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ORIGINAL RESEARCH ARTICLE

Magnets, magnetic field fluctuations and geomagnetic disturbances impair the homing ability of honey bees (*Apis mellifera*)

Thomas E Ferrari[1]*

[1]Botany & Horticulture, Pollen Bank, Bakersfield, CA, USA.

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*Corresponding author: Email: pollenbank@sbcglobal.net

Summary

Adult honey bees possess a magnetoreception sense similar to other animals such as birds, fish, whales, dolphins, insects, and microbes. Organisms use this sense for orientation purposes during migrations and traveling long distances. The sudden loss and disappearance of honey bees from a hive or apiary has been plaguing beekeepers for more than a century. This age-old disorder predates virtually all herbicides and pesticides, many diseases or pests and honey bee management protocols. To investigate possible involvement of a magnetoreception disorder (MRD) with loss of forager homing abilities: A. magnetized wires were glued to their abdomens; B. foragers were exposed to artificially induced fluctuating magnetic fields; and C. untreated foragers' return rates were monitored during naturally occurring disturbances to Earth's magnetosphere. Treated and untreated foragers were released at varying distances from their hives and their return rates were monitored. Significant differences in their return rates indicated that interactions existed between forager losses and exposure to both static and oscillating magnetic fields, as well as during fluctuations in the Earth's magnetosphere. In addition, D. decreases in untreated forager return rates also correlated with increasing intensity of extraterrestrial protons that entered Earth's atmosphere. Finally, winter colony losses in the northeast USA also correlated with annual geomagnetic storm occurrences. Collectively, these five observations indicate that coronal eruptions on the Sun are involved with interference of a forager's magnetoreception sense here on Earth. How abnormal magnetic fields and fluctuations relate to the epidemiology of honey bee losses is consistent with their behaviour and development.

Los imanes, las fluctuaciones de campos magnéticos y las perturbaciones geomagnéticas afectan la habilidad para volver a la colmena de las abejas melíferas (*Apis mellifera*)

Resumen

ALas abejas melíferas adultas poseen un sentido de magnetorrecepción similar al de otros animales como las aves, los peces, las ballenas, los delfines, otros insectos y ciertos microbios. Los organismos utilizan este sentido con fines de orientación durante las migraciones y viajes de larga distancia. La repentina pérdida y desaparición de abejas melíferas de sus colmenas o colmenares ha estado afectando a los apicultores desde hace más de un siglo. Este viejo problema es virtualmente anterior a la utilización de herbicidas y pesticidas, a muchas enfermedades o plagas y a los protocolos de manejo de abejas melíferas. Con el fin de investigar la posible implicación del desorden de la magnetorrecepción (MRD) en el fenómeno de la pérdida de habilidad para volver a la colmena de las abejas pecoreadoras: A. redes magnéticas fueron pegadas a los abdómenes de las abejas; B. abejas pecoreadoras fueron expuestas a fluctuaciones inducidas en campos magnéticos; y C. pecoreadoras no tratadas fueron monitorizadas para medir su tasa de retorno a la colmena durante la perturbación natural de la magnetosfera en la Tierra. Las pecoreadoras tratadas y no tratadas fueron puestas en libertad a diversas distancias de sus colmenas, y sus tasas de retorno fueron monitorizadas. Las diferencias significativas en sus tasas de retorno indicaron que existen interacciones entre las pérdidas de pecoreadoras y la exposición tanto a campos magnéticos estáticos como a los oscilantes, así como a las fluctuaciones de la magnetosfera terrestre. Asimismo, D. se encontró una correlación entre la disminución en las tasas de retorno de las pecoreadoras y el incremento de la intensidad de los protones extraterrestres que se introdujeron en la atmósfera de la Tierra. Finalmente E. se encontró una correlación entre las pérdidas de colonias durante el invierno en el noreste de EE.UU. y la aparición de las tormentas geomagnéticas anuales. Colectivamente, estas cinco observaciones indicaron que las erupciones en la corona solar interfieren en el sentido de magnetorrecepción de las pecoreadoras en la Tierra. La relación entre las fluctuaciones y anormalidades que se dan en los campos magnéticos y la epidemiología de las pérdidas de abejas melíferas es congruente con su comportamiento y desarrollo.

Keywords: Honey bees, orientation, magnetoreception, homing

Introduction

In 1891, R C Aikin observed a sudden and complete loss of adult honey bees (*Apis mellifera* L.) from colonies in an apiary he managed in Colorado, USA (Aikin, 1897). The hives still contained laying queens, healthy brood and young nurse bees caring for them. Since the adult bees seemed to him to evaporate and were nowhere to be found, he named the syndrome "evaporation." Notably, he reported: "The weather was so warm that there was no loss of brood; and as they had from four to seven combs well filled, the hives were soon very populous again." His observations and the ability of colonies to recover are inconsistent with a contagious disease or pest as causal agents for the sudden "evaporation" of only adult bees.

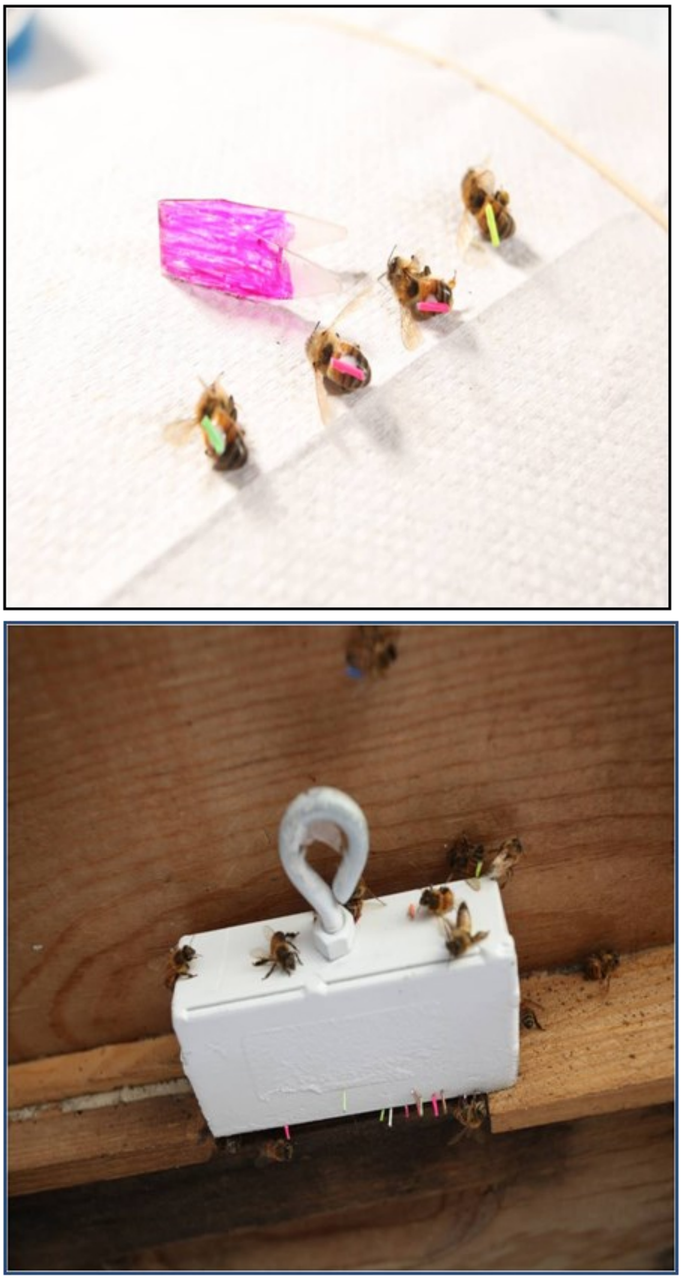

Fig. 1. A. Anesthetized bees with colour-coded wire magnets on abdomens. ***B.*** Magnet over hive entrance and removal of wires from returning foragers.

"Evaporation," "Disappearance Disease," "Dwindling Disease," "Autumn Collapse," "May Disease" and "Colony Collapse Disorder" (CCD) are various names used throughout history to describe similar observations: an unexpected, abrupt and severe loss of adult honey bees from a colony and apiary. Similar phenomena have been re-discovered and re-documented periodically around the world for more than a hundred years (Aikin, 1897; Oertel, 1965; Foote, 1966; Wilson and Menapace, 1979; Finley *et al.,* 1996; Underwood and vanEnglesdorp, 2007; Oldroyd, 2010).

It is important to recognize that honey bee colonies can "collapse," "fail" or "die-off" due to many maladies caused by viruses, fungi, bacteria, microsporidia, mites, pesticides and starvation (Neuman and Carreck, 2010; Ratnieks and Carreck, 2010; Van der Zee *et al.,* 2012; vanEnglesdorp *et al.,* 2012; Spleen *et al.,* 2013). But, what is unique concerning the "evaporation" disorder is the absence of victims: adult bees leave the hive and cannot be found. Therefore, autopsies cannot be performed. This key symptom sets the "disappearance" disorder apart from virtually all other maladies that are not only contagious, but also leave evidence of dead, sick or afflicted bees in or near the hive.

Seven symptoms identify the "dwindling" phenomenon: 1. a sudden, inexplicable loss of adult workers; 2. an absence of sick or dead bees; 3. presence of healthy brood; 4. existence of an egg-laying queen; 5. presence of fit, young adults; 6. an undersized cluster of bees; and 7. the condition is not contagious.

The seventh symptom is significant in that colonies afflicted with the "collapse" disorder can recover or be merged with other colonies without harm; moreover, equipment from affected hives can be used with healthy colonies without severe consequences (Aikin, 1897; Oertel, 1965; Foote, 1966; Wilson and Menapace, 1979; vanEnglesdorp *et al.,* 2008). Despite exhaustive studies, no single and demonstrable cause of CCD symptoms has yet been demonstrated (Cox-Foster *et al.*, 2007; vanEnglesdorp *et al.,* 2009). A study by Bromenshenk *et al.* (2010) linking invertebrate iridescent virus (Family Iridoviridae) with afflicted colonies was not reproducible (Tokarz *et al.*, 2011). Linking iridovirus and *Nosema* with the disorder is inconsistent with true "disappearance disease" because those infectious agents leave symptoms of their presence: dead or deformed bees in or near the hive; bees acting in an erratic crawling behaviour; faecal matter on hive bodies; and, moreover, both are contagious. Not so with the "collapse" disorder: healthy colonies are left behind and no adult bees can be found.

Repeatedly, studies have shown the "evaporation" disorder to be non-transmissible and not due to pathogens or parasites (Foote, 1966; Wilson and Menapace, 1979; Johnson, 2010). For example, extracts of bees from afflicted colonies have been mixed with live bees in small cages, and in no case was there an abnormal death rate (Ortel, 1965). "Combs containing honey and pollen, taken from dead colonies, were given to nuclei. No abnormal death rate was noted; development proceeded normally." (Ortel, 1965). "Colonies that survive the winter quickly build their adult populations. Beekeepers can then split these colonies by removing half of the immature and adult bee population, introducing them into the equipment of a dead colony, and adding a new queen. This practice permits beekeepers to build their colony numbers back up by mid-summer…" (vanEnglesdorp *et al.,* 2008). Also, a seldom recognized detail in many studies involving the "collapse" problem in the USA, is that it predates the introduction of many pesticides (Frazier *et al.,* 2011), diseases and pests which have been a focus of research in recent years, including neonicotinoids (Thany, 2010), *Nosema ceranae* (Williams *et al.,* 2008) and *Varroa destructor* (Wenner and Bushing, 1996), to name a few. A nagging problem with all research to date involving the "collapse" disorder is that only surviving bees were sampled for examination, because missing bees could not be found, resulting in an extraordinary and unavoidable statistical bias in experimental methods (e.g. Bromenshenk *et al.*, 2010; vanEnglesdorp *et al.*, 2009).

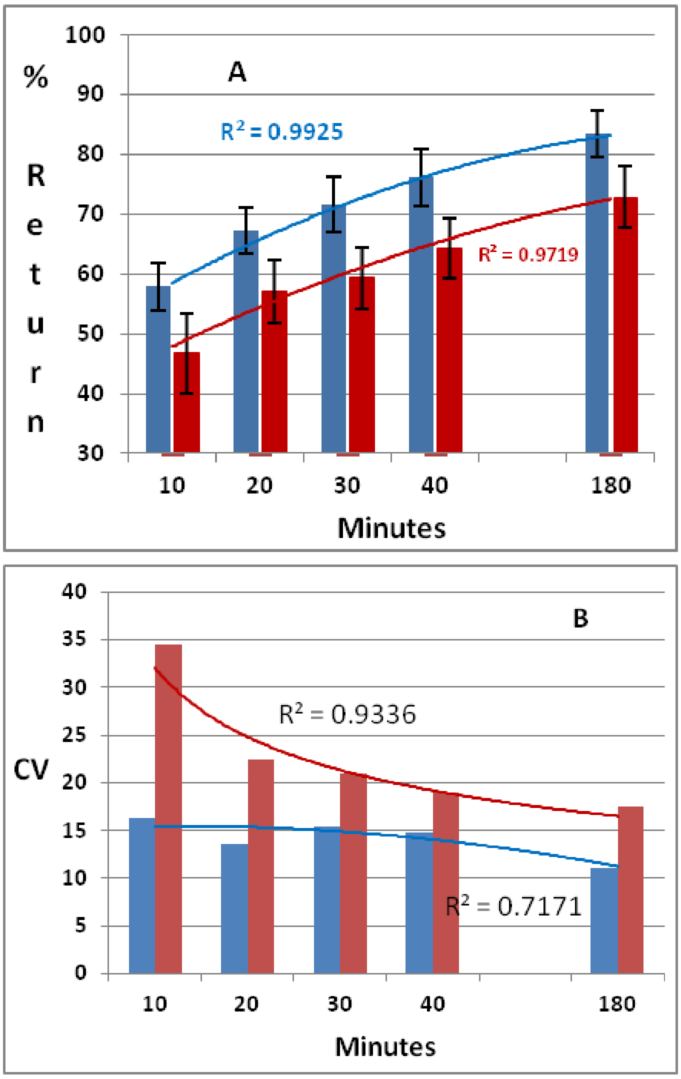

Fig. 2. A. Cumulative return rates at different time intervals for foragers returning with non-magnetized (blue) and magnetized wires (red) on their abdomens. Bees were released 80 m from their hives. Results represent the average of 15 experiments. Error bars are 90% confidence intervals. ***B.*** Coefficient of variation (CV) for returning bees at increasing 10-min. time intervals.

Behavioural scientists have accumulated decades of experimental evidence about honey bees' ability to perceive and orient themselves in magnetic fields. Their findings provide a novel theory as to a cause for the sudden, non-infectious loss of adult bees: it involves a sixth sense, termed "magnetoreception." Numerous organisms, including honey bees, extract directional information from Earth's ambient magnetic field (Lindauer and Martin, 1972; Gould *et al.,* 1978; Kirschvink *et al.*, 1985; Collett and Baron, 1994; Frier *et al.*, 1996; Kirschvink *et al.*, 1997; Gould, 1998; Galland and Pazur, 2005; Johnson and Lohmann, 2008; Frankel, 2009; Wajnberg *et al.,* 2010). A magnetoreceptive sense allows many organisms to use Earth's magnetic "lines" to migrate and travel long distances without using visual landmarks (for example, whales, dolphins, butterflies, salmon, geese, ducks, zebra and turtles). Indeed, experiments indicate that honey bees can be trained to respond to changes in local magnetic fields (Gould *et al.,* 1980; Tomlinsin *et al.,* 1981; Hsu *et al.,* 2010), and their sixth sense can be altered by exposure to abnormal magnetic fields (Lindauer and Martin, 1972; Towne and Gould, 1985; Walker and Bitterman, 1985, 1986, 1989). A magnetoreceptive sense opens the possibility that an environmental stress factor, involving severe fluctuations in Earth's magnetosphere following major coronal eruptions on the Sun, can interfere with a forager's homing ability and thereby lead to bee losses.

Experiments described herein provide evidence that experimentally induced changes in magnetic fields and solar-induced geomagnetic storms produces a "magnetoreception disorder" (MRD) in foragers, which causes them to get lost when returning to their colony. A review of past research indicates that bees use Earth's magnetosphere for orientation and that geomagnetic disturbances were likely to have contributed to, or caused the mysterious bee losses that have been documented in the past.

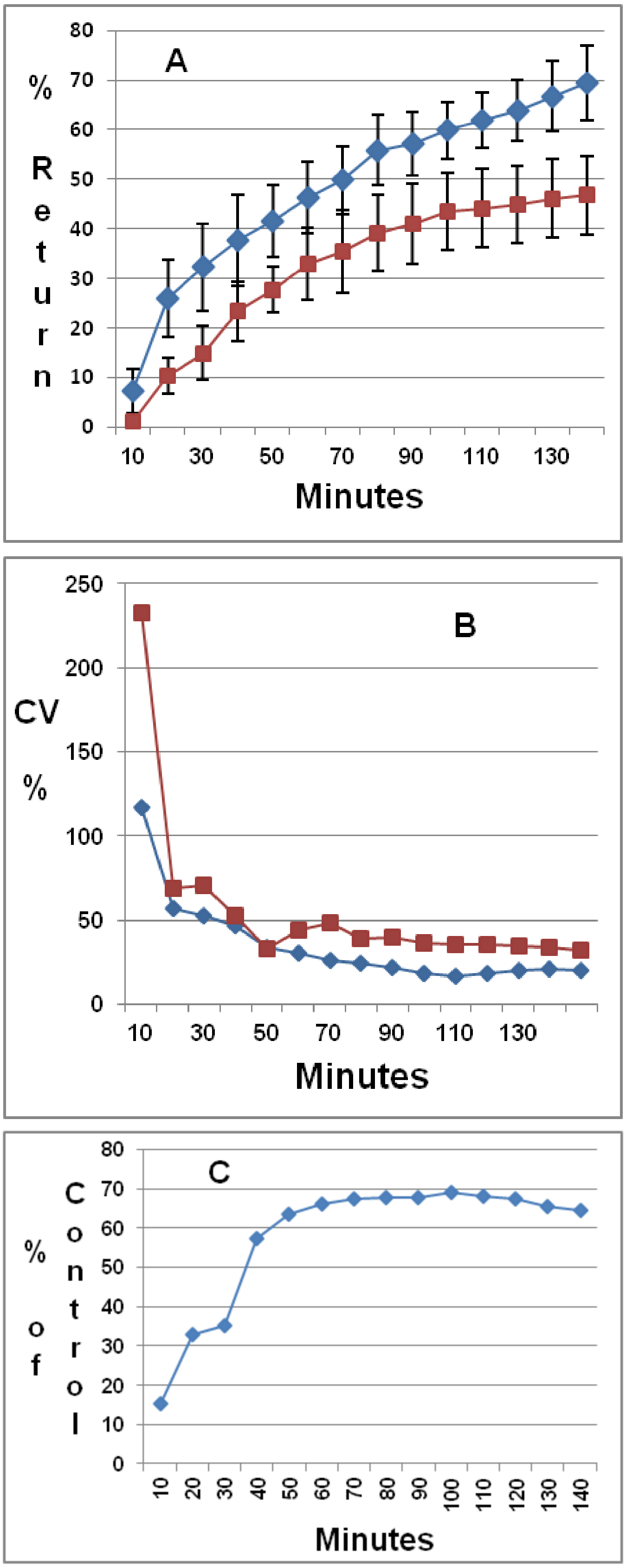

Fig. 3. A. Cumulative return rates of foragers bearing magnetized (red) or non-magnetized (blue) wires when released 800 m from their hives. Error bars are 90% confidence intervals. Each point represents an average of 11 experiments. ***B.*** Coefficient of variation (CV) for return rates. ***C.*** Inhibition of forager homing ability when bearing magnetized wires compared to controls.

Material and methods

Apis mellifera

Homing ability of honey bees was evaluated in the presence and absence of experimentally induced magnetic fields and during uncontrolled, natural fluctuations in Earth's magnetosphere. Colonies were feral swarms collected from suburban areas and maintained in Bakersfield, California, USA. After smoking the entrances of colonies to force guard bees and other non-foragers into hives, entrances were blocked. A few minutes later returning bees were collected by placing clear, plastic specimen cups (120 cc, 5-6 cm diameter) over them as they accumulated above the entrance. Cups were perforated to allow for air circulation. The cups were then slid onto a thin but firm plastic sheet to prevent bees from escaping. Captured bees were anesthetized by cooling them to 3-6°C for approximately 15 min. Bees with pollen on their legs were considered to be pollen gatherers. In one experiment, bees were separated based on colour of pollen pellets to associate them with different foraging sites. Nectar gatherers amongst the remaining bees were identified by gently pressing remaining bees on their abdomens and observing if they exuded a liquid from their mouth. Approximately 15 % to 20 % of them released a fluid that tested positive for glucose using a diabetic glucometer: they were considered to be nectar foragers.

Wire attachment

After nectar and pollen foragers were selected, magnetized and non-magnetized wires were attached to the mid-to-anterior dorsal region of their abdomens with the aid of handmade plastic forceps (Fig. 1A). A thin, flexible plastic strip (2 x 10 cm) with a v-shaped notch (4 x 4 mm) cut into a corner was placed between the thorax and abdomen to hold the bee's wings back while glue (circa 1.5 μl) was applied.

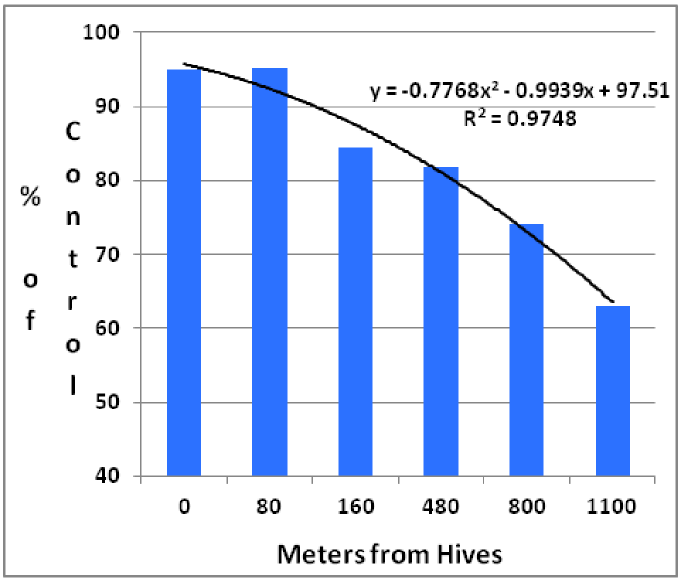

Fig. 4. Static magnetic fields increasingly inhibit return of foragers released at progressively longer distances from their hives.

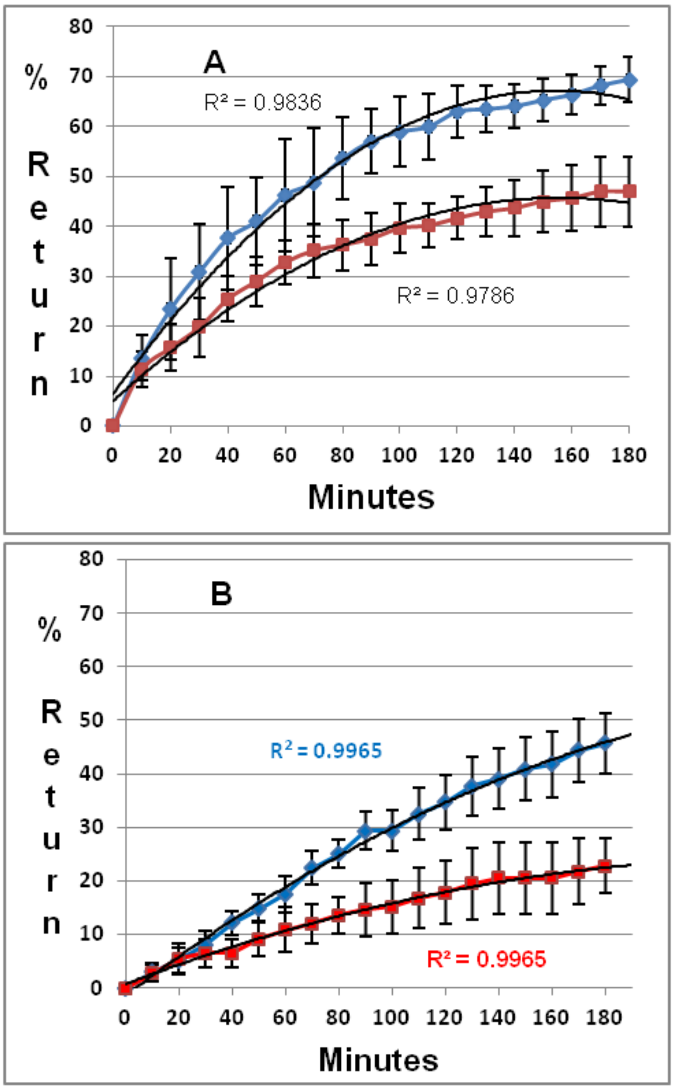

Fig. 5. Inhibition of foragers' homing ability after exposure to an oscillating magnetic field (red markers). Controls were not exposed (blue markers). ***A.*** Bees were released 480 m (9 experiments) or ***B.*** 800 m (12 experiments) from their hives.

Wires were then attached parallel to the bee's abdomen. Next, a clear plastic vial (25 cm^3) was placed over each bee at room temperature to allow glue to dry and allow for bee recovery (usually 1-5 min.). In all experiments, 15 to 21 (*n*) bees were used per treatment and release point. The procedure was minimally harmful based on return rates (90-100 %) when bees were released 1 m in front of their hives, or 80 m from their hive. Experiments involved 10 different colonies over a two-year period (2011, 2012, from June to November).

Wire preparation

Steel wires (www.forneyind.com) (30 cm x 0.89 mm dia.) were painted and colour-coded using acrylic paint. After drying, wires were cut to 4.0 - 4.5 mm lengths and each weighed approximately 15 mg (pollen pellets possess a similar weight). Magnetization was induced for a minimum of 15 mins by placing the cut wires onto neodymium-iron-boride ($Nd_2Fe_{14}B$) rare earth axially polarized rod magnets (5 cm x 2.5 cm dia.) (www.amazingmagnets.com). Magnetic field intensity at their poles for magnetized and non-magnetized wires was measured using a triple fluxgate magnetometer (Alpha lab Inc.; Salt Lake City, Utah, USA). Flux density values represent the Z-vector component of the wire's magnetic field when placed perpendicular to the instrument's sensor. Intensity averaged ≤0.2 x 10^{-6} Tesla (T) and ≥2.0 x 10^{-6} T, respectively, for control and magnetized wires. Wires with intermediate values were discarded. Repeat measurements indicated the intensity of magnetized wires did not become weaker within 48 hours.

Geomagnetic storms

Instability in Earth's geomagnetic field occurs constantly, and is logged by NOAA/SWPC daily at three hour intervals. Called the K-index, it ranges from 0 to 9. As a consequence, forager return experiments comparing different treatments were often subject to a varying background "geomagnetic noise." Disturbances of a K-index ≥5 are considered major storms (http:maar.us/ geomagnetic_storm_scale.html). When geomagnetic "contamination" occurred during experiments, comparisons of return rates between controls and treatments were not reproducible, therefore they were not included in data analysis. Experimental treatments were only compared and evaluated when K-indices of magnitude ≤4 occurred (considered minor fluctuations).

Treatment protocols

The homing ability of honey bees was evaluated in four ways: A. during the presence of a wire magnet on their body that induced a

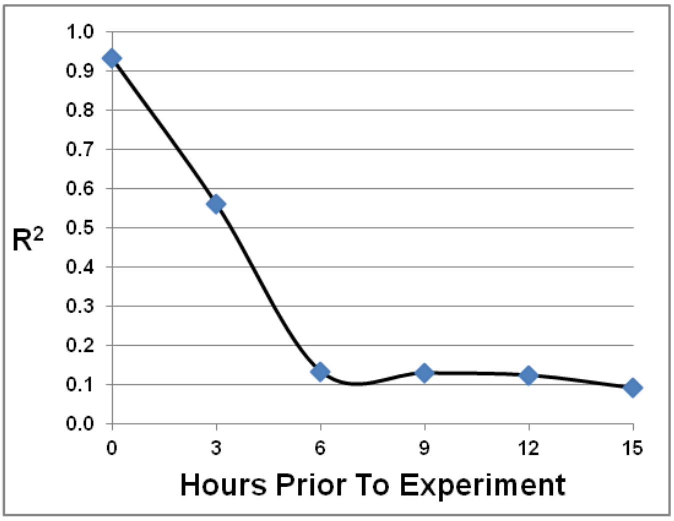

Fig. 6. Correlation coefficients for forager return rates during geo-magnetic disturbances (in nT) for 6 different time periods: 0 = *during* the 3 hour experiment; 3 = *during expt.* + prior 3 hrs; *during expt.* + prior 6 hrs; etc. Foragers were released 480 m and 800 m from their hives. Trendline is the average for both distances.

static magnetic field; B. after their exposure to an induced oscillating magnetic field; and C. during uncontrolled, natural fluctuations in Earth's magnetosphere. In addition, D. an independent survey of winter colony losses from 2000 to 2006 was compared to the record of geomagnetic disturbances in Earth's magnetosphere.

A. After bees were anesthetized, a nontoxic, fast-drying "Tacky" glue (www.duncancrafts.com) was used to attach wires onto their abdomens (n =15-21 per treatment). Each treatment took approximately 20-30 min. After they recovered, bees bearing magnetized and non-magnetized wires were transferred into separate

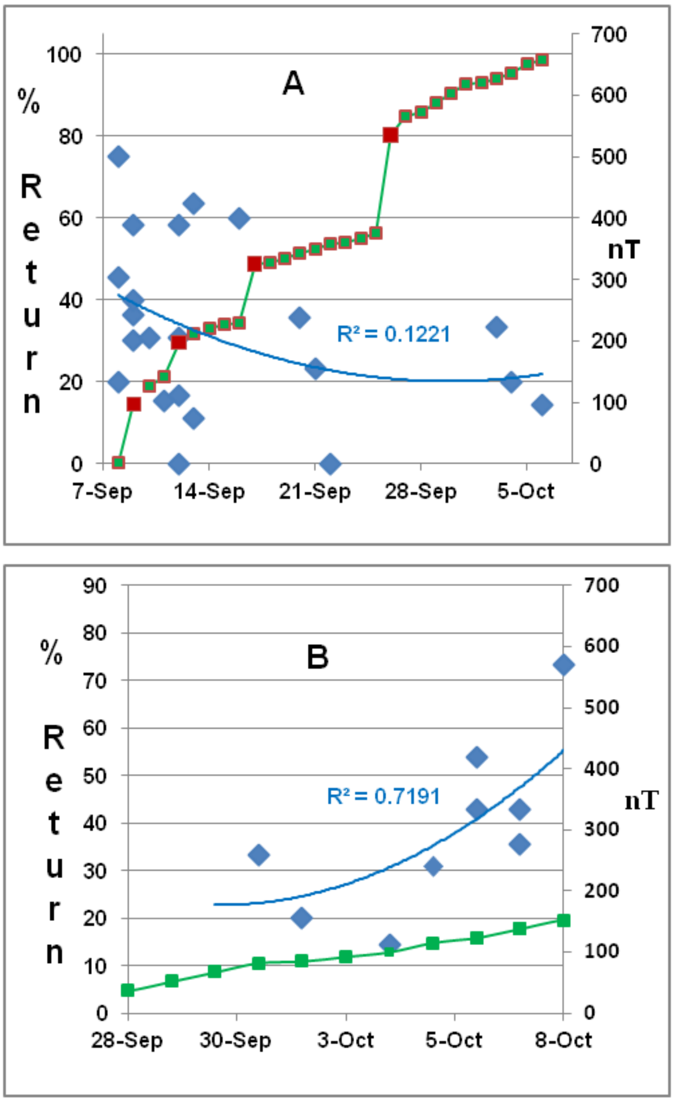

Fig. 7. A. Loss of returning foragers bearing non-magnetized wires (blue markers) in 2011 over a 29-day period***. B.*** Subsequent recovery of returning foragers during 11 days of relatively minor (K-index ≤4) geomagnetic disturbances (green markers). Green markers are the cumulative intensities of geomagnetic activity in nT from 18 to 21 hours GMT (9 AM to 12 AM pacific time). Four major disturbances to Earth's magnetosphere are indicated by red markers. Bees were released 800 m from their hives. Geomagnetic activity is represented by the cumulative sum of K-indices (nT) preceding (3 hrs.) and during (3 hrs.) each experiment.

clear plastic containers (32 x 19 x 11 cm) through a 3 cm hole in the lid. They were then taken to different locations and distances to be released: 15 to 21 bees were released per treatment per location. Hives bodies were not visible from all release sites. Bees that did not fly from containers were excluded from data analysis. Release distances were approximately 80 m, 100 m, 380 m, 800 m and 1,100 m from their hives. When released either at 380 m or at 800 m in easterly or westerly directions, or at 1,100 m in north or south directions, there was no statistically significant difference in forager return rates, indicating alignment of wire magnets with Earth's magnetic field made no difference. Therefore, data were pooled at equal release distances regardless of direction. Ambient temperatures ranged from 27 to 41°C.

Wires on returning foragers were removed automatically (Fig. 1B) from their abdomens by rectangular magnets (10 x 2.5 x 4.5 cm) placed 1.5 cm above hive entrances (9 cm wide). Wires were removed and counted at 10 min time intervals. Recovery of the colour coded wires from bees was 90 to 100 % when released 1 m in front of their entrances. Retrieval magnets were left on hive entrances for 24 hours to determine if additional bees returned after 3 h. Of 1,008 returning bees released at 80 m, 96.8 % returned within 3 h. Nearby hives were also fitted with retrieval magnets at entrances to determine if returning foragers drifted to neighbouring hives: only 2 bees in 1,000 did so.

B. Foragers were also exposed to a fluctuating magnetic field in a laboratory environment. Stationary cups containing freshly collected bees were placed 3 to 5 mm from the perimeter of a rotating circular wooden disk 35 cm in diameter. Two Neodymium magnets (the same as those used to magnetize wires) were attached on opposite sides of the disk's perimeter, with positive ends pointed in the same direction. The disk was rotated by hand 360°, 10 times in one direction, then

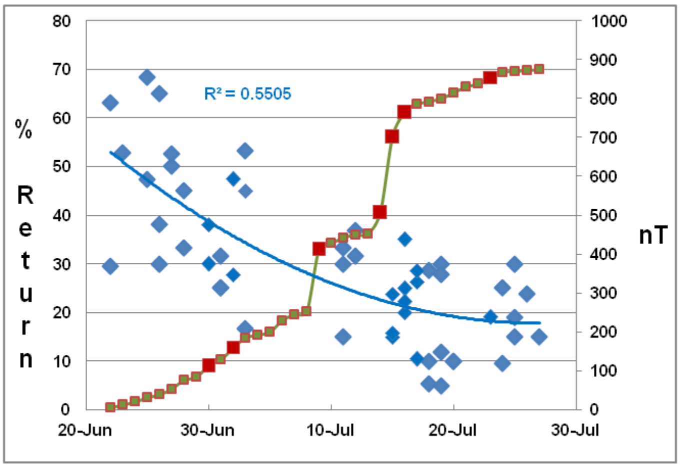

Fig. 8. Loss of returning foragers (blue markers) bearing non-magnetized wires during minor (green markers) and major (red markers) disturbances to Earth's magnetosphere in 2012. Foragers were released 800 m from their hives. Geomagnetic storms are represented by the cumulative sum of K-indices (in nT) preceding (3hrs) and during (3 hr) each experiment.

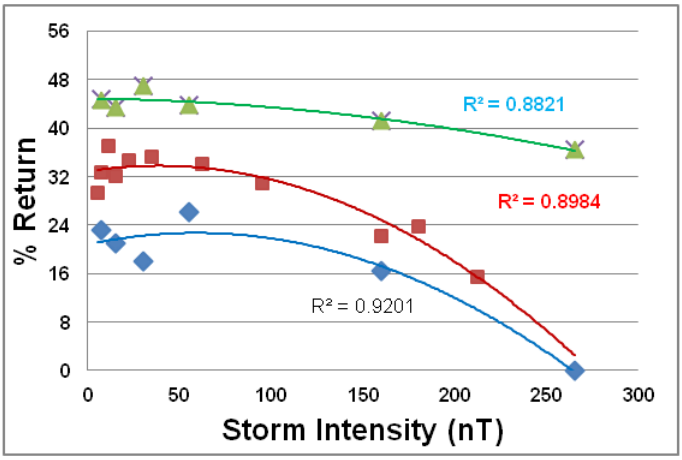

Fig. 9. Return of foragers during natural disturbances to Earth's magnetosphere. Release sites from hives were 380 m (green, triangles), 800 m (red, squares) or 1100 m (blue, diamonds). Magnetic disturbances are expressed in nT (Boulder, Colorado, USA, observatory).

10 times in the opposite direction, for a total of 4 cycles. The procedure lasted 80 seconds and created an alternating magnetic field (+/-, 2×10^{-4} T) positive to negative 20 times in one 10-cycle rotation, then negative to positive 20 times in the opposite direction (0.5 Hz). No wires were attached to bees during treatment. Bees were at room temperature and active during exposure to the oscillating magnetic field. During treatment, extra care was taken to not expose control bees, also in stationary cups and at a different location, to magnets, electromagnetic fields or batteries (including cell phones) in the lab environment. A magnetometer placed near control bees did not detect any magnetic field oscillations. After anesthetization, colour-coded, non-magnetized wires were attached to treated and non-treated foragers to monitor when they returned. Bees were then released at 480 m or 800 m distances from their hives and their return rates monitored at 10-minute intervals.

C. During each experiment, disturbances in Earth's magnetosphere were noted: K-index values reported herein were from the NOAA/SWPC observatory located in College Alaska, USA (N65°, W102°) (http.www.swpc.noaa.gov/ftpdir/indices/old_indices/2011_DGD.txt). Compared to other observatory locations in the world, it has the most comprehensive data and is most sensitive to fluctuations in Earth's magnetic field caused by solar flares. The K-index represents the sum of the maximum positive and negative horizontal fluctuation values recorded during each of 8, 3-hour periods. Because K-indices represent a semi-logarithmic scale, midpoints at each K-index range were converted to nT in tables and figures (www.swpc.noaa.gov/info/Kindex.html). For example, a magnitude 5 K-index fluctuates from 70 to 120 nT, for which the midpoint 95 nT was used in data analysis (Boulder Colorado, USA, observatory).

Extraterrestrial proton flux values were obtained from NOAA's geostationary operational environmental orbiting satellite (GOES-13). (http.www.swpc.noaa.gov/ftpdir/indices/old_indices/2012Q2_DPD.txt). The satellite monitors the proton flux arriving at Earth's outer atmosphere as a result of coronal eruptions on the Sun.

D. Six years of winter colony losses were surveyed by Burdick and Caron in northeast, USA (MAAREC Beekeeper Survey, 2006). States included New York, Pennsylvania, New Jersey, Maryland and Delaware. Averaged losses for each winter from 2000/2001 through 2005/2006 were, respectively: 41.7 %, 13.3 %, 30.0 %, 41.0 %, 33.7 % and 23.1 %. During those six winters, from the beginning of August to February (2001 to 2006), major geomagnetic storms that occurred during daylight hours (Eastern Time) were totalled for each of four different K-index ranges (≥5, ≥6, ≥7, ≥8). Then, bee losses per hour for each year were plotted versus each range's total hours (see Fig. 11, for example). Correlation coefficients were determined for each of the 4 graphs.

Data analysis

In appraising whether or not statistically significant differences occur between return rates for magnetically and non-magnetically treated foragers, it must be recognized that uncontrollable fluctuations in wind velocity, temperature and Earth's geomagnetic field occur on a daily basis; those variables can influence bee return rates. Moreover, it is important to recognize that "control" foragers are invalid controls when major geomagnetic disturbances occur during experiments, because their homing abilities are interfered with when K-indices ≥5 take place. In an uncontrollable geomagnetic environment, even minor fluctuations in the K-index probably affect reproducibility

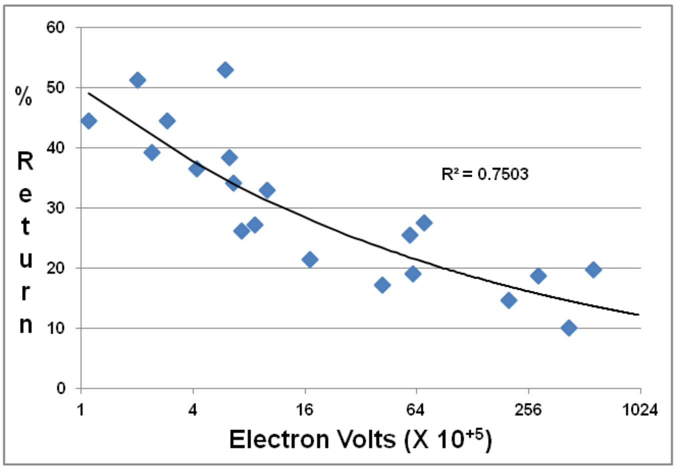

Fig. 10. Forager return rates as a function of the proton flux intensity reaching Earth's outer atmosphere as measured by the NOAA/SWPC Geosynchronous Operational Environmental Satellite (GOES-13). Measurements were from 26 June to 27 July, 2012, a 32 day period that included 8 days when geomagnetic storms of 5 and greater occurred during and 3 hours prior to experiments. Each point represents an average of multiple observations (total=58 observations). The proton flux is proportional to intensity of the sun's solar flares. (www.swpc.noaa.gov/fptdir/indices/old_indices.html).

between experiments. Hence, a relatively lenient 90 % confidence level was selected for use in data analysis. Statistical information involving return times involves the Pearson correlation coefficient (R^2). Histograms indicated return frequencies were skewed for both treatments, so a nonparametric Mann-Whitney test was used to evaluate statistical significance. Most bees returned within a 3-hour period. A similarity in forager return patterns consistently occurred at all release distances tested, usually within 3 hours, and studies involved over 300 experiments conducted over a 2-year period (from June to November). Considering the relevance of honey bees as pollinators and their value to agriculture and food production, null-hypothesis tests and significance levels should be assessed in light of such environmentally uncontrollable sources of variation. This is especially true when evaluating the theory that geomagnetic storms can cause a magnetoreceptive disorder (MRD) in foragers, and thereby lead to a disappearance of adult bees returning to a colony or apiary.

Results

Forager return rates represent the cumulative number of bees that came back to their hives at successive 10-minute time intervals after being released at sites 80 m, 480 m and 800 m from their hives in both easterly and westerly directions. At 1,100 m, bees were released in north and south directions.

A. When foragers bearing non-magnetized wires were released 80 m from their hives, 76.2 % returned within 40 minutes after release, compared to 64.4 % for bees bearing magnetized wires (Fig. 2A). In both cases, respectively, that represented 91.4 % and 88.3 % of all bees that returned after 180 minutes. No additional bees returned after 180 min. Ten minutes after release, the coefficient of variation (CV) was 2.1 times greater for "magnetized" foragers compared to

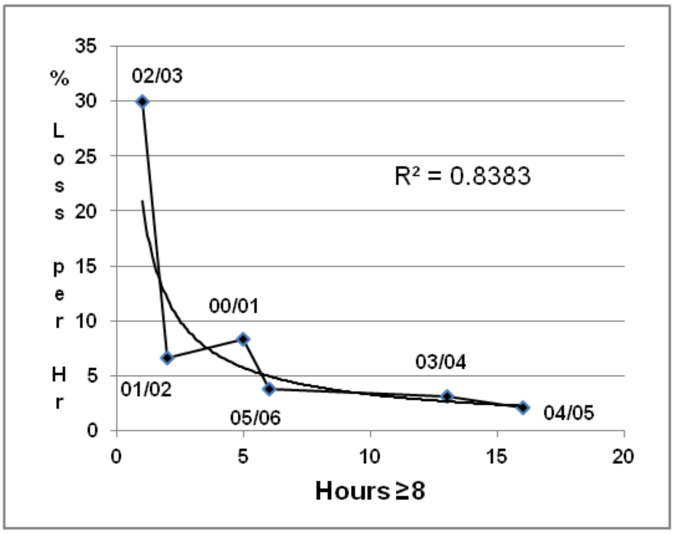

Fig. 11. Correlation of honey bee losses with total hours of K-indices ≥8 from August thru February. Winter bee losses were surveyed by Burdick and Caron (2006) from 2000/2001 to 2005/2006. K-indices ≥8 were from SWPC/NOAA.

control bees, but the difference gradually declined with time (Fig. 2B).

When foragers bearing non-magnetized or magnetized wires, respectively, were released at 800 m, 69.0 % and 47.3 % returned 140 minutes after release (Fig. 3A). As occurred at the 80 m location, there was a 2.0-fold increase in the CV at the 10 min time interval; thereafter, it declined (Fig. 3B). Nevertheless, there were greater variations in return rates for 13 of the later 14 observations. Compared to controls, the decrease in return rates for foragers bearing magnetized wires was strong for the first 30 minutes (Fig. 3C) but, thereafter, differences between treated and non-treated bees remained relatively constant and ranged from 27.7 % to 33.5 %. The difference between total return percentages for foragers bearing non-magnetized and magnetized wires was significantly different ($P<0.01$, two-tailed test). As release distances increased, there were progressively greater losses for bees bearing magnetized wires than those with non-magnetized wires (Fig. 4).

Return of untreated foragers during natural disturbances to Earth's magnetosphere were plotted at increasing geomagnetic fluctuation intensities (Fig. 9). As release distances and storm intensities increased, forager losses increased.

B. As with bees carrying magnetized wires, fewer foragers experimentally exposed to an oscillating magnetic field also returned than non-treated foragers. From a 480 m release distance, return rates at 180 minutes for treated foragers were 68.5 % of controls (Fig. 5A), and at the 800 m release distance, 49.9 % of controls (Fig. 5B).

C. When a three hour period (06.00 - 09.00, pacific coast time) was included prior to each experiment (beginning daylight hours), the correlation coefficient declined from 0.931 to 0.560; and when periods included prior 9, 12 and 15 hour periods (night time), correlations of return rates with K-indices declined, respectively, to 0.133, 0.129, 0.124 and 0.091 (Fig. 6).

D. From 7 September to 6 October, 2011, there were four major geomagnetic storms of magnitude 5 or 6 during experiments, and forager return rates declined (Fig. 7A). Thereafter, there were 13 days when the K-index was ≤ 4, and forager return rates gradually improved from approximately 20 % to 80 % (Fig. 7B). Note that variation in return rates between experiments was considerable when the four major geomagnetic storms occurred ($R^2=0.122$), compared to the recovery period ($R^2=0.719$) when major storms were absent, representing a 5.9-fold improvement in correlation coefficients. Geomagnetic intensities, expressed in nT, were expressed cumulatively (Figs 7 and 8) to graphically accentuate the increase in magnetosphere disturbances versus the gradual decline (%) in bee return rates.

From 22 June to 28 July 2012, seven major geomagnetic storms occurred of magnitude 5 or 6 during experiments (Fig. 8). During that 36 day period, return of foragers also gradually declined, ranging from 30 % to 70 % at the beginning of the period, to 5 % to 30 % at the end of the period.

As geomagnetic storm intensities and release distances increased, the number of foragers that returned decreased (Fig. 9). A similar decline in forager homing ability also occurred as proton flux intensity at Earth's outer atmosphere increased during that same period (Fig. 10).

E. Bee losses reported by Burdick and Caron (2006) for the winters from 2000/2001 through 2005/2006 were progressively more correlated as geomagnetic storm intensities increased from 5 to 8 (expressed as % loss each year vs. total number of hours each year, at K-index ranges ≥5, ≥6, ≥7 and ≥8). The resulting 4 correlation coefficients of bee losses per hour for each progressively increasing K-index range were, respectively, R^2=0.115, R^2=0.311, R^2=0.582 and R^2=0.838 (see Fig. 11, K ≥8, $\mathbf{R^2}$=0.838 for example). When correlation coefficients for each K-index range were plotted as dependently derived variables (y axis) versus increasingly intense independent storm ranges (x axis), a nearly perfect linear relationship of correlation coefficients resulted (R^2=0.998) (Fig. 12).

Discussion

Foragers selected for our experiments included nectar and pollen gatherers. When released at various distances from their hives, statistically significant decreases in numbers of returning bees occurred for those bearing magnetized wires compared to bees with non-magnetized wires. Losses occurred when bees were released in either north - south (1,100 m) or east - west directions (380 m, 800 m). It is noteworthy that variation in return rates for bees bearing magnetized wires were greater than controls in 18 of 19 cases (CVs, Figs 2B, 80 m; and 3B, 800 m). As release distances increased, progressively fewer bees with attached magnets returned to their hives compared to those without magnets (Fig. 4). At the longest distance (1,100 m) evaluated, 64.7 % of "magnetized" foragers returned relative to controls. When bees were exposed to a brief (80 sec) oscillating magnetic field, their return rates also decreased as release distances increased from 380 m to 800 m. Again, it appears a forager's magnetoreception sense is more involved with homing as distances increase. Of importance is that the colonies used in tests were examined during each experiment and exhibited no disease symptoms. Therefore, during these studies, which included multiple geomagnetic storm episodes in 2011 and 2012, failures of foragers to return were not due to a pathogen or pest: losses were more likely to have been due to an induced magnetoreception disorder (MRD).

It should be noted that initially, a 2.1 fold increase in variation of return rates occurred when magnetized bees were released at 80 m from their hives (Fig. 1B), a relatively short distance, which was close enough to their hives that visual or celestial orientation mechanisms would have been expected to be dominant (von Frisch, 1967). Since 95 % of bees eventually returned to their colony after 180 minutes at the 80 m release site (Fig. 1A), it appears that other homing cues eventually became overriding at short distances. In addition, a 2.0-fold increase in the coefficient of variation was initially obtained at the 800 M release site (Fig. 3B), also suggesting bees bearing magnets became confused or disoriented and that their magnetoreceptive sense was probably involved, at first, in their homing ability. The data supports a conclusion that orientation can rely on multiple senses, which is consistent with research reported by Dovey *et al.* (2013).

Foragers freed at north - south release sites (1,100 m) had magnets aligned with Earth's magnetic field. They too exhibited a MRD. Therefore, it was unlikely magnets were exerting a torque that may have interfered with homing capability when foragers were released in east - west directions. Because missing bees rarely returned 24 hours after release (at distances greater than 80 m), a beekeeper may well conclude, as in the past, that they had "evaporated", "disappeared" or "dwindled." Single bees from experimental colonies that were kept in cups either in a lab environment or outdoors on their hive lids did not survive longer than 10-12 hours.

Foragers used in these studies were healthy and from strong colonies, which were monitored regularly and showed no disease symptoms or pest problems (except for an occasional mite) and they continued to thrive after each experiment; so, a pathogen, parasite, pest or a combination of them was not the cause for their failure to return. These observations indicate a contagion was not involved (symptom #7). Moreover, bees were maintained and released in a suburban environment, so an agricultural pesticide was not likely the problem either. A reasonable conclusion is that induced magnetic fields caused their magnetoreception sense to malfunction. Thereafter, they became disoriented and eventually lost, an outcome that is consistent with symptom #1: a loss of adult foragers. These

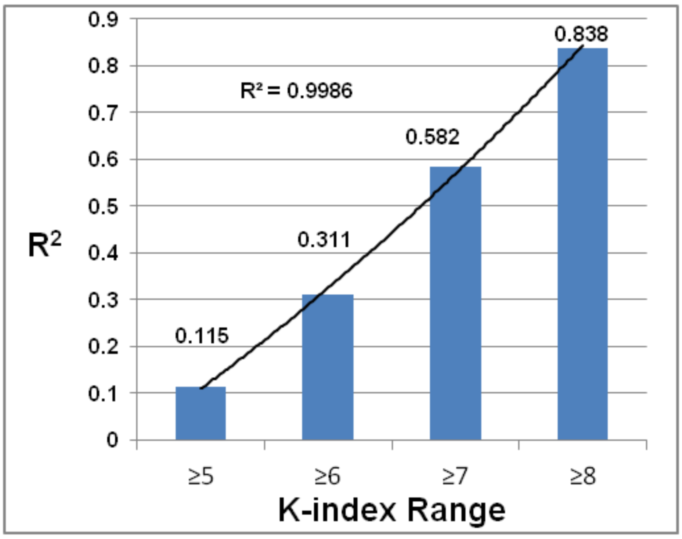

Fig. 12. Correlation of 4 geomagnetic storm ranges with independently derived correlation coefficients. The correlation coefficient indicated for each K-index range represents the value obtained when % colony losses per hour were plotted versus hours of storms for each of 4 K-indice ranges over 6 winter periods. (See Fig. 11, K ≥8, for example.) Graphs of the other K-index ranges (≥5, ≥6, ≥7) are not included: only their correlation coefficients are indicated.

Table 1. Colour of pollen pellets removed from foragers' corbiculae. Values represent percent of total.

SITE	POLLEN	Hive #1	Hive #2	Hive #3	Hive #4	Hive #5
1	Orange	0.0	3.7	0.0	39.5	4.5
2	Cream	80.0	14.8	17.1	13.2	68.2
3	Yellow	0.0	25.9	14.3	0.0	4.5
4	Brown	6.7	25.9	51.4	31.6	4.5
5	Green	6.7	18.5	8.6	2.6	13.6
6	Red	6.7	11.1	8.6	13.2	4.5

observations support the hypothesis that at long distances, an organism's magnetoreception sense becomes increasingly important for orientation and homing.

Lindauer and Martin (1972) also demonstrated direct evidence that a magnetic sense was involved in orientation of adult bees. They reported foragers' dance orientation changed when comb was placed in the presence of a compensated (weakened) magnetic field. Further proof of orientation using a magnetic sense in honey bees was also provided by Collett and Baron (1994). They reported a magnetic sense was involved in orientation in the rain under a completely overcast sky, and even when the sun's light was depolarized and its ultra violet radiation eliminated.

During the course of these studies, two series of major geomagnetic storms occurred (K-index 5 and 6) which altered Earth's magnetic field and untreated forager return rates declined progressively. This happened during fall 2011 (four storms, Fig. 7) and summer 2012 (seven storms, Fig. 8) when queens were actively laying eggs and building up the colonies population. One possible explanation for the gradual "dwindling" of return rates for bees on days when there were no storms is that immature bees had replaced adult foragers who had gone astray on days when storms occurred. Without a fully developed magnetoreception sense, immature bees that replaced adult foragers would be vulnerable to becoming disoriented and then lost, especially when released at long distances from their hive. This explanation is consistent with a 9 to 15 day period involved with development of their magnetoreceptive sense (Kuterbach and Walcott, 1986; Manning, 2009).

Consistent with this interpretation was the subjective observation that foragers collected after geomagnetic storms occurred were smaller and hairier in appearance, crude indicators used by beekeepers and entomologists to identify younger bees from older bees. This scenario too is consistent with symptom #2: an absence of sick or dead bees in or near the hive. Thus, one important side effect of geomagnetic storms is that foraging responsibly probably shifted onto a progressively younger work force whose magnetoreception sense was under developed. These observations are consistent with symptom #5: afflicted colonies contain fit, young adults. Under these circumstances, a colony can recover, unlike presence of a severe disease. However, in the fall when queens cease egg-laying responsibilities, a loss of foragers ("autumn collapse") would result in an undersized cluster of over-wintering bees, rendering a colony highly susceptible to die-off, especially in northern latitudes, which is consistent with symptom #6.

On 6 November 2001, Esquvel *et al.* (2007) were measuring the flight behaviour of the stingless bee Guirucu (*Scwarziana quadripunctata*) as it exited its earthen hive. A statistically significant difference occurred in the angle of departure when a spontaneous geomagnetic storm occurred (229 nT maximum fluctuation, K-index = 7): the departure angle decreased from 39° to 16°, a 23° difference. When seeking foraging sites, honey bees can fly about 30 km / h (20 mph). Theoretically, they would be nearly 90 km (60 miles) off course three hours after departing their entrance, which is well beyond their usual foraging range. At such long distances, it is unlikely foragers would have enough energy or be able to find their way back to their colony using visual, celestial, odour or magnetoreceptive senses, and is consistent with symptom #2 - no dead bodies in or near hives. Of equal importance is being 23° off-course when foragers return from a long foraging trip and unable to use other cues, thereby causing them to be substantially off course and, consequently, unable to locate their hive.

Data indicates, fortunately, that losses in homing ability during geomagnetic storms are not permanent. Most experiments reported herein began about three hours after sunrise. When major geomagnetic storm intensities were compared to forager losses during the course of experiments, a significant correlation resulted (R^2=0.93, Fig. 6). However, when major storm activity was considered at progressively earlier 3 hour time intervals extending back 15 hours, the correlations declined sharply, to approximately R^2=0.11. Apparently, adult foragers can "reset" their internal compass and regain their homing ability after storms occurred at night while they were clustered at the entrance or inside the hive body, which is nevertheless pervious to magnetic fluctuations. This appears not to be the case for captured foragers who were exposed to an oscillating magnetic field, taken to a distant site and then released. It appears, therefore, foragers need to put their hive's location in perspective while they are present in the hive's local magnetic field.

Iron in the form of super paramagnetic magnetite (Fe_3O_4) is a proposed magnetic field receptor molecule in adult honey bees (Hsu and Li, 1993). Iron accumulates gradually in bees after eclosion (Manning, 2009; Kuterbach and Walcott, 1986) and maximum levels peak at the time when honey bee workers commence foraging behaviour (Kuterbach and Walcott, 1986). It is important to recognize that homing ability is not an either / or condition, but develops gradually as bees develop.

During maturation, young bees must still leave the hive to defecate and in doing so visually familiarize themselves with surrounding areas. (Capaldi and Dyer, 1999; Collett and Baron, 1994). Therefore, before maturation, bees must rely on visual, celestial or odour cues for orientation when near their hives, but they would be at risk to becoming lost when released at longer distances. The recovery of homing ability after 13 days (Fig. 9B) is consistent with a 9 to 15 day period involved with their accumulation of iron and development of their magnetoreceptive sense (Kuterbach and Walcott, 1986). It is likely that the number of young workers remaining with the queen will vary depending on the reproductive proficiency of a queen. It is likely that after adult foragers suffer a MRD episode, younger workers can forage nearby food sources and use visual cues for homing. Consistent with these observations is the finding (Menzel *et al.*, 2005) that captured, displaced bees either exhibited a slow search flight with frequent changes of direction in which they attempt to "get their bearings" (those possessing an immature magnetoreception sense); or, they exhibit a direct path to their hive or feeding station (those possessing a mature magnetoreception sense). This difference likely resulted because researchers did not differentiate immature bees from mature foragers when they were captured.

Intracellular organelles involved with magnetoreception contain magnetite and are termed magnetosomes (Frankel, 2009; Galland and Pazur, 2005; Winklhofer, 2010). It has been hypothesized that the receptor molecule contains a pair of radicals that are involved in detection of the geomagnetic field (Lau *et al.,* 2010). The positive correlation of intense proton flux intensities detected by the GOES-13 satellite with forager losses provides another mechanism as to why adult foragers become lost, in addition to major fluctuations in Earth's magnetosphere caused by solar storms. Following a coronal eruption and after protons enter Earth's atmosphere those subatomic particles have potential to interfere with the separation, orientation and 3-dimentional rotation of the dual electron fields in the proposed magnetoreceptor molecule (Lau *et al.,* 2010). Interactions between protons and electrons would likely annihilate the molecule's anisotropy, and thereby result in reduced directional sensitivity.

Magnetic fields induced by magnetized wires were static, relatively weak and ranged from 2 to 2.5 nT, about 5 % of Earth's magnetosphere at 50° latitude, and more than 10 times greater than control wires. Induced magnetic fields were to some extent comparable to a geomagnetic K-index of 3 (20 to 40 nT), which fluctuates (non static), and is considered a minor perturbance to Earth's magnetosphere. Though magnetized wires attached to foragers were relatively weak, an interference of homing ability was detected, indicating bees are more sensitive than previously estimated (4.3 nT) (Kirschvink *et al.*, 1997).

It seems reasonable that as storm intensities increase beyond magnitudes 5 and 6 - the most intense encountered during these studies - a forager's ability to return would diminish proportionately. Indeed, this appears to be the case. Losses that occurred during the six year survey reported by Burdick and Caron (2006) were plotted against four different ranges of geomagnetic disturbances: K-indices ≥5, ≥6, ≥7 and ≥8 (Fig. 11). Each of the four independently derived correlation coefficients of bee losses, for each individual range, were positively and linearly correlated with storm intensities which extended from magnitudes 5 to 8 (Fig. 12). Such extensive bee loss surveys are rare and geomagnetic records only date back to 1995; nevertheless, the correlations support research described herein involving loss of returning foragers as fluctuations in Earth's geomagnetic field increase. Interestingly, colony losses per hour declined rapidly with time (Fig. 11). A simple explanation for this pattern is that a rapid loss of foragers occurs at first. Then, a colony's subsequent exposure to additional geomagnetic activity has less of an effect because most foragers have already become "lost."

The MAAREC survey is unique in that it included colony loss data near a peak in a sunspot cycle (2000-2003) as well as a trough (2004 -2006). Honey bee losses, like sunspot cycles, seem to occur in cycles as well (Wilson and Menapace, 1979). Information from the northeast correlated extraordinarily well (R^2=0.998) with geomagnetic storm intensities. More recent national surveys contain an unacceptable amount of anchoring bias in that they were conducted only during a lull in the sunspot cycle (2007-2011) (vanEnglesdorp *et al.*, 2012). Obviously, to be unbiased and statistically legitimate for comparative purposes, honey bee loss surveys need to occur during a peak in a sunspot cycle as well.

A MRD is consistent with the sudden loss of adult bees observed by beekeepers and entomologists involving CCD. Two of their common observations are that some apiaries with CCD symptoms have been identified near neighbouring apiaries with no CCD symptoms; and, colonies within an apiary often exhibit symptoms but others do not. Apiculturists should recognize that foragers from different colonies do not forage at the same sites or in equal numbers (Table 1). Moreover, they should be aware that beekeepers often use different genetic strains of queens (Carnolian, Italian, Russian, etc.) in different apiaries. These conditions explain why specific apiaries and / or colonies exhibit MRD symptoms and others do not, for the following reasons.

Firstly, evidence presented indicates honey bee losses due to aberrant magnetic fields grow more severe as foraging distances increase. Therefore, colonies foraging at long distances would be affected more than those foraging nearby sites, where visual cues would predominant. Thus, not all colonies would be affected equally. Nor would subtle differences in return rates be noticed unless precise measurements of returning bees were made. For example, five colonies were examined regarding what colour pollen their returning foragers had on their legs (Table 1). Evidence clearly demonstrates the diversity of pollens that different colonies were foraging and the relative numbers (%) of foragers doing so. Assuming the cream-coloured pollen that colonies # 1 and # 5 collected came from a site 5,100 m (3 miles) from their hives, then they would be extremely affected by a geomagnetic storm when returning, and suffer CCD like symptoms – adult bee losses of 80.0 % and 68.2 %, respectively. Colonies #2, #3 and #4 would be relatively unaffected (losses of 14.8 %, 17.1 % and 13.2 %): this hypothetical example assumes the other three foraging sites are closer to hives. The same scenario would occur for colony #3 whose foragers were collecting brown-coloured pollen (51.4 %). The colony would lose nearly half their adult foragers if they were gathering that pollen at a long distance from their hive. The other four colonies would show losses to lesser degrees, ranging from 4 % to 32 %. In both examples, geomagnetic storms would produce the common observation that some hives appear to be affected, others do not.

Secondly, an important consideration of why some colonies and apiaries demonstrate MRD symptoms during a geomagnetic storm and others do not involves genetics. A honey bee's phenotype is the composite of its observable characteristics or traits, such as homing behaviour. Natural selection only acts on phenotypes of organisms. Genes responsible for resistance or susceptibility to extreme geomagnetic fluctuations are the entities that are ultimately reproduced and transmitted over generations. It is likely that no queen breeder has ever selected for resistance to severe geomagnetic disturbances. Nor has natural selection by "Mother Nature" since the last ice age 10,000 years ago, a mere speck in an evolution time-scale. That's when bees migrated northward from the equator where DNA and fossil evidence indicates they evolved (Whitfield *et al.,* 2006), and where Earth's magnetic disturbances are less than half that of the northern hemisphere. It is reasonable to expect, therefore, there is diversity amongst honey bee strains as to their susceptibility. Once more, variation amongst queens regarding genetic vulnerability would account for observations of why some apiaries or colonies are affected by geomagnetic storms and others are not.

Earth's magnetosphere is usually relatively stable, providing a reliable reference for honey bee orientation purposes; but, it is disrupted periodically. Severe coronal mass ejections on the Sun result in solar storms containing sub atomic particles along with their magnetic fields that typically take about 1 to 2 days to reach Earth. Major storms can occur at any time, even during lulls in sunspot cycles. Upon impact with Earth, they disturb its ambient magnetosphere, causing geomagnetic storms and intense proton fluxes that typically last 2 to 4 days. Under severe circumstances, those organisms that rely on Earth's magnetic "lines" for orientation can become disoriented during migrations or foraging at relatively long distances from their nests.

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