritsen & Ritz, 2005). Birds are also capable of using fluctuations in magnetic intensity as proverbial signposts which allows them to memorise a specific area that they need to navigate like a magnetic map (Mouritsen & Ritz, 2005).

In mammals, red foxes (*Vulpes vulpes*) have been suggested to utilise magnetic alignment to their advantage during hunting behaviour (Červený, *et al*. 2011). Foxes hunt small rodents underneath snow and thick vegetation using an aerial attack by jumping high into the air to surprise their prey, meaning that each attempt must be calculated perfectly. Findings suggested that the foxes had a significantly greater prey attainment success rate when they approached their attack from a northern position, thus it was discovered that most attacks were approached from approximately within the north-eastern compass direction (Červený, *et al*. 2011). Other mammals such as bats, have been shown to exhibit behavioural changes in response to magnetic manipulations, such as having their homing directional path skewed by an artificial manipulations to the magnetic field both clockwise and anticlockwise, as well as hanging at the opposite end of their roosting basket when the horizontal component of the magnetic field is altered (Holland, *et al*. 2006; Wang, *et al*. 2007). Cattle and deer have also been the topic of some debate over the last decade, as it has been suggested that they orientate themselves with the magnetic north when resting and grazing (Begall, *et al*. 2008). Also, in 2009 a study conducted by Burda, *et al*. suggested that extremely low-frequency magnetic fields deriving from high-voltage power lines disturbed the cattle's ability to align themselves with the magnetic North-South axis, suggesting that a magnetic sense is present. These studies were then contested in 2011 by Hert, *et al*. who suggested that cows did not orientate themselves across the North-South axis based on 232 images of individual herds taken from Google Images. Then, two years later in 2013, Slaby, *et al*. produced a study which suggested that cattle are capable of aligning themselves along the magnetic North-South axis, however it is dependent on the mutual proximity between individuals.

In amphibians, magnetoreception has been studied in several different species. Early studies suggest that red-bellied newts (*Taricha rivularis*) are capable of relocating to their home ranges after significant displacement (Twitty, *et al*. 1964; Twitty, *et al*. 1966; Twitty, *et al*. 1967). In 1977, Phillips carried out an experiment on cave salamanders (*Eurycea lucifuga*) during which individuals were trained to associate magnetic field strengths with specific compartments of the experimental arena. One group of salamanders was trained to associate the Earth's magnetic field with one compartment whereas the second group was trained to associate a manipulated magnetic field with another compartment. It was concluded that salamanders were able to distinguish between the respective magnetic intensities and entered the correct compartments when released from the same central position in the experimental arena (Phillips, 1977).

Currently, there are two respective mechanisms which have been suggested to be responsible for animals' magnetic sensitivity. Early publications focussed on a newly discovered species of magnetotactic bacteria which possess iron-based magnetoreceptors comprised of chains of crystal-like particles, described as magnetotactic cells (Blakemore, 1975). Honeybees (*Apis mellifera*) have been suggested to possess superparamagnetic iron oxide crystals within the anterior end of their abdomen which could potentially be responsible for the magnetoreception capabilities in both the larvae and adult bees (Gould, *et al*. 1978). Another article published by in 1980 focussed on the demagnetisation of honeybees to determine whether the iron based magnetoreceptor is the mechanism which is responsible for the bees' capabilities of sensing magnetic fields (Gould, *et al*. 1980*)*. This study, however, yielded results showing that bees were unaffected by the demagnetisation, meaning that honeybees utilise different domains to detect magnetic fields, or they use an entirely different and unrelated mechanism for magnetoreception. A potential iron-based magnetoreceptor was also suggested in higher animals in 2003 by Fleissner, *et al*. It was suggested that superparamagnetic magnetite crystalline clusters (Fe_3O_4) are housed within a trigeminal nerve terminal occurring along the cell membrane in the upper beak of homing pigeons (*Columba livia*) (Fleissner, *et al*. 2003). Another study which was again carried out within the Fleissner laboratory in 2007, suggested similarly that iron-based structures predominantly comprised of maghemite (90%) as well as a small part magnetite (10%) could be the mechanisms which serve as magnetoreceptors in *Columba livia* (Fleissner, *et al*. 2007). These results remained relatively uncontested until 2012 when the Keays laboratory produced results suggesting that the iron-rich particles which were found within the upper beak and trigeminal nerve of pigeons were in fact macrophages (Treiber, *et al*. 2012). These macrophages are mobile and pursue and consume foreign bodies and pathogens such as bacteria within respiratory mucosa, the spleen and dermis of many species (Treiber, *et al*.

2012). As well as being vital for host defence, these macrophages are also imperative for the process of iron homeostasis, during which they accumulate iron which is then stored as ferritin during the process of the breaking down of haemoglobin (Wang & Pantopoulos, 2011; Mebius & Kraal, 2005). It is suggested that within the class of macrophages known as siderophages, ferritin builds up within the membrane-bound siderophages during a biological process known as proteolytic processing (Simson & Spicer, 1972; Meguro, *et al*. 2005). These ferritin build ups were highlighted using Prussian blue stain (PB). Analysing results yielded from several different methods, it was suggested by Treiber, *et al* that 95% of the PB positive cells observed within the upper beak of the pigeon were in fact macrophages as opposed to magnetosensitive neurons. In 2012, Eder, *et al*. suggested that they had isolated iron molecules within the olfactory epithelial tissue of rainbow trout (*Oncorhynchus mykiss*) and had been successful in highlighting these particles as being capable of rapidly sensing and spinning in tandem with a relatively weak external magnetic field. These particles were perceived to be single-domain magnetite crystals which should in theory meet the criteria necessary for magnetoreception (Eder, *et al*. 2012). This study was heavily contested in a 2014 study by Edelman, *et al*. which highlighted that a large proportion of the iron crystals which were observed within the epithelial tissue was contamination. This contamination was suggested to have been partly derived from reagents which are commercially available and widely used within laboratories such as sodium chloride ($NaCl$), potassium chloride (KCl), calcium chloride ($CaCl_2$) and magnesium chloride ($MgCl_2$) (Edelman, *et al*. 2014). The other suggestion was that there is always uncontrollable omnipresent iron particles and dust present in the air, often appearing as a biproduct of equipment and other objects which are ever-present within laboratories (Edelman, *et al*. 2014). This article, therefore made it evidently clear that a method for classifying iron-rich particles located within the animal body is both complicated and essential for any future studies.

Despite the lack of evidence of a magnetosensory substrate or cell within the animal body, there is still evidence to support the presence of an iron-based magnetoreceptor within passerine birds. In 2010, Holland performed a study in which passerine birds were treated with strong magnetic pulses in order to re-magnetise iron minerals within the purported magnetosensory system contained within the beak. This treatment resulted in the birds migrating in a different direction to the control birds when they were both treated in natural conditions (Holland, 2010).

The second hypothesised molecular magnetoreceptors are known as cryptochromes, which are blue light photoreceptor flavoproteins that control light-influenced processes in both plants and animals (Cashmore, *et* al. 1999; Lin & Shalitin, 2003; Li & Yang, 2007; Ozturk, *et al*. 2011; Foley & Emery, 2019). It is widely accepted that in many organisms the presence of a radical-pair system within the cryptochrome is (partly) responsible for their magnetic alignment capabilities (Schulten, *et al*. 1978; Ritz, *et al*. 2000; Ritz, *et al*. 2004; Wang & Ritz, 2006; Rodgers & Hore, 2009; Mouritsen & Hore, 2012; Wiltschko & Wiltschko, 2014). Several studies have been carried out on birds whereby the animals' migratory direction was tested under specific light intensities, colours and wavelengths, resulting in disorientation (Muheim, *et al*. 2002; Wiltschko & Wiltschko, 2002; Wiltschko, *et al*. 2008). Furthermore, it is also generally accepted that birds use both known mechanisms for magnetoreception; the radical-pair mechanism's function is to sense the direction of the magnetic field, whereas the magnetite-based mechanism's function is to perceive the intensity of the magnetic field (Wiltschko & Wiltschko, 2006; Wiltschko & Wiltschko, 2019). *Drosophila melanogaster* is a widely utilised and renowned model species for a vast array of biological fields including magnetoreception. It has been suggested that *Drosophila* requires the use of the ultraviolet A-/blue light photoreceptor cryptochrome in order to sense magnetic fields (Gegear, *et al*. 2008). This was illustrated using manipulation by blocking the cryptochrome-sensitive ultraviolet A-/blue light photoreceptor cryptochrome component of the spectrum, ultimately resulting in the flies' incapability of orientating with the artificial magnetic field (Gegear, *et al*. 2008). Despite these novel findings, the experiment that was carried out by Gegear, *et al* in 2008 was not designed to fully consider directional behaviour as the flies were only provided with a binary choice of direction meaning that the compass points that could be explored were limited to only two. This means that the results gathered could not be successfully related to orientation nor with navigation. Cryptochromes have been reported to be capable of exhibiting the necessary photochemistry to be able to react to magnetic fields (Maeda, *et al*. 2012). Despite this, however this serves only as prerequisite information, as there is no evidence to suggest that animals are capable of utilising these proteins to navigate (Maeda, *et al*. 2012).

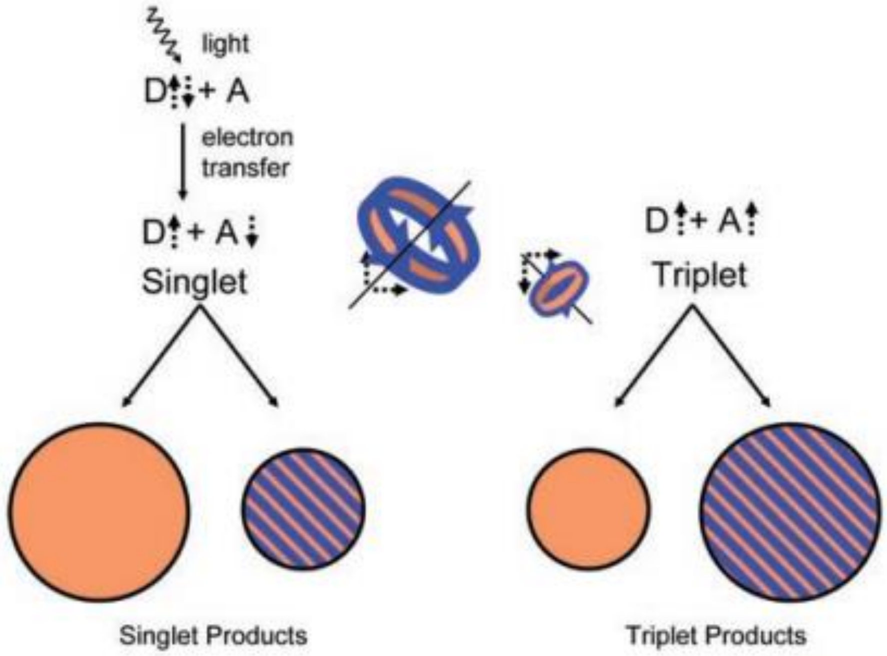


Figure 2: Diagram showing the theorised cryptochrome magnetosensory mechanism. Light initiates an electron transfer which produces a donor acceptor pair (D + A). These pairs spin independently and are active within surrounding magnetic fields which changes their relative orientation. These orientations are known as singlet or triplet states. These determine what products can be formed and how frequently. Weak magnetic fields represented by the small, blue, circular arrow can differentially affect the motion of acceptor and donor molecules (Ritz, et al., 2010, p. 25).

Invertebrates have been extensively studied for their magnetoreception capabilities. Bees have often been the focal species for magnetoreception studies due to their high mobility rate, the relative ease of accessibility, biological importance and apparent possession of biogenic magnetite crystals (Gould, *et al*. 1978; Gould, *et al*. 1980). Bees, however, are not the only species of the order Hymenoptera that have been suggested to possess biogenic magnetic nanoparticles within their body. *Pachycondyla marginata* is a species of migratory ant which commonly predates on the termite species *Neocapritermes opacus* (Hölldobler, *et al*. 1996). This species has been suggested to use magnetoreception based on the presence of the iron oxides, magnetite and maghemite within the abdomen, the thorax and the head (Acosta-Avalos, *et al*. 1999). Lepidopterans are another relatively well-studied order of insects regarding studies on magnetoreception. The large yellow underwing moth (*Noctua pronuba*) is a migratory species with a wide distribution covering a large proportion of the Earth's continents. This particular species has been suggested to use celestial cues for orientation and navigation. Tethered individuals were observed to be able to orientate in light winds despite wind direction and were suggested to have been utilising the moon’s azimuth to direct themselves (Sotthibandhu & Baker, 1979). Furthermore, individuals flying on starry nights when the moon was invisible, exhibited orientation behaviour that indicated that they utilised stars located approximately 95° away from the pole star (Sotthibandhu & Baker, 1979). Another study on *Noctua pronuba* indicated that individuals were still capable of orientation when placed within an orientation cage with no celestial cues, however the magnetic field was reversed which caused the moths to adapt to the altered magnetic field, suggesting that they possess at least one magnetosensory mechanism (Baker & Mather, 1982). Another aerial hexapod that has been studied extensively within laboratory conditions is the fruit fly (*Drosophila melanogaster*). Evidence suggests that *Drosophila* exhibit behaviours that are consistent with a light-dependant magnetoreception mechanism, as male individuals are able to align themselves with an ambient horizontal magnetic field when trained under 365nm light and were also capable of aligning themselves with the magnetic field under 500nm light, although they exhibited a 90˚ clockwise directional shift (Phillips & Sayeed, 1993). In Florida, an experiment carried out on western Atlantic spiny lobsters (*Panulirus argus*) involved the introduction of individual lobsters to a magnetic coil which were then exposed to three distinct treatments; the reversal of the vertical magnetic field lines, the reversal of the horizontal field lines, and no change in the magnetic field at all (Lohmann, *et al*. 1995). Results showed that these lobsters only exhibited a change in their orientation behaviour when the horizontal field lines were altered, suggesting that the mechanism which this species possesses is based on the polarity of the magnetic field as opposed to the field inclination (Lohmann, *et al*. 1995). In 2003, another study found that spiny lobsters also possess a magnetic map sense which allows individuals to return to a specific capture site despite the lobsters being displaced by approximately 37km and being influenced by magnetic fields that imitate fields found at specific locations within their habitat (Boles & Lohmann, 2003). This study confirmed that *P. argus* could be classified as the only (extant) invertebrate to be known to possess a magnetic map and compass simultaneously (Boles & Lohmann, 2003). Termites are highly abundant hexapods that can be observed all over the world building complex tunnels and impressive mounds. *Trinervitermes geminatus* is a species of grass harvester termite common in Nigeria and across Western Africa which is reported to be capable of distinguishing between the outward and homeward directions of their residence by using the surrounding magnetic fields even when the local magnetic field has been substituted for an artificial, weak permanent field (Ohiagu, 1979; Rickli & Leuthold, 1988). To back this up, in 1998, Maher produced a pilot study reporting that two species of termites possess biogenic iron particles within their abdomen and thorax, with small traces also being observed within the head, suggesting that other related species may also possess this material (Maher, 1998).

Chelicerata is a large subphylum of arthropods which envelopes Arachnida, Xiphosura, Pycnogonida and two extinct classes Eurypterida and Chasmatapspidida (Dunlop, 2010). There appears to be a significant gap in the literature regarding magnetoreception in arachnids. Orb-weaving spiders construct radial webs which they utilise for residence and capturing fast-moving prey (Lin, *et al*. 1995). This web building behaviour is repeated many times in the lifetime of a spider due to the prevalence of high-quality construction sites (Chmiel, *et al*. 2000). Based on the fact that the structure of an orb-web spider's web is relatively predictable and almost identical each time, it could be hypothesised that spiders are influenced by a magnetic force or celestial cues to enable them to replicate the same patterns and structures consistently each time. Sedentary spiders from the genera *Atypus* (purseweb spiders) and *Eresus* (ladybird spiders) among other species, live their entire lives almost exclusively within burrows constructed in high quality soil (Řezáč, *et al*. 2018). It could potentially be hypothesised that these spiders use magnetoreception-based learning to remember where burrows and high-quality soil is located. Both red-bellied newts (*Taricha rivularis*) and cave salamanders (*Eurycea lucifuga*) have also been suggested to be capable of this (Twitty, *et al*. 1964; Twitty, *et al*. 1966; Twitty, *et al*. 1967; Phillips, 1977). Despite these theories however, thus far, no studies have been carried out to provide any evidence to support them.

Due to the current scarcity of studies and literature surrounding arachnid magnetoreception, it is important to determine whether any potentially magnetosensitive species exist within the arachnid class and whether they can be used as model species in future studies. Within Arachnida along with spiders, scorpions and harvestmen, lies the subclass Acari (mites and ticks). Despite the diversity and specialisation of the respective species belonging to Acari, there is a significant gap in the literature where magnetoreception appears to have been overlooked. From the human perspective, mites are almost omnipresent. Examples of such mite species which dwell within anthropogenic habitats include the house dust mites (*Dermatophagoides*) which are regular inhabitants of homes and vacuum cleaners and possess potentially harmful antigens, causing breathing problems and worsening the effects of asthma in humans (Miyamoto, *et al*. 1968; Wharton, 1976). Other species include ubiquitous, symbiotic and otherwise parasitic *Demodex* mites (*brevis* and *folliculorum*) which inhabit the hair and skin follicles of almost all living humans and are regarded as being potential contributors to the development of the skin condition rosacea due to pathogen transport and mechanical follicle obstruction (Bonnar, *et al*. 1993). Storage mites (*Lepidoglyphus*, *Tyrophagus*, *Glycyphagus*, *Acarus* and *Blomia*) are prolific pests of stored foods such as grain, animal feed and aged products such as cured ham and cheese (Hage-Hamsten & Johansson, 1992; Thind, 2005). The storage mites *Lepidoglyphus destructor* and *Tyrophagus putrescentiae* have been found to be as influential in the development of occupational rhinitis in dairy farmers in Finland as cow dander, meaning that they are of medical significance (Terho, *et al*. 1985).

The aforementioned storage mite species *Tyrophagus putrescentiae* and its sister species *Tyrophagus longior* are cosmopolitan storage-mite species often observed in the vicinity of nesting animals such as bees, birds and mice (Fan & Zhang, 2007*a*). *T. longior* is regarded as a fungivore, however this particular species has been recorded damaging seeds and plants through direct feeding within greenhouses (Ribrioux, 1970; Buxton, 1989). This species has also been recorded somewhat unusually, infesting a mouse larder consisting of dried dog biscuits located underneath the floorboards within a house in the UK (Baker & Swan, 2013). These mites were hypothesised to have been introduced via the family dog, as well as the mice which had previously infested the house, suggesting that this was an anomalous occurrence (Baker & Swan, 2013). *Tyrophagus putrescentiae* is a mite with similar feeding habits to *T. longior* in that it is regularly found on aged or mouldy stored food products, although they can also be observed in mushroom beds (Kheradmand, *et al*. 2007). In one study, in 38 of 450 samples of mouldy Turkish Surk (a traditional spiced cheese) the only mite that was recorded feeding on the surface of the cheese was *T. putrescentiae*, suggesting that despite the many distinct species of fungivorous storage mites that have been identified, this specific species is a particularly prolific pest within the global food industry (Aygun, *et al*. 2007;

Hayaloglu & Fox, 2008). These mites not only damage and destroy food products, but they also introduce preferentially selected foreign micromycetes to food products through direct contact, as well as through their faeces (Hubert, *et al*. 2003). Fortunately, however, due to their small size (females = 320-420µm, males = 280-350µm), mites are limited in the number of fungal spores which they are capable of inadvertently relocating onto such products (Zhang, *et al*. 2018; Hubert, *et al*. 2003). In a study conducted in 2004 by García, it was suggested that both *T. longior* and *T. putrescentiae* were prominent on dry cured hams. However, the most commonly observed mite species differed depending on the location of the ham, with *T. longior* being more common on hams within drying rooms, whereas *T. putrescentiae* were more commonly observed on hams within cellars (García, 2004). Furthermore, it was concluded that humidity levels below 60% inhibited the growth of both mite species on the perimeter of the ham, but these low humidity levels caused individuals to find shelter within crevices in the ham and failed to eradicate them (García, 2004). The ideal temperature that *Tyrophagus putrescentiae* females require in order to lay eggs is approximately between 8 and 36°C which highlights the flexibility and hardiness of this species which allows it to survive and proliferate so successfully within stored goods (Zhang, *et al*. 2018). *Tyrophagus putrescentiae* requires a high relative humidity to ensure that they can develop through each of their life stages effectively (Sánchez-Ramos, *et al*. 2007). It has been observed that *T. putrescentiae* individuals adopt a 'huddling' behaviour when the humidity in the surrounding environment drops and becomes desiccating (Cutcher, 1973). The purpose of this is to reduce the surface area of the individual mites to minimise water transpiration and decrease the risk of dehydration (Cutcher, 1973). Based on the literature and preliminary studies, it is important to highlight that people within the food industry predominantly perceive storage mites as being detrimental to both food consumers and the food economy (Freitag & Kells, 2013). Despite this, similar species are also traditionally utilised as ripening coadjuvants to improve the flavour of cheeses such as Mimolette or in the production of cheeses like Milbenkäse in countries such as Brazil, Germany and France (Carvalho, *et al*. 2018*a*). Often however, these generally unconventional methods of cheese production are frowned upon by foods standards organisations based on the lack of conclusive evidence regarding the health implications resulting from the consumption of the mites (Carvalho, *et al*. 2018*b*). The importance of the biology of the focal species is highlighted to contextualise the findings in relation to behaviour. This, if the findings suggest that these mite species are capable of magnetoreception, will aid in explaining why this sense may be necessary in non-migratory species.

Tyrophagus putrescentiae and *T. longior* have been selected as the focal species for this study based on their relative abundance and simple and inexpensive husbandry. Of the many *Tyrophagus* species that have been identified, these two species were specifically selected due to the fact that they are sister species and almost identical morphologically, except from the fact that *T. longior* lacks the ability to sense visual cues due to the absence of eyes or simple light-perceiving photoreceptors, whereas *T. putrescentiae* possesses simple, light-sensitive eyes (Fan & Zhang, 2007*a*; Fan & Zhang, 2007*b*; Zhang, *et al*. 2018). Phylogenetic analyses have shown that mite species which possess eyespots have formed a separate lineage from those species which do not possess eyespots (Murillo, *et al*. 2018).

Because of the lack of knowledge surrounding these two species, the importance of this study is to first identify whether either of them is capable of spontaneously orientating themselves and aligning with the Earth's magnetic field. If either species is capable of magnetoreception, then this will aid in the development and planning of future studies and furthermore, it may encourage biologists to carry out a higher number of studies on species within Acari instead of overlooking them as they appear to have done thus far. Additionally, the nature of this particular study requires live mites to be used under experimental conditions and therefore, means that mites must be accommodated for and nourished sufficiently under laboratory conditions. As there have been few papers published on the conditions that these mite species require in order to optimally reproduce and survive under controlled conditions, this study will also benefit laboratories planning on using these mites in further studies on both magnetoreception and other fields by providing information on how to care for them. Finally, this study may also result in conclusions which could potentially aid in the control of these two pest species. If the evidence resulting from this study can suggest that mites are either attracted or repelled by specific magnetic field intensities, then it could provide information which could help to remove *T. putrescentiae* and *T. longior* from locations in which stored foods are maintained and aged. This study may hopefully provide enough evidence to suggest that closely related species with subtle physiological differences should be studied in greater depth. Due to the absence of eyes in *Tyrophagus longior*, it can be hypothesised that this species should possess a magnetoreceptor mechanism to compensate for its non-existent visual sense. On the other hand, as *Tyrophagus putrescentiae* possesses eyes, it can by hypothesised that this species will not exhibit magnetosensitivity as it would be arbitrary. These species will, therefore, be tested against one another and have their magnetoreception capabilities compared.

Materials and Methods

Data collection and laboratory work was initiated in January 2019 and ceased in June 2019 at Bangor University. Due to the fact that magnetoreception studies had not yet been carried out on *Tyrophagus putrescentiae* nor *Tyrophagus longior* prior to this study, many of the techniques and materials that were used were reliant on trial and error. It involved the use of both unconventional methods, as well as methods that had been used in earlier studies on magnetoreception in different species. Prior to the initiation of this study, it was essential that all paperwork involving ethics and welfare was completed carefully to ensure that there could be no future legal issues. Because the focal species involved in this study were both invertebrates, it meant that they did not require filing under the Animals (Scientific Procedures) Act (ASPA). Prior to all laboratory work, the appropriate health and safety checks and risk assessments were carried out and approved. Also, after the experiments had been concluded, the petri dishes and mites within them were either disposed of in a sterile manor, or the mites were transferred back into their home tissue flask to be used in other experiments.

Data collection was scheduled in order to allow a sufficient length of time to collate literature and background knowledge on the phenomena and focal species that were to be involved in this study. Both *Tyrophagus* species were acquired in their earliest forms (eggs and larval) from The University of Reading, where they are carefully categorised into specific species colonies. Because they were sent as eggs and larvae, it meant that they required a significant amount of time to mature, also resulting in the simultaneous growth of the individual mite population. Both species were housed within separate transparent plastic 12cm (175ml) tissue flasks. Before the mites were added to the flasks, each flask was labelled and dated accordingly to avoid any chance of confusion and therefore unwanted contamination. Next, a medium was formulated from a combination of approximately 70% wholegrain flour and 30% dried yeast which was prepared in a clean glass beaker and mixed using a clean stainless-steel spoon or a stainless-steel scoop. This substrate was then added to the flask and homogenously spread across the inner base. The purpose of this medium was to fabricate a desirable environment and habitat for the mites which they can both hide in amongst, as well as feed upon, ultimately reducing mortality rates as well as escape attempts. Once the substrate had been prepared, the mites were then introduced to the flasks using the stainless-steel scoop. The flasks were enclosed using a screw-cap lid with six ventilation holes covered with a thin layer of card, allowing air to get in to maintain mite respiration, but prohibiting any mites from escaping and disallowing any foreign solid objects from entering the flask.

It became apparent relatively early on in the study that there are several factors that can detrimentally affect the survival of both storage mite species. The population size of both mite species can increase rapidly due to their high reproductive rate. Because of this, the food/substrate and the size of the tissue flask cannot sustain the continuous growth of the colonies. Overpopulation inevitably occurs and results in overcrowding combined with escalated amounts of faeces which ultimately results in uninhabitable conditions for the mites. This became apparent when the mites began crowding at the top of the flasks near the screw cap where the ventilation holes were located (see appendix 1). It took approximately two weeks without any interference for the mites to reach their maximum capacity and approximately three weeks for the colony to have entirely perished. As the population increased, the top layer of substrate changed colour from light brown to a dark brown/golden colour. This was the result of a build-up of the mites' faeces, thus meaning that the amount of fresh food was dwindling. Because of this, it was imperative that the mites were introduced to a fresh labelled flask and substrate when the population began to approach maximum capacity. This was carried out using the stainless-steel scoop and a glass beaker, underneath which a sheet of kitchen roll was placed to catch any mite conglomerations that may have dropped off the scoop. Any equipment used during the experiments was washed thoroughly using detergent and hot water when they were no longer required. Another factor that appeared to affect the survival rate of the mites was the surrounding humidity. When mites were left in the tissue flasks without any humidity control, they rapidly expired. In order to prevent this from regularly occurring, all the 12cm flasks were assigned to large 18cm plastic tubs, also with screw-on lids. These tubs were capable of accommodating two 12cm tissue flasks at a time. Prior to adding the tissue flasks to the tubs, a single sheet of absorbent kitchen roll dampened with lukewarm water was added as a base layer within the tub. The two tissue flasks were then place atop one another as well as the wet kitchen roll. The lid was then screwed on, meaning that any individual mites that may have escaped the tissue flasks through small crevices in the lid were not able to escape any further and become airborne. The use of a hygrometer was not necessary for this study as the humidity scale that these mites require in order to reproduce and survive is relatively flexible provided that it is above 60%. Another key environmental factor that is capable of influencing the behaviour and reproductive success of *Tyrophagus* mites is temperature. The temperature within the laboratory was maintained at a consistent temperature of approximately 26-35°C throughout the duration of time that the mites were stored within. Based on the knowledge that individual female *Tyrophagus* mites ideally require a temperature of between 8-36°C in order to lay their eggs, it meant that the temperature could be set at a reasonably flexible number within that scale. Despite the room temperature being set within the 8-36°C scale, it was vital that the mites were placed in a location out of the vicinity of the radiators within the laboratory to ensure that the mites were not dying unnecessarily. As adult *Tyrophagus* mites can only grow to a size of between 320-420µm in females and 280-350µm in males, it meant that it was essential that a method of visualising the mites was available to be capable of monitoring their population sizes. Therefore, a microscope and an in-built lamp were used to monitor the progress of mite maturation and population density expansion. The microscope also meant that observations could be made on general mite behaviour and colony interactions. This then meant that later observations made after potentially behaviour altering manipulations could be better understood. To back up these pilot observations, both Google Scholar and Web of Science (all databases) were utilised. This resulted in a more thorough understanding of the mites' behaviour, nourishment requirements and habitat preferences that were necessary for the accommodation of the focal species as well as the understanding of observations made during the course of the imminent experiments.

As previously stated, the methods used during this study were largely improvised to allow the highest chance of yielding the most meaningful results possible. This meant that several variations of the same experiment were practiced, optimising the likelihood that the results gathered were the most realistic representations of an experiment carried out under natural conditions. This included the eradication of potential confounding factors which appeared across the course of the study. The same individual observer, photographer and technician was used throughout the study to certify that each repetition was as accurate and replicable as possible, as well as to remove potential observer bias.

Experiments

1.1. The first experiment to be carried out on the mites was designed to function as a pilot study involving live mites. This experiment involved the use of the 12cm tissue flasks as the experimental arenas. Identical to the 12cm tissue flasks that accommodated the concentrated mite colonies, the tissue flasks used as experimental arenas also had a substrate layer (~3mm) of wholegrain flour combined with dried yeast coating their inner base. This functioned to feed and house the mites that were later introduced to the experimental arenas. The substrate also functioned as an indirect barrier which prevented the mites from escaping the flasks. This was because both species are highly food orientated, meaning that they had no reason to leave the flasks full of a fresh and preferred food source. The Idea behind the pilot experiment was to introduce a high concentration of both respective mite species separately into the experimental arena. The mites were relocated from their home tissue flasks and instated at the entrance of the identical experimental arena atop the fresh substrate. The colour contrast between the substrate concentrated with mites and the fresh substrate was immediately evident, as the old substrate was considerably darker. The flasks were then placed in an 18cm plastic tub with the humidity control in place and stored in a dark cupboard within the laboratory for approximately 24 hours. The flasks were then removed and observed using the naked eye. This was carried out by using the darker substrate patch as an indicator for the direction(s) in which the mites had moved. However, after observations had been made using the microscope it was concluded that the experimental arena was too large for the small number of mites being introduced into the arena resulting in sparse distribution and high mortality. Because only a small number of individuals had survived the 24-hour period, it was decided that any results yielded from this particular experiment may not be truly representative of the mites' magnetoreception capabilities. This was because it was unclear how many of the mites were alive to participate in the experiment. So that the lives of the mites were not unnecessarily wasted, each of the tissue flasks that were originally used as experimental arenas were kept and stored within the humidity controlled plastic tubs. This meant that the mites could survive and also, meant that the mite stocks were replenished after each repetition due to their high reproductive rate.

1.2. The next experiment to be set up involved an almost identical setup to experiment *1.1*. However, the 12cm tissue flasks were substituted for 5cm tissue flasks as the experimental arenas. It was hypothesised that the smaller arena would result in more decipherable results and could potentially have reduced the individual mortality rate. The scoop of mites introduced to the arenas were this time slightly smaller to accommodate the smaller experimental arenas. The number of mites added into the experimental arena each time did not have to be specific as the individual mites were not used as the experimental units. Despite this, care was taken to ensure that each scoop was approximately the same size. Once the mites had been introduced to the arena, they were placed within plastic tubs and left for 24 hours. The next day the mites were again observed using the naked eye and a microscope. This time, the mites had successfully survived, and the brown patch had been deformed since the day prior, indicating mite movement. It became apparent after microscopy, however, that the smaller size of the flask meant that the mites were not capable of moving as far as they perhaps might have if the flask provided enough space. This was brought to attention after microscopy, as the majority of the mites were predominantly observed to have been located right next to the edges of the flask. Also, the cuboidal shape of the flask meant that it was difficult to measure the directional information of the mites' paths because the flasks are longer than they are wide. This meant that their East and West directional capabilities were physically hindered, as the flasks were set up with the cap facing North. As the mites were initially placed so close to the entrance of the tissue flask and there was no accurate method of placing them in the middle, it meant that the mites were only capable of moving forwards or remaining in the same position. This was because the corners of the flask did not heavily deviate from the centre of the flask. *Tyrophagus putrescentiae* and *Tyrophagus longior* could relocate using air currents due to their minute size and weight. This meant that the mites could move from their original position to the edges of the flask in less than a second. Another problem that was encountered whilst using the tissue flasks was that mites appeared to be showing a bias towards the single origin of the tissue flasks' air currents. This meant that the mites showed a preference for the screw cap as the airflow was not homogenous throughout the flasks. Therefore, it was again decided that the experiments should be postponed until a more practical solution could be formulated.

Like the 12cm flasks, the 5cm tissue flasks were also maintained to increase the mite stocks and reduce unnecessary mortality.

2.1. After the realisation that the shape of the tissue flasks was going to be problematic for the data collection process, a new experimental arena was introduced. For this experiment 9cm radial petri dishes were utilised. The circular shape of the petri dishes meant that they could coincide with the compass points, thus allowing the yielded measurements to be taken significantly more easily and accurately. The ideas behind the initial pilot experiments were also transferred over to the experiments using the petri dishes. This is because they could be carried out simplistically, effectively and efficiently and it was the design that was postulated to be most capable of yielding the optimum results. This experimental design could also be applied more fittingly to the petri dishes than the tissue flasks. This is because the petri dishes have loose, dorsal, non-screw cap lids which improved the accessibility for introducing the mites into the arena, therefore improving the accuracy of colony placement. The loose-fitting lids also meant that the air flow was homogenous across the entire arena, thus eliminating the mites' abilities to preferentially direct themselves based on air quality. Because the petri dishes were circular, it meant that the mites could be placed at the centre of the experimental arena, allowing the mites to move in any direction. Care was taken to make sure that the mounds at the centre of the dishes were almost perfectly circular to ensure that each unit was approximately the same. This suggested that any potential results gathered during the petri dish experiment would be a significantly more accurate representation of the mites' capabilities of sensing and utilising magnetic fields for orientation and alignment. Separately, both mite species were introduced to the centre of 12 petri dishes (n=12 per species). These dishes were then placed on top of one another and added to the humidified plastic tub. These were also left for the standard time of 24 hours per species to allow the mites to move in their intended direction(s). Each tub was housed within a cupboard raised high enough from the ground so that they would not be disturbed by other researchers using the laboratory. The purpose of this experiment was to determine whether the mites exhibited behaviour suggesting that they were capable of simultaneously aligning and orientating with the relatively weak, natural magnetic field. After the allotted movement time, the mites' directional behaviour was recorded.

Because the petri dishes did not have screw-on lids, it meant that the escape rate was high and many of the mites had migrated from the petri dishes into their respective plastic tubs. As a competent method of quantifying the results had not yet been established at this stage in the study, directional information was recorded based on the deformation of the dark patch of substrate that was visible on top of the fresh lighter coloured substrate.

Prior to the initiation of experiment *2.2.* it was realised that lighting had not been properly considered, as there were no measures in place to control it. One particular study suggested that mites were deterred by bright lights, suggesting that they are nocturnal. However, based on the lack of observational literature found using both Google Scholar and Web of Science (all databases), it was unclear whether the focal *Tyrophagus* species were either nocturnal or diurnal. This meant that the experiment had to be designed in a way which could accommodate these uncommon circumstances. To remove any potential light-based confounding factors, a relatively unorthodox experimental arena was constructed. A blackened box technique currently used in magnetoreception experiments on another species was arranged and constructed. A 30cm x 30cm cardboard box was used as the basic frame of the experimental arena. One end of the box was left open so that an artificial base could be easily slotted in underneath it. With the open end placed at the base, one side was then cut halfway vertically on both the left- and right-hand sides parallel to one another. This was then fashioned into a makeshift door flap using a cable tie and an adhesive plastic cable tie lock. This door would function to allow easy access in and out of the experimental arena so that the mites could be efficiently introduced and removed from the experiment. The inside walls of the cardboard box were then thoroughly painted using three coatings of plain black paint. This was then left to dry before finishing the painting with an unscented transparent varnish. The purpose of the paint and varnish was so that the *Tyrophagus* species with eyes were not allowed to focus on any otherwise uncontrollable visual cues within the arena. The black paint meant that there was a constant absence of colour during both day and night. As the blackened box experiment was too large to carry out within the aforementioned laboratory cupboards, it meant that potential visual cues stemming from ambient light entering the room through doors and windows required counteraction. To abolish this potentially detrimental confounding factor, a 21cm x 30cm (A4) illuminated drawing table was placed within the box to act as the base of the experimental arena. This drawing table remained illuminated throughout the entire duration of the remaining experiments to ensure that any light that entered the laboratory was invisible from within the box. The varnish that was applied as an additional coating atop the black paint resulted in the homogenous reflection of light from the illuminated drawing table. This eradicated any possibility that the visually capable mites' movement would be influenced in any way by visual cues. Finally, to further ensure that there was no interspecific contamination occurring during the experiments, one blackened box was crafted per species. To avoid any confusion, both boxes were labelled with their respective species names using a permanent marker.

2.2. The next experiment also involved the utilisation of 9cm circular petri dishes as the experimental arenas. For this experiment however, one radial adhesive 1cm^3 neodymium and cobalt artificial magnet was placed North-side-up on the outer base of each experimental unit. The purpose of these magnets was to determine whether strong magnetic fields either deterred or attracted the mites. Either of these outcomes would have suggested that the mites were magnetosensitive to some degree. The setup was the same as experiment *2.1.* with a thin layer of substrate covering the inner base of the petri dishes. The mites were then arranged radially and centrally with the magnet set up near the edge of the petri dish. This was so that results would show a significant deviation from the centre of the petri dish in either the direction of the magnet if attracted to the magnet, or towards the three unmagnetised compass points if deterred by the magnetic field. This was because magnetic fields decay as the distance away from the source increases, resulting in the assumption that the mites would move away from the magnet. As practiced with experiment *2.1.*, a day was again left between using different species during the experiment to prevent interspecies contamination. As this experiment was carried out within the blackened box, it would not have been practical to have used the 18cm plastic tubs to store the experimental units within. Therefore, a storage method was put in place to ensure that the introduction of the mites to the box was as efficient as possible. ~11cm x 11cm Ziploc polypropylene freezer bags were utilised to function as a space efficient petri dish storage mechanism. A single sheet of kitchen roll dampened with lukewarm water was added to each freezer bag to maintain the relatively high humidity level. Prior to the introduction of the petri dishes to the freezer bags, each of the 20 dishes

(10 petri dishes per species) were photographed from above using a digital camera so that the dark mound containing the mites was clearly visible atop the fresh lighter substrate. Each petri dish was then placed on top of the damp kitchen roll within the freezer bags. The bags were then carefully labelled with the species names, date and individual bag number with a permanent marker. To make sure that each repetition was of the highest quality, only four petri dishes were involved in the experiment at any one time. This minimised the risk of errors and meant that observations could be carried out efficiently over the course of a single day. This was imperative as it meant that each colony of mites was exposed to the treatment for the same amount of time. Each dish was placed atop the illuminated drawing table and left for approximately 24 hours. Once the time had elapsed, the freezer bags containing the petri dishes were each carefully removed. The dishes were then removed from the bags and placed upon the laboratory bench. Theoretically, the darkened patches containing the mites should have been deformed by the mites' movements. This meant that further photographs were necessary so that before and after comparisons could be made. Often, the petri dish lids had to be removed for photography because of the condensation resulting from the damp kitchen roll obstructing the observer's view of the mites.

2.3. This penultimate experiment required the utilisation of more sophisticated technology than used in the previous experiments. The setup of the mites remained relatively unaltered. The same 9cm petri dishes were used at the units and the mites were introduced to the same measurements of substrate as in the experiments prior. The blackened boxes were also used during this experiment along with the illuminated drawing table. However, instead of the neodymium/cobalt artificial magnets, a wooden/copper Helmholtz coil was introduced. This coil had previously been used during studies on bird magnetoreception and navigation. The idea behind this method was to use the Helmholtz coil to produce a magnetic field comparable to the intensity of the geomagnetic field, however with a distinguishable deviation of the North-South axis. The coil was setup and attached to a power supply within the laboratory. The coil itself was placed upon a large polypropylene plastic garden table. The material was carefully selected previously to ensure that it did not have any influence on magnetic fields utilised during various other magnetoreception experiments. A small wooden plinth was then placed in the centre of the plastic garden table, within the Helmholtz coil. This was used to balance and support the experimental arena. The drawing table was then placed atop the wooden plinth, before the blackened box was also finally introduced. The Helmholtz coil was set up so that there was a magnetic field deviation of -45° (anticlockwise) meaning that the North direction now sat at 315° on an unaltered compass. The purpose of this was to determine whether the mites were able to adapt to the anomaly in the magnetic field. This would mean that the mites would still be able to sense the magnetic field, however their preference would be shifted to coincide with the anomaly. If the mites did not respond to the field interference, then it would suggest that they were unable to sense magnetic fields and their distribution would be statistically uniform. Photographs were taken prior to the experiment using a digital camera. The petri dish lids were then sealed using cello tape and were then placed in allocated freezer bags. These were then placed within the blackened box atop the illuminated drawing table. Four petri dishes were exposed to the altered magnetic field for approximately 24 hours each to ensure that there was enough time allotted for the mites to be affected by the magnetic anomaly. Each petri dish was then removed and photographed once again so that analysis could later be carried out on the mound deformations. A 3-axis milli-gaussmeter was utilised to take readings of the artificial magnetic field before and after each treatment to ensure that the magnetic flux (nT) was not fluctuating and detrimentally affecting the yielded results. The National Oceanic and Atmospheric Administration (NOAA) magnetic field calculator was used to specifically pinpoint the behaviour of the normal magnetic field (NMF) in the specific location in which the experiment was being carried out. This meant that if necessary, it was possible to change the intensity of the artificially changed magnetic field (CMF) to coincide with and override the NMF of the specific location(s).

2.4. The next and final experiment to be carried out combined and refined each of the previous experiments. This experiment was carried out without the intervention of artificial magnets. Some of the darkened mounds during the previous experiments had either minimally changed shape or had not changed at all. This led to the introduction of a new data collection method. To accurately quantify the directional information yielded from the experiments, the mites were to be counted individually under a microscope. To accommodate the newly introduced method, the setup required alteration. Firstly, it was evident that counting individual translucent mites would not be practical if the substrate consisted of white flour. This meant that a new approach had to be undertaken in order to improve the mites' visibility. For the inner base of the petri dishes, radial 9cm filter paper was used. To make sure that the mites could be properly visualised under the microscope, the filter papers were coated in unscented violet food colouring. Because the mites were translucent, it meant that the darker coloured violet background would result in the mites appearing white (Figure 2 & Figure 3). However, it was also vital to maintain the desirability of the substrate that the mites were living amongst. Before the filter paper dried, it was impregnated with a dissolved whole-wheat flour and water solution. Theoretically, this would maintain the smell of the whole-wheat flour, ultimately resulting in the retention of the mites within the petri dishes. The mites may also have been capable of feeding on the surface of the filter paper. These filter papers were then left to dry for several hours prior to the initiation of the experiment. Once the papers were dry, they were applied flat to the inner base of the 9cm petri dishes (Figure 2 & Figure 3). Prior to the beginning of the treatments involved with experiment *2.3.*, the mites were relocated from Bangor, North Wales to Durham, North-East England. The room type therefore, also changed along with the location from a laboratory setting to an unheated garage setting. This meant that the experiments had to be carried out prior to the arrival of the cold winter weather to avoid excessive colony mortality. To ensure that this was possible, four of the petri dishes were set up simultaneously per repetition. This meant that the blackened boxes were filled to capacity with petri dishes for each repetition, resulting in a time efficient method of collecting the necessary data.

Figure 3: Photograph showing the setup used for experiment 2.4. The image shows a mound of *Tyrophagus longior* mites combined with whole-wheat flour and yeast, carefully centred within a stained, flour impregnated, circular piece of filter paper. This photograph was taken before the initiation of the experiment using an iPhone 6s camera.

Figure 4: Photograph showing the setup used for experiment 2.4. The image shows a mound of *Tyrophagus longior* mites combined with whole-wheat flour and yeast. It is evident from the photograph that the mound has become significantly deformed relative to the mound shown in *figure 2*. This photograph was taken after the cessation of the experiment using an iPhone 6s camera.

The next stage of the setup involved the mites' introduction to the petri dishes. Two scoops of mites combined with their home substrate was applied radially in the centre of the filter paper on the base of each petri dish. These mite mounds were then photographed using a digital camera. The lids were then returned to the petri dishes and secured using cello tape. This was added to the setup because it could not be guaranteed that the mites would remain within the petri dishes due to the absence of a purely edible substrate. These secured petri dishes were then added to their own individual freezer bags. Next, the blackened box with the drawing table base was carefully placed on a stable wooden chair. This abolished any possibility that the experiment may fall during the waiting period. A caution sign was also added to the top of the blackened box to ensure that the equipment was not tampered with in any way. It was ensured that the chair was placed next to an available power supply so that the drawing table could be operated. The mites were then placed within the illuminated blackened box and left for 12-24 hours. This timeframe was theorised to be sufficient for the mites to move due to the absence of a desirable food source. The mites were then removed individually from the blackened box and photographed to comparatively determine whether the mound deformation correlated with the mites' directional movement. The petri dishes were then moved and placed within a freezer at -19°C. This rapidly incapacitated the individual mites; however, they were each left for at least five hours to ensure that there were no rogue survivors. The purpose of this procedure was to make sure that the mites could be counted efficiently and accurately underneath the microscope without the mites moving around. The tape and lids were removed from each dish and they were carefully examined in an office away from any potential contaminants. A fine detail Taklon paint brush was used to move the mites aside once they had been counted to ensure that there was no double-counting. One paint brush was used per species to prevent interspecies contamination. These were each kept in separate, labelled ~11cm x 11cm Ziploc polypropylene bags as an extra precaution to prevent room contamination.

The mites were each counted individually using a microscope and the paint brushes for additional assistance. Each mite that had been counted was pushed into a desolate area of the petri dish to avoid confusion. Measurements were then carefully taken using a magnetic compass before the petri dishes were resealed and disposed of. Each measurement was taken at the central point of each individual compass direction (North = 359°, South = 180… etc.) to ensure that there was enough data to coincide with the specific direction in which the mites had moved.

Data Analysis

Data analysis was carried out using the circular statistics programme 'Oriana'. This data was categorised using the species names *Tyrophagus putrescentiae* and *Tyrophagus longior*. Individual mites per colony were counted and the compass direction with the highest number of mites was selected to represent the colony. This meant that the colony was the experimental unit as opposed to individual mites. This would have been problematic to carry out based on the mites' small size and high mortality rate. Also, it would not have been practical to focus on one single individual mite as there is no way to distinguish between individuals and they are too small to apply identity marks.

The statistical test that was selected for this particular data type was the Rayleigh z Test for uniformity ($z = nr^2$). The function of this test is to determine whether the movements of an individual unit or units were uniform. If the data was uniform, then the species did not predominantly move in a specific direction and therefore was not influenced by a specific phenomenon or cue. This was the most suitable test as it focusses on data relating to compass directions in which both low and high integers are arbitrary.

H_1: Both mite species will show a non-uniform distribution around the compass points, therefore showing orientation.

H_0: Both mite species will show a uniform distribution around the compass points, therefore showing that they are incapable of orientation.

Results

Several datasets were compiled over the course of this study. However, only the data collected from experiment *2.4* has been used (see Tables 1 and 2 and Appendices 2 and 3). This is because the experimental design of the previous experiments contained severe flaws that required immediate intervention. Experiment *2.4* is, therefore a combination of each of the improved preceding experiments.

To determine whether either of the focal species involved in this study were capable of magnetic orientation, directional statistics had to be carried out. Both mite species were tested separately and split into ten respective colonies (n=10). Also, each petri dish containing a mite colony was treated as a unit, as the mites could not be tested individually as their minute size would have been highly impractical.

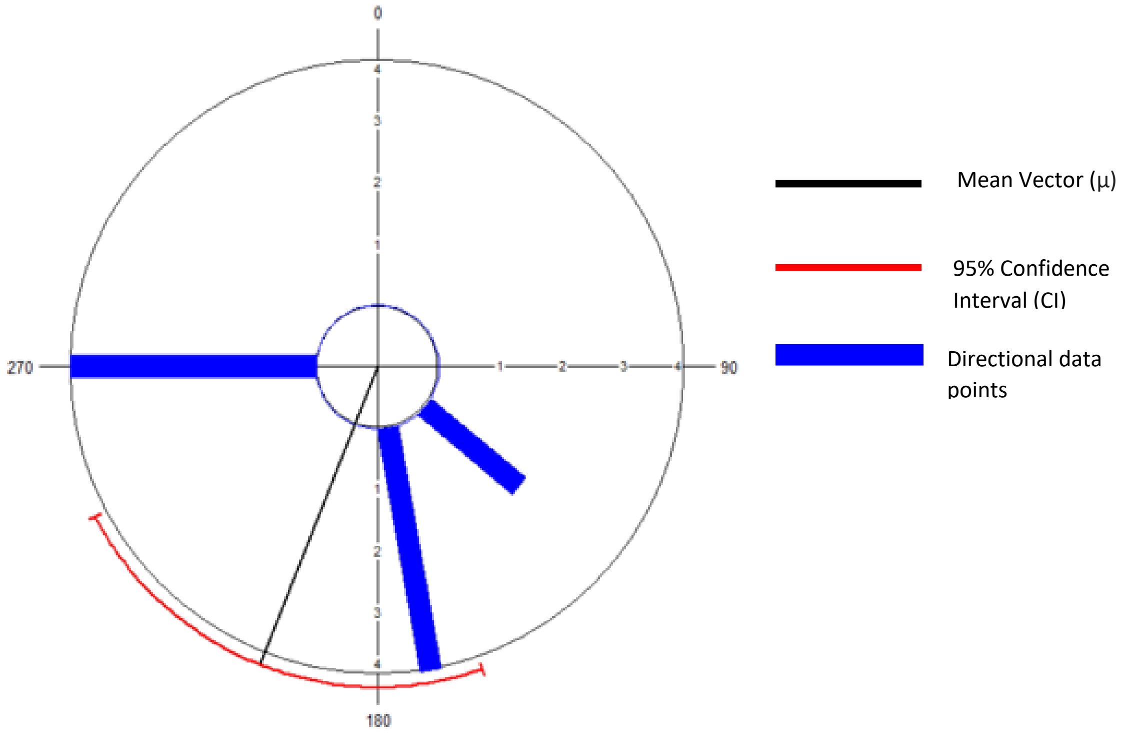
Tyrophagus longior

Table 1: Circular statistics data representing the directional preferences of Tyrophagus longior when tested under experimental conditions

Species	**Number of observations (n)**	**Mean vector (µ)**	**Length of mean vector (r)**	**Rayleigh test (p*)***
Tyrophagus longior	10	201.50	0.584	0.02

As the length of the mean vector was relatively high (~0.58) it was suggested that the observations that were analysed for *Tyrophagus longior* were primarily non-uniform. This meant that the mean vector (µ) could be used as an accurate representation of the directional preferences of *T. longior* (µ = 201° = South South West). The p-value attained from the Rayleigh test for uniformity suggested also, that the observations that were recorded from experiment *2.4* were non-uniform, meaning that *T. longior* showed a preference for a specific compass direction (p = 0.02).

To further illustrate these results, a radial histogram was formulated showing the directional preferences of *T. longior*.



Tyrophagus longior
Circular Statistics

Figure 5: Radial histogram representing the directional movement preferences of Tyrophagus longior (n = 10). In this case, the 95% confidence interval is relatively small (~90°), suggesting that the clustered directional results gathered for T. longior are more likely to be representative of the entire species. The mean vector (µ) was sat at 201˚ South South West.

These results were concluded to be non-uniform, therefore meaning that the null hypothesis (H_0) could be confidently rejected. As the controlled experiments removed confounding factors, it meant that only tactile and magnetoreception senses could be utilised by the mites (if they indeed possessed a mechanism for magnetoreception).

Tyrophagus putrescentiae

Table 2: Circular statistics data representing the directional preferences of *Tyrophagus putrescentiae* when tested under experimental conditions

Species	**Number of observations (n)**	**Mean vector (μ)**	**Length of mean vector (r)**	**Rayleigh test (p)**
Tyrophagus putrescentiae	10	50.96	0.301	0.414

As the length of the mean vector was relatively low (<0.5) it was suggested that the observations that were analysed for *Tyrophagus putrescentiae* were uniform. This meant that the mean vector (μ) could not be used as an accurate representation for *T. putrescentiae* as a species (μ = 50° = North East). The p-value attained from the Rayleigh test for uniformity suggested that the results collected from experiment 2.4 were also uniform, suggesting that *T. putrescentiae* did not appear to show a preference for a specific compass direction (p = 0.41).

A radial histogram was also formulated in order to exhibit the findings attained for *Tyrophagus putrescentiae* more clearly.

Tyrophagus putrescentiae
Circular Statistics

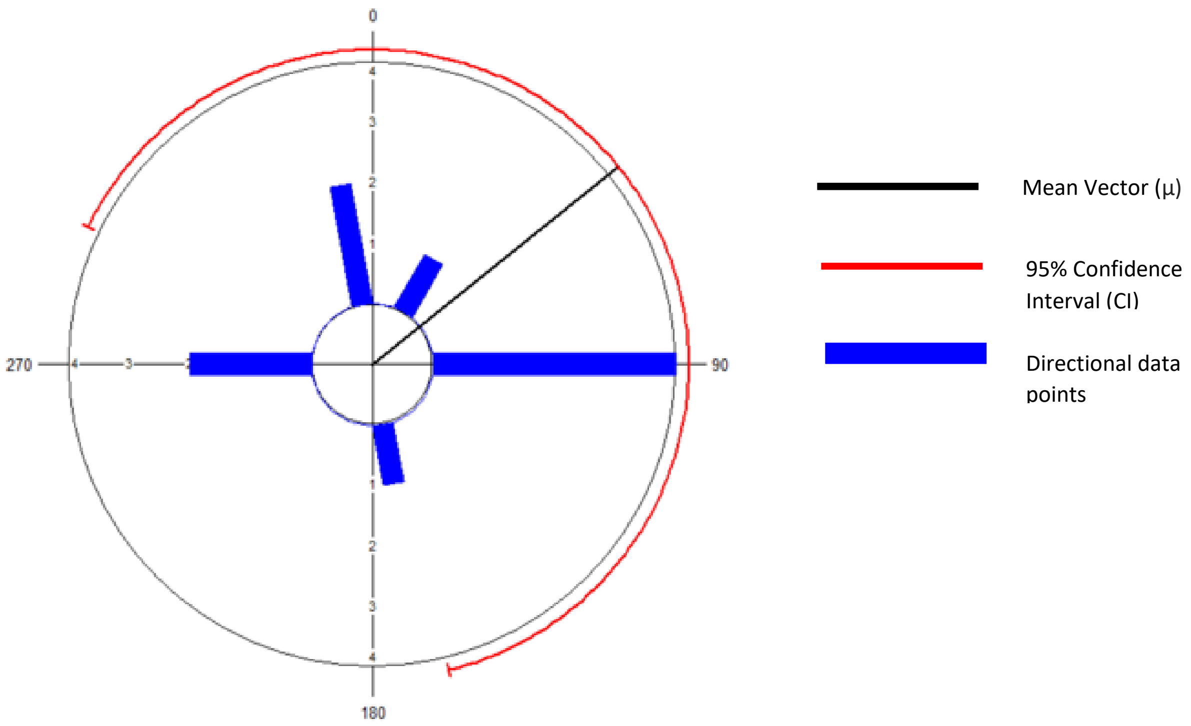


Figure 6: Radial histogram representing the directional movement preferences of *Tyrophagus putrescentiae* (n=10). In this case, the 95% confidence interval (CI) is large (~180). This indicates that the data is scattered, therefore meaning that the CI must be larger to fit the true mean within it. The mean vector (μ) was sat at 50˚ North East.

These results were concluded to be not different from uniform, meaning that the null hypothesis (H_0) could not be rejected in this case. Like with the *T. longior* experiment, all the controllable confounding factors were removed with the utmost care. This meant that only the mites' tactile and magnetoreception senses could be utilised (assuming that the mites possessed a magnetosensory mechanism).

Discussion

Like many other species with the possible exception of various endoparasites, mites require mechanisms which aid in their abilities to move in specific directions. This is a vital component of life for most species, as this allows them to efficiently find food, mates and nesting grounds respectively. Some animals such as bats have a well-developed auditory sense, as well as sophisticated echolocating calls to detect lepidopteran prey (Waters & Jones, 1996). Whilst others such as canids possess a highly defined and complex olfactory sense (Galibert, *et al*. 2016). Many species within the animal kingdom also possess simple light-detecting or complex eyes which enable them to perceive the environment and the organisms within it. There are, however, many species for which these senses are less advanced or absent entirely. Fossorial species such as moles have adapted to life in absolute darkness. This has resulted in the eyesight of mole species becoming rudimentary and almost vestigial, whilst their other senses are more refined in order to compensate (Crish, *et al*. 2003). Troglobitic species such as olms (*Proteus anguinus*) have adapted to inhabiting perpetually dark cave waters by losing their eyesight entirely, instead relying heavily on chemoreception (Parzefall, *et al*. 1980).

Tyrophagus longior is a species that possesses neither the simplest light-sensitive photopigments, nor ineffective or vestigial eyes (Fan & Zhang, 2007*a*; Fan & Zhang, 2007*b*, Murillo, *et al*. 2018). *Tyrophagus putrescentiae* on the other hand, does possess light-sensitive photoreceptors (Zhang, *et al*. 2018). Because these two species are so closely related, yet their visual sensory anatomy differs so significantly, it meant that the two species could be studied for magnetosensitivity simultaneously and then compared without species specific confounding factors proving to be detrimental to the results. This study aimed to test whether *Tyrophagus* species, *T. longior* would be the species which was most likely to exhibit magnetoreception capabilities. This objective was based on the knowledge that blind and visually impaired species generally possess either unique senses such as echolocation, magnetoreception or electrosensitivity, or alternatively, their common senses such as olfactory, auditory and tactile senses are more well-developed than visually capable species. Therefore, *Tyrophagus putrescentiae* was used as a control during this study. The intent of this was to investigate whether the visually capable species was less likely to possess a magnetosensory mechanism than the visually incapable species.

The results accumulated from the Rayleigh test for uniformity suggested that *T. longior* was capable of magnetic orientation, whereas *T. putrescentiae* exhibited uniform directional behaviour. The data collected for *T. putrescentiae* indicates that they are incapable of specific directional orientation. Data yielded from the experiment for *T. longior* on the other hand supported the argument that this species was capable of alignment of some sort. The 95% confidence interval that was generated using the data for *T. putrescentiae* spanned from West to South clockwise. This means that the directional data points could have fallen within any of three primary directions within approximately 75% of the entire compass. This indicates further that *T. putrescentiae* does not utilise colonial alignment to influence directional behaviour, instead using other senses. The 95% confidence interval that resulted from the data points collected from *T. longior* was significantly shorter, only covering approximately 25% of the overall compass between South and South West. The results from ten observations clearly suggest that *T. longior* shows a preference for the south-south western pole of the Earth's magnetic field. The reason for this, however is yet unstudied.

Prior to this study, there has been a distinct literary void surrounding *Tyrophagus* mite species and their magnetoreceptive capabilities. Not only has the data collected during this study suggested that *Tyrophagus longior* may be capable of a form of orientation, but it also unearths new questions about the variation in physiologies of sister species. There have been certain studies which have focussed on magnetoreception in animals that acknowledge the comparison between the focal species and their sister species, however the extent to which they are compared has been greatly limited. In batoid elasmobranchs it has been suggested that the sister species the round stingray (*Urobatis halleri*) and the yellow stingray (*Urobatis jamaicensis*) are both capable of utilising magnetic fields to memorise geographical points associated with vital resources (Newton & Kajiura, 2017). Despite ephemeral comparisons between sister species' magnetoreception capabilities, there is a considerable gap in the literature where this has been the focus of an entire study. This could be because many sister species are very similar in anatomy and physiology to one another. Unless magnetoreception studies on anatomically similar species are designed using strong artificial magnets and therefore the weakened geomagnetic field as a control, then it may be difficult to justify the study if they cannot be hypothesised to potentially show different results. This is one of the main reasons why this particular study is so novel and important. *T. putrescentiae* in this case functioned as a natural control as it can now be assumed that magnetoreception is not a necessity in a visually capable, non-migratory species. The assumption that the explanation for the alignment capabilities of *Tyrophagus longior* however, is indirect. This assumption is based on the restriction of all other confounding cues using the blackened box and it must be emphasised that artificial magnetic field manipulation should be explored using both of these species in future studies to further back up these findings.

It can be assumed that the primary explanation for these findings is that *T. longior* does not possess their main sense, vision. However, why a species such as *T. longior* would possess such a sensory mechanism is not yet understood. *T. longior* is not a nesting species, nor do they feed in the same specific place at a recurring time of year. Like *T. putrescentiae*, *T. longior* is a communal species, sharing its environment with conspecifics in large colonies. It could be postulated that *T. longior* may use magnetoreception to determine its position in relation to the colony. If this is the case, then it could provide evidence to suggest that *Tyrophagus* mites are also capable of memorising positional information by utilising a present magnetic field. This has previously been observed in cave salamanders (*Eurycea lucifuga*) (Phillips, 1977). The mites were tested with the colonies as the experimental units, meaning that this species can orientate as a colony. This may suggest that they use magnetoreception to maintain the colony’s seemingly erratic structure to ensure that they have the highest possible chance of reproducing and surviving. *T. longior* is frequently observed inhabiting the nests of various bird species, as well as the nests of bumblebees (Fan & Zhang, 2007*a*). They have also previously been discovered inhabiting a mouse larder comprised of dried dog food, suggesting habitat opportunism (Baker & Swan, 2013). These habitats are capricious and relatively complex in structure, meaning that residing organisms require methods of navigating through them. As *T. longior* does not possess eyespots, their apparent magnetosensory capabilities could provide an explanation as to how they navigate these habitats whilst maintaining the structure of the colony.

It is understood that one of the two postulated mechanisms which animals utilise for magnetoreception is dependent on blue light photoreception (Cashmore, *et al*. 1999). The process of magnetoreception can be easily skewed by thermal fluctuations, however, which create noise (Ritz, *et al*. 2010). The necessary radical-pair processes are formed by light-mediated electron transfers between a donor and an acceptor molecule (Ritz, *et al*. 2010).

Both of these molecules possess unpaired electrons which spin indefinitely and create a magnetic moment which is sensitive enough to detect the relatively weak geomagnetic field (Ritz, *et al*. 2010). These occur quickly enough so that thermal noise does not affect their magnetosensitivity (Ritz, *et al*. 2010). It has been suggested that one of the primary molecules which is responsible for the electron transfer in animals is the photopigment-protein, cryptochrome. These proteins occur within the eyes of several studied species, including birds. It is understood that *Drosophila melanogaster* possesses at least five eye types which perform functions unique to each respective structure. This includes their cryptochrome-dependent, magnetosensitive circadian clock (Rieger, *et al*. 2003; Yoshii, *et al*. 2009). *Tyrophagus longior* is absent of any eye structures which potentially suggests that they do not possess the necessary photopigments for them to detect magnetic fields using the radical-pair process mechanism. Studies focussing on plants contradict this assumption, however. This is based on the evidence that suggests that *Arabidopsis* possesses cryptochrome which is comprised of a similar sequence to DNA photolyases which activate the restoration of ultraviolet light-damaged DNA (Li & Yang, 2007).

As well as magnetoreception, this study also unearthed questions about the basic behaviour of *Tyrophagus* mites. The initial observations of both species were that they appeared to move randomly within their colony with very little structure. This, however, was suggested to be untrue by the results of this study. Another observation of the mites was that they crowded at the screw-on lid as close to the ventilation holes as possible when the population size grew. Whilst the cap was removed, the scent that emanated from the flask was pungent. It has been discovered that *Tyrophagus putrescentiae* is capable of producing an alarm pheromone comprised of neryl formate when they become distressed (Kuwahara, *et al*. 1975). This pheromone has been observed to be secreted latero-abdominally from specialised scent glands (Kuwahara, *et al*. 1979). When mites are squashed or disturbed, this pheromone is released causing a repellent effect to the undisturbed conspecifics (Kuwahara, *et al*. 1979). The purpose of this repellent effect is to deter conspecifics away from the disturbance in order to improve the survival rate of the overall colony. Another study, this time focussing on *Tyrophagus perniciosus* indicated that this species also produces an alarm pheromone in the form of 2-hydroxy-6-methyl-benzaldehyde (Leal, *et al*. 1988). These studies indicate firstly that the reason for the crowding behaviour near the lids of the tissue flasks was potentially to escape alarm pheromones released in large quantities by mites close to death due to a lack of food and overcrowding. The findings resulting from these studies also indicate that *Tyrophagus* mite species possess a sophisticated olfactory sense. During the experiments conducted during this study, the mites were placed in petri dishes containing stained filter paper across the inner bases. Once the mites were introduced to this medium, their 'home substrate' became less desirable, as it was brown and defiled by both pheromones and faeces. This meant that the mites were persuaded towards the more preferable medium. Based on the knowledge that mites are capable of chemoreception, it could be assumed that the mites use their olfactory sense to locate the fresher food source. This fresh food provided the mites with the opportunity to move from the centre flour mound, however it did not influence the direction in which they moved. It is imperative that the mites' refined olfactory sense is taken into consideration for future studies on *Tyrophagus* magnetoreception. This is because it evidently influences their movement behaviour to an extent, meaning that scents must be homogenous throughout the experimental arenas to ensure that their directional behaviour is not influenced.

Another observation that was made throughout the course of the study was an apparent 'jumping' behaviour exhibited by both of the focal mite species. Because these mite species do not possess limbs nor appendages adapted to hopping, it was clear that they were relying on airflow to relocate. This behaviour resembled ballooning which is an aeronautic behaviour observed in various species within the order Araneae (Greenstone, 1982; Coyle, 1983). Spiders of multiple genera have been observed to utilise a combination of silk, wind intensity and electrical fields to become airborne when their current habitat becomes uninhabitable or undesirable (Humphrey, 1987). All identified spider species are significantly larger than *Tyrophagus* mites which could potentially explain why the spiders' silk is required to become airborne. Mite chaetotaxy has previously been suggested to allow individual mites to interact with substrates and the environment. Predatory mite species belonging to the Phytoseiidae family are regular predators of spider mites belonging to the Tetranychus family. This feeding behaviour requires Phytoseiidae mites to navigate the spider mites' complex web structures. Due to their ambulatory locomotive strategy, it means that Phytoseiidae mites risk becoming caught in the webs. The setae of the Phytoseiidae mites, function as protectors, allowing the mites to move uninterrupted through the web conglomerations (Sabelis & Bakker, 1992). The significance of this is that *Tyrophagus* mites appear to use a similar strategy to manoeuvre within a substrate. It was observed that during every microscopy session with the mites there were individuals with grains of flour attached to their dorsal setae. This is thought to be one of the functions of the setae of *Tyrophagus* mites. This allowed them to remain within the colony and prevented them from being carried away by rogue air currents. When the mites were moved from the tissue flasks to the petri dishes however, it appeared to trigger the jumping behaviour as they attempted to remove themselves from the area of disturbance. This appeared to be an adaptation to evading predatory threats as they were actively removing themselves from the food substrate in order to escape. The mites were capable of moving from one side of the petri dish to the inner edges approximately within a single second. This behaviour was highly significant during the data collection process of this study because of the specific focus on magnetoreception. If this jumping behaviour was reactive in response to a disturbance stimulus and they were counted, then this could have negatively affected the results. Because it could not be assumed that this secondary method of locomotion was based on the Earth's magnetic field and not merely the direction of the present air current, it was decided that mites within 0.5cm of the edge of the petri dish would not be quantified.

Once it became evident that the mites were capable of rapidly escaping in relatively high numbers through aerial relocation, it was essential that methods had to be put in place to inhibit the risk of interspecific contamination. It was unlikely that single individual mites would be capable of reproducing at a high enough rate to decimate the opposing species if they were inadvertently introduced to the wrong petri dish. Despite this, at least 24 hours of inactivity was left between days where different species were tested, and equipment was cleaned thoroughly.

It is understood based on early studies that arachnids such as spiders reduce their metabolic rates in response to durations of involuntary fasting and influxes in temperature (Anderson, 1970; Anderson, 1974). Theoretically, mites should require a similar resting pattern to ensure that they are able to function appropriately. Observations on the mites' resting periods were difficult to carry out due to the proliferation of individuals in each colony. Post-mortem, the mites became rapidly desiccated, suggesting that the mites that were stationary and attached to the substrate were in fact still alive and resting. Upon observation, the individual mites evidently did not carry out this behaviour simultaneously, meaning that their activity levels were not clock dependant. As both of these species are colonial and are rarely observed singly, it can be assumed that the function of this behaviour is to increase colony vigilance and reduce the risk of predation and mass mortality. As both species appeared to be cathemeral, it meant that the light inflicted upon the mites did not affect their activity patterns, however it extinguished the potential of *T. putrescentiae* being able to use light patches as navigational aids (Gonçalves-Souza, *et al*. 2014).

This study presented several opportunities to try and apply novel and creative methods to each of the experiments that were carried out. A method was discussed whereby a material impermeable to magnetic fields could be used to construct the blackened box. This would mean that the Earth's external magnetic field could not be tested under these conditions, however weak artificial mimics could be used within the box without environmental magnetic noise affecting the results. The most effective material for this construction appeared to be mu-metal. Mu-metal is a highly conductive alloy often used to protect equipment and experiments from external magnetic fields in institutions around the world (Brake, *et al*. 1991). A small mu-metal chamber could potentially have been constructed to test artificial magnetic fields on the mites within, however this idea was abandoned as time and money was relatively scarce.

The overall effectiveness and power of the results that were yielded from these experiments could potentially have been significantly improved. To achieve this, more time could have been spent concentrating on a single experiment to attempt to achieve the results that were ultimately successfully gathered. This would have resulted in a larger sample size and more time could have been allotted for counting the mites under the microscope. The considerable gap in the literature surrounding the magnetoreceptive capabilities of Acarid mites meant that the initial methods and experiments that were used required trial and error treatment. This took a considerable proportion of time to carry out. This was to ensure that the experimental design was unflawed as many confounding factors could have potentially hindered the final results. Alongside the primary experiments that were conducted, other avenues of potential experimental designs were explored from the literature. A potential T-maze design utilised to present a binary choice for focal test species using 2 artificial magnetic coils was proposed in 2008 by Gegear, *et al*. This method was originally intended to test magnetosensitivity in *Drosophila melanogaster*, however with the appropriate measurement alterations it was hypothesised that it could also be used to treat both *Tyrophagus putrescentiae* and *Tyrophagus longior*. Because of this, future studies should focus partly on constructing the T-maze experimental arena, or a similar experimental design to test the directional behaviour of the two *Tyrophagus* mite species. This is because the T-maze would provide a more controlled experimental environment than the petri dishes due to a lower mite escape rate and a more easily controlled and manipulated artificial magnet setup. The T-maze experiment could also be used in future studies to determine whether *T. longior* is capable of learning geographical points treated with magnetic fields. This simultaneously may also be used to explain whether these mites are able to be deterred by specific magnetic intensities to repel them from desirable foodstuffs. Another method that was proposed involved the use of a disintegration technique on the mites. This method was proposed as a way of determining whether the *Tyrophagus* mites possessed an iron-based magnetoreception mechanism. To achieve this, the mites were to be collected in species groups with measures in place to ensure that there was no interspecies contamination. They would then be incinerated into a fine dust which would be genetically analysed. When the mites had been farmed within the tissue flasks for a sufficient length of time with a large enough food source, they began crowding around the lid. Therefore, this meant that they could be removed from the flask and analysed with minimal flour contamination. A washing-up detergent can be used to separate most of the remaining flour from the mites. The hypothesis was that if iron was found in the DNA sequences of the ashen mites, then there was a possibility that the mites could possess an iron-based magnetoreceptor if the results from the related experiments suggested that the mites were capable of magnetoreception. The problem with this method however, is that iron is an essential element found in the bodies of most organisms including mites, as a component of their body composition as well as a biproduct from food, prey and the environment (Zaitsev & van Straalen, 2001; Rousch, *et* al. 2009). This experiment could, however potentially serve as an interesting preliminary investigation for future studies.

Conclusion

Prior to the initiation of this study, it was hypothesised that both *Tyrophagus longior* and *Tyrophagus putrescentiae* would be able to sense magnetic fields. This was assumed based on the fact that the mites are sister species. Despite this, if it was to be discovered that only one of the two species could use magnetoreception, then it was predicted that *Tyrophagus longior* would be the most likely to possess this capability. This was based on the knowledge that *Tyrophagus longior* does not possess eyes, meaning that along with other potentially heightened senses such as olfaction, it would require another sense to compensate for the lack of vision. Both of these species occupy similar niches and live in colonies with almost identical structures and behaviours. These niches are often complex and relatively unpredictable with constant changes. This means that navigation and orientation are essential to maintain colony structure and reduce mortality rates.

T. longior was discovered to orientate itself towards the South-South West compass points, whereas *T. putrescentiae* appeared to show a uniform distribution across the majority of the compass points. Because of the uniformity of the directional behaviour of *T. putrescentiae*, it is assumed that this species is reliant on visual cues to influence directional preference. This is because their only sense that they were able to use effectively during the blackened box experiments was vision. Because the food-based environment was consistent throughout the experimental arena, it appeared to produce a random movement effect in the individual mites. Food size preferences may also have been an individually subjective factor that influenced the mites' behaviour.

These results provide an insight into the potential magnetosensory capabilities of mite species in general. Future studies may incorporate several different species of the *Tyrophagus* genus to further compare sister species. Mite species which possess eyes function as the experimental controls, as it is predicted and supported by the results in this study that these animals may not require a magnetosensory mechanism to orientate and navigate. Other methods involving binary choice experiments should be further implemented with a higher number of repetitions to make proceedings more efficient and to make the results more powerful. The structure of the colonies of *Tyrophagus* mites should also be investigated further, to provide more insight into why these mites preferentially direct themselves towards the south western direction. The husbandry involved with accommodating

Tyrophagus mites is both time efficient and inexpensive, suggesting that they could be useful for future laboratory experiments focussing on animal magnetoreception. Ultimately, the results from this study function as evidence to support that there may be many overlooked species within the animal kingdom that in future studies could serve as essential model species in the field of magnetoreception. The mechanisms that *Tyrophagus longior* uses in order to align itself is not yet understood. Based on these results, this should be investigated further during future studies with more resources and time to improve the knowledge on this subject and on this specific potential model species. Experiments using magnetic field manipulations should also be undertaken to fully understand whether *T. longior*'s alignment capabilities are in fact based on magnetoreception, or if they use phenomena that could not be controlled during the experiments carried out during this study. It is unknown whether *Tyrophagus putrescentiae* possesses a magnetic sense but does not require it when light is available. Therefore, it would benefit knowledge on this species and potentially species of other genera to investigate whether this sense can be used as a compensatory sense when all others are present but inhibited.

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References

Acosta-Avalos, D., Wajnberg, E., Oliveira, P. S., Leal, I., Farina, M., Esquivel, D. M. 1999. Isolation of magnetic nanoparticles from *Pachycondyla marginata* ants. Journal of Experimental Biology. **202**, 2687-2692

Anderson, J. F. 1970. Metabolic rates of spiders. Comparative Biochemistry and Physiology. **33**, 51-72, doi: 10.1016/0010-406X(70)90483-4

Anderson, J. F. 1974. Responses to starvation in the spiders *Lycosa lenta* Hentz and *Filistata hibernalis* (Hentz). Ecology. **55** (3), 576-585, doi: 10.2307/1935148

Aygun, O., Yaman, M., Durmaz, H. 2007. A survey on occurrence of *Tyrophagus putrescentiae* (Acari: Acaridae) in Surk, a traditional Turkish dairy product. Journal of Food Engineering. **78** (3), 878-881, doi: 10.1016/j.foodeng.2005.11.029

Baker, A. S. and Swan, M. C. 2013. A puzzling domestic infestation of the storage mite *Tyrophagus longior*. Journal of Stored Products Research. **54**, 64-66, doi: 10.1016/j.jspr.2013.05.004

Baker, R. R. and Mather, J. G. 1982. Magnetic compass sense in the large yellow underwing moth, *Noctua pronuba* L. Animal Behaviour. **30** (2), 543-548, doi: 10.1016/S0003-3472(82)80067-5

Begall, S., Červený, J., Neef, J., Vojtěch, O., Burda, H. 2008. Magnetic alignment in grazing and resting cattle and deer. Proceedings of the National Academy of Sciences of the United States of America. **105** (36), 13451-13455, doi: 10.1073/pnas.0803650105

Blakemore, R. 1975. Magnetotactic bacteria. Science. **4212** (190), 377-379

Boles, L. C. and Lohmann, K. J. 2003. True navigation and magnetic maps in spiny lobsters. Nature. **421**, 60-63

Bonnar, E., Eustace, P., Powell, F. C. 1993. The *Demodex* mite population in rosacea. Journal of the American Academy of Dermatology. **28** (3), 443-448, doi: 10.1016/0190-9622(93)70065-2

Brake, H. J. M. t., Wieringa, H. J., Rogalla, H. 1991. Improvement of the performance of a mu-metal magnetically shielded room by means of active compensation (biomagnetic applications). Measurement Science and Technology. **2** (7), 596-601

Burda, H., Begall, S., Červený, J., Neef, J., Němec, P. 2009. Extremely low-frequency electromagnetic fields disrupt magnetic alignment of ruminants. Proceedings of the National Academy of Sciences of the United States of America. **106** (14), 5708-5713, doi: 10.1073/pnas.0811194106

Buxton, J. H. 1989. *Tyrophagus longior* (Gervais) (Acarina; Acaridae) as a pest of ornamentals grown under protection. Plant Pathology. **38** (3), 447-448, doi: 10.1111/j.1365-3059.1989.tb02167.x

Carvalho, M. M., Oliveira, E. E., Matioli, A. L., Ferreira, C. L. L., Silva, N. M. D., Lindner, J. D. D. 2018*a*. Stored products mites in cheese ripening: Health aspects, technological and regulatory challenges in Brazil. Journal of Stored Products Research. **76**, 116-121, doi: 10.1016/j.jspr.2018.01.010

Carvalho, M. M., Silva, N. M. D., Matioli, A. L., Oliveira, E. E., Ferreira, C. L. L., Lindner, J. D. D. 2018*b*. Morphological and molecular characteristics of stored-product mites found on Brazilian ripened cheeses. Journal of Stored Products Research. **79**, 79-82, doi: 10.1016/j.jspr.2018.09.003

Cashmore, A. R., Jarillo, J. A., Wu, Y. J., Liu, D. 1999. Cryptochromes: blue light receptors for plants and animals. Science. **284** (5415), 760-765, doi: 10.1126/science.284.5415.760

Červený, J., Begall, S., Koubek, P., Nováková, P., Burda, H. 2011. Directional preference may enhance hunting accuracy in foraging foxes. Animal Behaviour. **7** (3), 355-357, doi: 10.1098/rsbl.2010.1145

Chmiel, K., Herberstein, M. E., Elgar, M. A. 2000. Web damage and feeding experience influence web site tenacity in the orb-web spider *Argiope keyserlingi* Karsch. Animal Behaviour. **60** (6), 821-826, doi: 10.1006/anbe.2000.1541

Coyle, F. A. 1983. Aerial dispersal by mygalomorph spiderlings (Araneae, Mygalomorphae). Journal of Arachnology. **11** (2), 283-286

Crish, S. D., Comer, C. M., Marasco, P. D., Catania, K. C. 2003. Somatosensation in the superior colliculus of the star-nosed mole. Journal of Comparative Neurology. **464** (4), 415-425, doi: 10.1002/cne.10791

Cutcher, J. 1973. The critical equilibrium activity of nonfeeding *Tyrophagus putrescentiae* (Acarina: Acaridae). Annals of the Entomological Society of America. **66** (3), 609-611, doi: 10.1093/aesa/66.3.609

Dunlop, J. A. 2010. Geological history and phylogeny of Chelicerata. Arthropod Structure & Development. **39** (2-3), 124-142, doi: 10.1016/j.asd.2010.01.003

Edelman, N. B., Fritz, T., Nimpf, S., Pichler, P., Lauwers, M., Hickman, R. W., Papadaki-Anastasopoulou, A., Ushakova, L., Heuser, T., Resch, G. P., Saunders, M., Shaw. J. A., Keays, D. A. 2014. No evidence for intracellular magnetite in putative vertebrate magnetoreceptors identified by magnetic screening. Proceedings of the National Academy of Sciences of the United States of America. **112**, 262-267, doi: 10.1073/pnas.1407915112

Eder, S. H. K., Cadiou, M., Muhamad, A., McNaughton, P. A., Kirschvink, J. L., Winklhofer, M. 2012. Magnetic characterization of isolated candidate vertebrate magnetoreceptor cells. Proceedings of the National Academy of Sciences of the United States of America. **109** (30), 12022-12027, doi: 10.1073/pnas.1205653109

Fan, Q. H. and Zhang, Z. Q. 2007*a*. *Tyrophagus* (Acari: Astigmata: Acaridae). Fauna of New Zealand. **56**, 5-291, doi: 10.7931/J2/FNZ.56

Fan, Q. H. and Zhang, Z. Q. 2007*b*. Revision of some species of *Tyrophagus* (Acari: Acaridae) in the Oudemans collection. Systematic and Applied Acarology. **12** (3), 253-280, doi: 10.11158/saa.12.3.11

Fleissner, G., Stahl, B., Thalau, P., Falkenberg, G., Fleissner, G. 2007. A novel concept of Fe-mineral-based magnetoreception: histological and physiochemical data from the upper beak of homing pigeons. Naturwissenschaften. **94** (8), 631-642, doi: 10.1007/s00114-007-0236-0

Fleissner, G., Holtkamp-Rötzler, E., Hanzlik, M., Winklhofer, M., Fleissner, G., Petersen, N., Wiltschko, W. 2003. Ultrastructural analysis of a putative magnetoreceptor in the beak of homing pigeons. Journal of Comparative Neurology. **458** (4), 350-360, doi: 10.1002/cne.10579

Foley, L. E. and Emery, P. 2019. *Drosophila* cryptochrome: variations in blue. Journal of Biological Rhythms. **35**, 16-27, doi: 10.1177/0748730419878290

Freitag, J. A. and Kells, S. A. 2013. Efficacy and application considerations of selected residual acaricides against the mold mite *Tyrophagus putrescentiae* (Acari: Acaridae) in simulated retail habitats. Journal of Economic Entomology. **106** (4), 1920-1926, doi: 10.1603/EC13038

Galibert, F., Azzouzi, N., Quignon, P., Chaudieu, G. 2016. The genetics of canine olfaction. Journal of Veterinary Behaviour. **16**, 86-93, doi: 10.1016/j.jveb.2016.06.012

García, N. 2004. Efforts to control mites on Iberian ham by physical methods. Experimental and Applied Acarology. **32** (1-2), 41-50, doi: 10.1023/B:APPA.0000018165.80420.c9

Gegear, R. J., Casselman, A., Waddell, S., Reppert, S. M. 2008. Cryptochrome mediates light-dependent magnetosensitivity in *Drosophila melanogaster*. Nature. **454**, 1014-1018

Gonçalves-Souza, T., Santos, A. J., Romero, G. Q., Lewinsohn, T. M. 2014. Conservation along a hotspot rim: spiders in Brazilian coastal restingas. Biodiversity and Conservation. **24**, 1131-1146, doi: 10.1007/s10531-014-0846-8

Gould, J. L., Kirschvink, J. L., Deffeyes, K. S. 1978. Bees have magnetic remanence. Science. **201** (4360), 1026-1028

Gould, J. L., Kirschvink, J. L., Deffeyes, K. S., Brines, M. L. 1980. Orientation of demagnetised bees. Journal of Experimental Biology. **86**, 1-8

Greenstone, M. H. 1982. Ballooning frequency and habitat predictability in two wolf spider species (Lycosidae: *Pardosa*). Florida Entomologist. **65**, 83-89

Hage-Hamsten, M. V. and Johansson, S. G. O. 1992. Storage mites. Experimental and Applied Acarology. **16** (1-2), 117-128, doi: 10.1007/BF01201495

Hayaloglu, A. A. and Fox, P. F. 2008. Cheeses of Turkey: 3. Varieties containing herbs or spices. Dairy Science & Technology. **88** (2), 245-256, doi: 10.1051/dst:2007015

Hert, J., Jelinek, L., Pekarek, L., Pavlicek, A. 2011. No alignment of cattle along geomagnetic field lines found. Journal of Comparative Physiology A. **197** (6), 677-682, doi: 10.1007/s00359-011-0628-7

Holland, R. A., Thorup, K., Vonhof, M. J., Cochran, W. W., Wikelski, M. 2006. Bat orientation using Earth’s magnetic field. Nature. **444** (1720), 702

Holland, R. A. 2010. Differential effects of magnetic pulses on the orientation of naturally migrating birds. Journal of the Royal Society Interface. **7** (52), 1617-1625, doi: 10.1098/rsif.2010.0159

Hölldobler, B., Janssen, E., Bestmann, H. J., Kern, F., Leal, I. R., Oliveira, P. S., König, W. A. 1996. Communication in the migratory termite-hunting ant *Pachycondyla* (= *Termitopone*) *marginata* (Formicidae, Ponerinae). Journal of Comparative Physiology A. **178**, 47-53, doi: 10.1007/BF00189589

Hubert, J., Stejskal, V., Kubátová, A., Munzbergová, Z., Váňová, M., Žd’árková, E. 2003. Mites as selective fungal carriers in stored grain habitats. Experimental and Applied Acarology. **29** (1-2), 69-87, doi: 10.1023/A:1024271107703

Humphrey, J. A. C. 1987. Fluid mechanic constraints on spider ballooning. Oecologia. **73** (3), 469-477, doi: 10.1007/BF00385267

Johnsen, S. and Lohmann, K. J. 2008. Magnetoreception in animals. Physics Today. **61** (3), 29-35, doi: 10.1063/1.2897947

Kheradmand, K., Kamali, K., Fathipour, Y., Goltapeh, E. M. 2007. Development, life table and thermal requirement of *Tyrophagus putrescentiae* (Astigmata: Acaridae) on mushrooms. Journal of Stored Products Research. **43** (3), 276-281, doi: 10.1016/j.jspr.2006.06.007

Kramer, G. 1961. Biology and comparative physiology of birds: volume 2, volume II. 341-369, Academic Press London

Kuwahara, Y., Ishii, S., Fukami, H. 1975. Neryl formate: alarm pheromone of the cheese mite, *Tyrophagus putrescentiae* (Schrank) (Acarina, Acaridae). Experientia. **31** (10), 1115-1116, doi: 10.1007/BF02326740

Kuwahara, Y., Fukami, H., Ishii, S., Matsumoto, K., Wada, Y. 1979. Pheromone study on acarid mites II Presence of the alarm pheromone in the mold mite, *Tyrophagus putrescentiae* (Schrank) (Acarina: Acaridae) and the site of its production. Medical Entomology and Zoology. **30** (4), 309-314, doi: 10.7601/mez.30.309

Leal, W. S., Nakano, Y., Kuwahara, Y., Nakao, H., Suzuki, T. 1988. Pheromone study of acarid mites XVII. Identification of 2-hydroxy-6-methyl-benzaldehyde as the alarm pheromone of the acarid mite *Tyrophagus perniciosus* (Acarina: Acaridae), and its distribution among related mites. Applied Entomology and Zoology. **23** (4), 422-427, doi: 10.1303/aez.23.422

Li, Q. H. and Yang, H. Q. 2007. Cryptochrome signalling in plants. Photochemistry and Photobiology. **83**, 94-101, doi: 10.1562/2006-02-28-IR-826

Lin, C. and Shalitin, D. 2003. Cryptochrome structure and signal transduction. Annual Review of Plant Biology. **54**, 469-496, doi: 10.1146/annurev.arplant.54.110901.160901

Lin, L. H., Edmonds, D. T., Vollrath, F. 1995. Structural engineering of an orb-spider’s web. Nature. **373**, 146-148

Lohmann, K., Pentcheff, N., Nevitt, G., Stetten, G., Zimmer-Faust, R., Jarrard, H., Boles, L. 1995. Magnetic orientation of spiny lobsters in the ocean: experiments with undersea coil systems. Journal of Experimental Biology. **198**, 2041-2048

Maeda, K., Robinson, A. J., Henbest, K. B., Hogben, H. J., Biskup, T., Ahmad, M., Schleicher, E., Weber, S., Timmel, C. R., Hore, P. J. 2012. Magnetically sensitive light-induced reactions in cryptochrome are consistent with its proposed role as a magnetoreceptor. Proceedings of the National Academy of Sciences of the United States of America. **109** (13), 4774-4779, doi: 10.1073/pnas.1118959109

Maher, B. A. 1998. Magnetite biomineralization in termites. Proceedings of the Royal Society B. **265** (1397), 733-737, doi: 10.1098/rspb.1998.0354

Meguro, R., Asano, Y., Odagiri, S., Li, C., Iwatsuki, H., Shoumura, K. 2005. The presence of ferric and ferrous iron in the nonheme iron store of resident macrophages in different tissues and organs: histochemical demonstrations by the perfusion-Perls and -Turnbull methods in the rat. Archives of Histology and Cytology. **68** (3), 171-183, doi: 10.1679/aohc.68.171

Meibus, R. E. and Kraal, G. 2005. Structure and function of the spleen. Nature Reviews Immunology. **5**, 606-616

Miyamoto, T., Oshima, S., Ishizaki, T., Sato, S. 1968. Allergenic identity between the common floor mite (*Dermatophagoides farinae* Hughes, 1961) and house dust as a causative antigen in bronchial asthma. Journal of Allergy. **42**, 14-28, doi: 10.1016/0021-8707(68)90128-7

Mouritsen, H. and Hore, P. J. 2012. The magnetic retina: light dependant and trigeminal magnetoreception in migratory birds. Current Opinion in Neurobiology. **22** (2), 343-352, doi: 10.1016/j.conb.2012.01.005

Mouritsen, H. and Ritz, T. 2005. Magnetoreception and its use in bird navigation. Current Opinion in Neurobiology. **15**(4), 406-414, 10.1016/j.conb.2005.06.003

Muheim, R., Bäckman, J., Åkesson, S. 2002. Magnetic compass orientation in European robins is dependent on both wavelength and intensity of light. Journal of Experimental Biology. **205**, 3845-3856

Murillo, P., Klimov, P., Hubert, J., OConnor, B. 2018. Investigating species boundaries using DNA and morphology in the mite *Tyrophagus curvipenis* (Acari: Acaridae), an emerging invasive pest, with a molecular phylogeny of the genus *Tyrophagus*. Experimental and Applied Acarology. **75**, 167-189, doi: 10.1007/s10493-018-0256-9

Newton, K. C. and Kajiura, S. M. 2017. Magnetic field discrimination, learning, and memory in the yellow stingray (*Urobatis jamaicensis*). Animal Cognition. **4** (20), 603-614, doi: 10.1007/s10071-017-1084-8

Ohiagu, C. E. 1979. A quantitative study of seasonal foraging by the grass harvesting termite, *Trinervitermes geminatus* (Wasmann), (Isoptera, Nasutitermitinae) in Southern Guinea savannah, Mokwa, Nigeria. Oecologia. **40** (2), 179-188, doi: 10.1007/BF00347935

Ozturk, N., Selby, C. P., Annayev, Y., Zhong, D., Sancar, A. 2011. Reaction mechanism of *Drosophila* cryptochrome. Proceedings of the National Academy of Sciences of the United States of America. **108** (2), 516-521, doi: 10.1073/pnas.1017093108

Parzefall, J., Durand, J. P., Richard, B. 1980. Chemical communication in *Necturus maculosus* and his cave-living relative *Proteus anguinus* (Proteidae, Urodela). Ethology. **53** (2), 133-138, doi: 10.1111/j.1439-0310.1980.tb01045.x

Perdeck, A. C. 1958. Two types of orientation in migrating starlings, *Sturnus vulgaris* L., and chaffinches, *Fringella coelebs* L., as revealed by displacement experiments. Ardea. **55**, 1-2, doi: 10.5253/arde.v1i2.p1

Phillips, J. B. 1977. Use of the earth's magnetic field by orienting cave salamanders (*Eurycea lucifuga*). Journal of Comparative Physiology. **121** (2), 273-288, doi: 10.1007/BF00609616

Phillips, J. B. and Sayeed, O. 1993. Wavelength-dependent effects of light on magnetic compass orientation in *Drosophila melanogaster*. Journal of Comparative Physiology A. **172** (3), 303-308, doi: 10.1007/BF00216612

Řezáč, M., Tošner, J., Heneberg, P. 2018. Habitat selection by threatened burrowing spiders (Araneae: Atypidae, Eresidae) of central Europe: evidence base for conservation management. Journal of Insect Conservation. **22**, 135-149, doi: 10.1007/s10841-018-0048-x

Ribrioux, Y. 1970. Injuries by a mite to cucumbers in greenhouse cultures on balls of straw. Phytoma. **22** (223), 27-29

Rickli, M. and Leuthold, R. H. 1988. Homing in harvester termites: evidence of magnetic orientation. Ethology. **77** (3), 209-216, doi: 10.1111/j.1439-0310.1988.tb00204.x

Rieger, D., Stanewsky, R., Helfrich-Förster. 2003. Cryptochrome, compound eyes, Hofbauer-Buchner eyelets, and ocelli play different roles in the entrainment and masking pathway of the locomotor activity rhythm in the fruit fly *Drosophila melanogaster*. Journal of Biological Rhythms. **18** (5), 377-391, doi: 10.1177/0748730403256997

Ritz, T., Adem, S., Schulten, K. 2000. A model for photoreceptor-based magnetoreception in birds. Biophysical Journal. **78** (2), 707-718, doi: 10.1016/S0006-3495(00)76629-X

Ritz, T., Thalau, P., Phillips, J. B., Wiltschko, R., Wiltschko, W. 2004. Resonance effects indicate a radical pair mechanism for avian magnetic compass. Nature. **429**, 177-180

Ritz, T., Yoshii, T., Helfrich-Foerster, C., Ahmad, M. 2010. Cryptochrome: a photoreceptor with the properties of a magnetoreceptor? Communicative and Integrative Biology. **3**, 24-27, doi: 10.4161/cib.3.1.9865

Rodgers, C. T. and Hore, P. J. 2009. Chemical magnetoreception in birds: the radical pair mechanism. Proceedings of the National Academy of Sciences of the United States of America. **106** (2), 353-360, doi: 10.1073/pnas.0711968106

Rousch, J. M., Simmons, T. W., Kerans, B. L., Smith, B. P. 2009. Relative acute effects of low pH and high iron on the hatching and survival of the water mite (*Arrenurus manubriator*) and the aquatic insect (*Chironomus riparius*). Environmental Toxicology and Chemistry. **16** (10), 2144-2150, doi: 10.1002/etc.5620161022

Sabelis, M. W. and Bakker, F. M. 1992. How predatory mites cope with the web of the tetranychid prey: a functional view on dorsal chaetotaxy in the Phytoseiidae. Experimental and Applied Acarology. **16** (3), 203-225, doi: 10.1007/BF01193804

Sánchez-Ramos, I., Alvarez-Alfageme, F., Castañera, P. 2007. Effects of relative humidity on development, fecundity and survival of three storage mites. Experimental and Applied Acarology. **41** (1-2), 87-100, doi: 10.1007/s10493-007-9052-7

Schulten, K., Swenberg, C. E., Weller, A. 1978. A biomagnetic sensory mechanism based on magnetic field modulated coherent electron spin motion. International Journal of Research in Physical Chemistry and Chemical Physics. **111**, 1-5, doi: 10.1524/zpch.1978.111.1.001

Simson, J. V. and Spicer, S. S. 1972. Ferritin particles in macrophages and in associated mast cells. Journal of Cell Biology. **52** (3), 536-541, doi: 10.1083/jcb.52.3.536

Slaby, P., Tomanova, K., Vacha, M. 2013. Cattle on pastures do align along the North-South axis, but the alignment depends on herd density. Journal of Comparative Physiology A. **199** (8), 695-701, doi: 10.1007/s00359-013-0827-5

Sotthibandhu, S. and Baker, R. R. 1979. Celestial orientation by the large yellow underwing moth, *Noctua pronuba* L. Animal Behaviour. **27** (3), 786-800, doi: 10.1016/0003-3472(79)90015-0

Terho, E. O., Husman, K., Vohlonen, I., Rautalahti, M., Tukiainen, H. 1985. Allergy to storage mites or cow dander as a cause of rhinitis among Finnish dairy farmers. European Journal of Allergy and Clinical Immunology. **40**, 23-26, doi: 10.1111/j.1398-9995.1985.tb04150.x

Thind, B. B. 2005. A new versatile and robust mite trap for detection and monitoring of storage mites in the cereal and allied industries. Experimental & Applied Acarology. **35** (1-2), 1-15, doi: 10.1007/s10493-004-2950-z

Treiber, C. D., Salzer, M. C., Riegler, J., Edelman, N., Sugar, C., Breuss, M., Pichler, P., Cadiou, H., Saunders, M., Lythgoe, M., Shaw, J., Keays, D. A. 2012. Clusters of iron-rich cells in the upper beak of pigeons are macrophages not magnetosensitive neurons. Nature. **484**, 367-370

Twitty, V., Grant, D., Anderson, O. 1964. Long distance homing in the newt *Taricha rivularis*. Proceedings of the National Academy of Sciences of the United States of America. **51**, 51-58, doi: 10.1073/pnas.51.1.51

Twitty, V., Grant, D., Anderson, O. 1966. Course and timing of the homing migration in the newt *Taricha rivularis*. Proceedings of the National Academy of Sciences of the United States of America. **56** (3), 864-871, doi: 10.1073/pnas.56.3.864

Twitty, V., Grant, D., Anderson, O. 1967. Home range in relation to homing in the newt *Taricha rivularis* (Amphibia: Caudata). Copeia. **1967** (3), 649-653, doi: 10.2307/1442244

Wang, J. and Pantopoulos, K. 2011. Regulation of cellular iron metabolism. Biochemical Journal. **434** (3), 365-381, doi: 10.1042/BJ20101825

Wang, K. and Ritz, T. 2006. Zeeman resonance for radical-pair reactions in weak static magnetic fields. Molecular Physics. **104** (10-11), 1649-1658, doi: 10.1080/00268970600564869

Wang, Y., Pan, Y., Parsons, S., Walker, M., Zhang, S. 2007. Bats respond to polarity of a magnetic field. Proceedings of the Royal Society B. **274** (1627), 2901-2905, doi: 10.1098/rspb.2007.0904

Waters, D. and Jones, G. 1996. The peripheral auditory characteristics of noctuid moths: responses to the search-phase echolocation calls of bats. Journal of Experimental Biology. **199**, 847-856

Wharton, G. W. 1976. Review article: house dust mites. Journal of Medical Entomology. **12** (6), 577-621, doi: 10.1093/jmedent/12.6.577

Wiltschko, R., Munro, U., Ford, H., Stapput, K., Wiltschko, W. 2008. Light-dependant magnetoreception: orientation behaviour of migratory birds under dim red light. Journal of Experimental Biology. **211**, 3344-3350, doi: 10.1242/jeb.020313

Wiltschko, R. and Wiltschko, W. 2006. Magnetoreception. Bioessays. **28** (2), 157-168, doi: 10.1002/bies.20363

Wiltschko, R. and Wiltschko, W. 2014. Sensing magnetic directions in birds: radical-pair processes involving cryptochrome. Biosenses. **4**, 221-242, doi: 10.3390/bios4030221

Wiltschko, R. and Wiltschko, W. 2019. Magnetoreception in birds. Journal of the Royal Society Interface. **16** (158), 20190295, doi: 10.1098/rsif.2019.0295

Wiltschko, W. and Wiltschko, R. 1972. Magnetic compass of European robins. Science. **176** (4030), 62-64

Wiltschko, W. and Wiltschko, R. 2002. Magnetic compass orientation in birds and its physiological basis. Naturwissenschaften. **89** (10), 445-452, doi: 10.1007/s00114-002-0356-5

Yoshii, T., Ahmad, M., Helfrich-Förster, C. 2009. Cryptochrome mediates light-dependent magnetosensitivity of *Drosophila*'s circadian clock. PLoS Biology. **4** (7), e1000086, doi: 10.1371/pbio.1000086

Zaitsev, A. S., and van Straalen, N. M. 2001. Species diversity and metal accumulation in oribatid mites (Acari, Oribatida) of forests affected by a metallurgical plant. Pedobiologia. **45** (5), 467-479, doi: 10.1078/0031-4056-00100

Zhang, X., Hendrix, J. D., Campbell, Y. L., Phillips, T. W., Goddard, J., Cheng, W. H., Kim, T., Wu, T. L., Schilling, M. W. 2018. Biology and integrated pest management of *Tyrophagus putrescentiae* (Schrank) infesting dry cured hams. Journal of Stored Products Research. **79**, 16-28, doi: 10.1016/j.jspr.2018.08.001

Appendix 1 – Mites crowded at lid of tissue flask

(All photographs were taken using a Canon digital camera under laboratory conditions.)

Appendix 2: Raw data table representing the directional behaviour of 10 colonies of *Tyrophagus longior* mites.

This data was collected during experiment 2.4.

***Tyrophagus longior* (°)**
174
269
269
134
134
269
269
174
174
174

Appendix 3: Raw data table representing the directional behaviour of 10 colonies of Tyrophagus putrescentiae mites.

This data was collected during experiment 2.4.

***Tyrophagus putrescentiae* (°)**
90
90
359
21
269
179
359
90
269
90