Light Affects the Homing Ability of Solenopsis invicta (Hymenoptera: Formicidae) Foraging Workers

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Light affects the homing ability of *Solenopsis invicta* (Hymenoptera: Formicidae) foraging workers

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Abstract

Ants have evolved a wide variety of ways to take advantage of available food resources and to distribute them to colony members. For the red imported fire ant, *Solenopsis invicta* Buren (Hymenoptera: Formicidae), at least 3 major stages are involved: A) foraging or scout workers leave the nest and take a looping path as they forage an area for resources; B) the scout must orient back to its nest after food discovery either with food or to recruit workers to a food source too large for a single forager to take back to the colony, and C) the food resources must be efficiently distributed to colony members (queen, workers, and brood). Fire ant recruitment has been well studied behaviorally and chemically. However, initial homing of the foraging worker back to its colony after food discovery has only been investigated relative to the sensitivity of the fire ant to geomagnetism under dark conditions, where the time-to-trail-formation was significantly increased when the magnetic field direction was reversed. Here, we focus on light in the context of a homing cue used by foraging workers above ground. We demonstrate that fire ants use light as a powerful homing/orientation cue that allows them to orient directly back to their nest after locating food, instead of retracing their previous random foraging path. The light source needs to be relatively fixed, as rotating light inhibited trail formation. Light does not have to be very bright as there was no degradation of homing ability even at 1 lux (equivalent to moonlight). We also showed time-to-trail-formation under red light was indistinguishable from under dark conditions. An experiment that changed the visual cues but kept the light fixed suggested that in the presence of a light source, visual cues had no effect on fire ant homing. Our study documents the use of light in fire ant homing and contributes to our understanding of another component of the complex fire ant recruitment system.

Key Words: fire ant; illumination; orientation; recruitment; hunting

Resumen

Las hormigas han desarrollado una amplia variedad de formas de aprovechar los recursos alimenticios disponibles y distribuirlos entre los miembros de la colonia. Para la hormiga de fuego roja importada, Solenopsis invicta Buren (Hymenoptera: Formicidae), están involucradas al menos 3 etapas principales: A) las obreras exploradoras o en busca de alimento abandonan el nido y toman un camino circular mientras buscan recursos en un área; B) el explorador debe orientarse de regreso a su nido después del descubrimiento de alimentos, ya sea con alimentos o para reclutar trabajadores a una fuente de alimentos demasiado grande para que un solo recolector los lleve a la colonia, y C) los recursos alimentarios deben distribuirse de manera eficiente entre los miembros de la colonia (reina, obreras y cría). El reclutamiento de hormigas de fuego roja importada ha sido bien estudiado desde el punto de vista conductual y químico. Sin embargo, el regreso inicial de la obrera en busca de alimento a su colonia después del descubrimiento de alimento solo se ha investigado en relación con la sensibilidad de la hormiga de fuego al geomagnetismo en condiciones de oscuridad, donde el tiempo hasta la formación del rastro aumentó significativamente cuando la dirección del campo magnético fue invertido. Aquí, nos enfocamos en la luz en el contexto de una señal de búsqueda utilizada por los trabajadores que buscan alimento en la superficie. Demostramos que las hormigas de fuego usan la luz como una poderosa señal de orientación/búsqueda que les permite orientarse directamente de regreso a su nido después de localizar el alimento, en lugar de volver sobre su camino de búsqueda de alimento aleatorio anterior. La fuente de luz debe ser relativamente fija, ya que la luz giratoria inhibe la formación de estelas. La luz no tiene que ser muy brillante ya que no hubo degradación de la capacidad de orientación incluso a 1 lux (equivalente a la luz de la luna). También mostramos que el tiempo de formación de estelas bajo luz roja era indistinguible por de bajo de condiciones de oscuridad. Un experimento que cambió las señales visuales pero mantuvo la luz fija sugirió que, en presencia de una fuente de luz, las señales visuales no tenían ningún efecto sobre el retorno de las hormigas de fuego. Nuestro estudio documenta el uso de la luz en la búsqueda por las hormigas y contribuye a nuestra comprensión de otro componente del complejo sistema de reclutamiento de las hormigas de fuego.

Palabras Clave: hormiga de fuego; iluminación; orientación; reclutamiento; caza

Ants (Hymenoptera: Formicidae) inhabit virtually every ecosystem on Earth, exceed the combined biomass of wild birds and mammals and equate to about 20% of total human biomass (Schultheiss et al. 2022). With diverse habitats and huge demands for resources, ants have evolved a wide range of mechanisms for discovery and return of food resources to the colony. This process can be broken down into: A) the search for food, where foraging worker ants leave the nest and forage an area for resources; B) orientation of the forager back to its nest after food discovery; C) recruitment of additional workers to large resources; D) guidance of these workers to the discovered food; and E) efficient distribution of food resources to other colony members. An exemplary model for the recruitment process is the fire ant, *Solenopsis invicta* Buren. Mature monogyne colonies may contain more than 200,000 workers and have population densities over 120 colonies per

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hectare (Lofgren 1986; Tschinkel 2005). Resources to support this large biomass requires an efficient foraging strategy (Wilson 1962a, 1962b, 1971). Research has focused on several parts of the recruitment process and their associated chemistry (Vander Meer et al. 1981; Vander Meer 1986; Vander Meer et al. 1988; Vander Meer et al. 1990). However, little attention has been given to how foraging fire ants find their way back to the nest after discovering food (initial homing), except for research on a specific homing mechanism in *S. invicta*, that utilizes detection of the earth's magnetic field (Anderson & Vander Meer 1993). Here we report an initial homing orientation mechanism in *S. invicta* that utilizes light cues.

A variety of orientation mechanisms have been discovered for ants. However, most deal with post-initial homing situations, e.g., visual landmarks, and chemically marked trails that help maintain fidelity to trunk trails in the harvester ant, *Pogonomyrmex barbatus* (F. Smith) (Hölldobler 1976). Initial homing in ants has centered on astronavigation mechanisms (Wehner 1984). *Cataglyphis bicolor* (Fabricius) workers forage individually for food, navigating very effectively by polarized light, celestial compass, and landmarks (Wehner et al. 1983). Scouts of the parasitic ant, *Polyergus breviceps* Emery, return to their nest after finding a target nest using the position of the sun and polarized light. The returning scout deposits a chemical trail for recruited workers to follow back to the target host nest (Topoff et al. 1984). Canopy pattern is used by the forest dwelling stink ant, *Paltothyreus tarsatus* (Fabricius), in finding its way back to its nest after food discovery (Hölldobler 1980). Laboratory studies with a Y-maze have implicated visual, chemical, or kinesthetic senses for orientation in several ant species (Jaffe et al. 1990).

A fire ant nest is composed of a tumulus with no openings or worker activity. Foraging tunnels radiate from the mound and contain exit holes to the surface that allow foraging workers to search the ground and plants for food. After exiting the colony, these workers walk in an irregular looping pattern until food is found. If the food material is too large to take back by itself the worker lays a pheromone trail directly back to the nest, regardless of the worker's random movements (Wilson 1962a). Once the scout reaches its nest and nestmates, the recruitment pheromone motivates workers to follow the trail to the food source (Vander Meer et al. 1990). Fire ants forage night and day (Kidd & Apperson 1984), depending mainly on temperature, as illustrated by a bell-shaped curve with low to no activity at low and high temperatures (Porter & Tschinkel 1987). Thus, efficient homing abilities under a variety of conditions are essential for the effective use of this resource gathering strategy.

Fire ant workers following a well-established pheromone trail become alarmed when the light intensity or the position of the light source is changed (Marak & Wolken 1965). Also, the path of workers removing dead ants from a colony is influenced by artificial changes in the position of a light source, as well as gravitational cues (Howard & Tschinkel 1976). Thus, we investigated the hypothesis that foraging workers use light as an orientation cue in homing to their nest after initial food discovery. We evaluated the ability of the ants to orient back to their nest in complete darkness, as well as with a moving light source and a variety of light intensities and colors.

Materials and Methods

ANT COLONIES

Solenopsis invicta colonies were collected and reared from newly mated queens or by excavation from field populations near Gainesville, Florida, USA, at sites previously established to be monogyne (single queen). Newly mated queens were field collected and those weighing >15 mg were set up for colony development in the laboratory (Banks et al. 1981). Field colonies were collected by excavation into a large bucket. Workers, brood, and queen (if present) were recovered from the soil by floating out as previously described (Banks et al. 1981) and placed in a standard colony rearing tray (40 × 50 × 6 cm). The inner sides of the rearing trays were coated with Fluon® (ICI Americas, Exton, Pennsylvania, USA) to prevent escape. Each rearing tray contained 1 or 2 plastic Petri dish rearing cells (12 cm in diameter) depending on the number of workers and brood. Each Petri dish had a 5 mm layer of Castoneã dental stone (Ransom and Randolph, Maumee, Ohio, USA) on the bottom that acted as a moisture reservoir. The lid of each Petri dish had a hole placed in the center to allow ant movement in and out of the Petri dish(es). After several days, field collected colonies organized themselves into the Petri dish(es) and the presence or absence of the queen could be determined. Colonies were kept only if a single physogastric queen was found. Field collected and newly mated queen derived colonies were fed crickets (*Acheta domesticus* [Linnaeus]; Orthoptera: Gryllidae), or American cockroaches (*Periplaneta americana* [Linnaeus]; Blattodea: Blattidae) and 10% sugar solution absorbed onto wads of tissue. Colonies were maintained under ambient laboratory conditions (RH = 35–45%; 27–28 °C). Colonies derived from newly mated queens were mature (>1 yr old) and well established in the laboratory. Each colony consisted of 1 or 2 Petri dish rearing cells, and each cell contained approximately 15,000 workers and brood.

TIME-TO-TRAIL FORMATION

One rearing cell from a colony unit was removed and centered 5 cm from one end of a bioassay tray, i.e., a tray the same type and size as a rearing tray (40 × 50 × 6 cm). After 10 mins the number of workers in the foraging area was adjusted by removal or addition of workers to obtain similar numbers of foraging workers for each bioassay tray. The ants were allowed to acclimate to their new environment for at least 60 mins prior to initiation of the experiment. The initial time for each experiment started when a single American cockroach (killed by freezing and thawed prior to use) was placed on its back 22 cm from the rearing cell at the opposite end of the bioassay tray. A single observer directly recorded time-to-trail-formation for each series of experiments, by recording the time at which a discernable trail could be seen. This was not difficult as the number of workers per rearing cell and bioassay tray was large and ants in the foraging arena visually represent randomly moving rectangles, until a trail develops, and they start to line up. If a bioassay unit did not develop a trail by 60 mins the experiment was stopped, and time-to-trail-formation was recorded as 60 mins. Results for treatment and control with the same colony (replicate unit) were obtained within a 24 h period. After each bioassay, the rearing cell was returned to their rearing tray. The bioassay trays were cleaned with hexane to remove residual trail pheromones and other ant deposits from the surface.

LIGHT VERSUS DARK

A room with no windows was chosen for all experiments and the door was closed and sealed in such a way that no external light entered the room. A centrally located single incandescent ceiling light (150 W) was used to measure the time-to-trail-formation with a fixed light source. The same room was used to measure the time-to-trail-formation under complete darkness. In the dark, trail formation was observed by the intermittent use of a handheld red filtered flashlight. The experiment was replicated with a rearing cell from the same colony for each condition (light and dark) within 24 h. The time-to-trail-formation was recorded. This process was repeated with 10 colonies.

EFFECT OF VISUAL CUES

The time-to-trail-formation experiment was conducted in a bioassay room that contained furniture that created visual asymmetry that could be used by foraging fire ant workers to track their position and home back to the nest after finding food (natural visual cues). A second setup included placing the tray within a solid black cloth tent equipped with a single incandescent light (150 W), which eliminated furniture associated visual cues from the bioassay room. The bioassay tray was placed at the center of the tent and 100 cm from the light source. In addition, a 10 cm high × 17 cm diameter white plastic cylinder (artificial visual cues) was modified with 3 symmetrically placed 1.5 mm x 10 cm notches cut in the bottom to allow foraging ants access to the surface within the cylinder. The cylinder was placed at one end of the bioassay tray. The inside and outside bottom third of the cylinder wall was painted with Fluon® (ICI Americas, Exton, Pennsylvania, USA) to prevent the ants from crawling on the cylinder surfaces. A rearing cell of test ants was placed at the opposite end of the tray from the cylinder and the ants were allowed to acclimate for at least 1 h as previously described. The food material (American cockroach) was placed at the center of the cylinder on the tray floor 18 cm from the colony rearing cell and the time-to-trail-formation was recorded. The natural cues setup consisted of the same experimental setup without the tent and the cylinder, but with the light source in the same position. The comparison is between two sets of visual cues (natural and artificial), both in the presence of the same light source. The experiment was replicated 6 times.

FIXED VERSUS ROTATING LIGHT

Two methods were used to rotate the light source to test the effect of light movement on fire ant homing. Method A: four 150 W incandescent lights were fixed to the ceiling at the corners of a 106 × 106 cm square located 128 cm above the center of the bioassay tray. The hour of ant acclimation was carried out with 1 of the 4 lights on. After the cockroach was put in place the lights were sequentially turned on and off such that the on light rotated clockwise by 90° every 15 sec, for 1 rpm (N = 10). Method B: a goose-necked lamp (with 150 W incandescent bulb) was attached to a turntable centered 120 cm above the bioassay tray, such that the bulb remained in a parallel plane to the bioassay tray, 75 cm from the center and 120 cm above the tray. The single light was manually rotated 90° every 15 sec for 1 rpm (N = 6). The control for each setup was the turntable light in 1 place. If for any of the rotating light experiments the colony workers did not form a trail by 60 mins, the rotation was stopped, but the light was left on, and the time-to-trail-formation was determined for these colonies with the now fixed light (N = 12). After the worker ants in 10 of these replicates formed a discernable trail under fixed light conditions, a single light was sequentially turned on and off such that the light rotated clockwise every 15 sec for 1 rpm. The objective was to determine whether rotating lights after trail formation would interfere with the existing trail. The existing trails were observed for trail disruption or unusual trailing worker movement (N = 10).

EFFECT OF LIGHT INTENSITY

The effects of light intensity on time-to-trail-formation were evaluated by using a single 150 W incandescent light, as described above. Light intensity was modulated by adjusting the voltage using a Variac® voltage regulator (ISE, Cleveland, Ohio, USA) and measured using a Weston Illumination Meter, Model 756 and Viscor filter (Weston Instruments, Inc. Newark, New Jersey, USA). Variac settings of 140, 100, 60, 20, and 0 corresponded to 312, 140, 22, 1, and 0 (dark) Lux, respectively. The experiments were set up as described for a fixed light source. Only the light intensity was changed (N = 6).

EFFECT OF COLOR

For each part of this experiment a 75 W incandescent light bulb (white, blue ~ 475 nm, yellow ~ 570 nm, and red ~ 650 nm) was oriented 1 m above the nest cell end of the bioassay tray. The time-to-trail-formation was determined for each of the light colors. In addition, the time-to-trail-formation was recorded for the same colonies in complete darkness and light regimens. Each color plus the 2 controls (light and dark) were replicated 10 times.

STATISTICAL ANALYSIS

Statistical procedures and graphical representations were carried out using GRAPHPAD PRISM, Version 6 (GraphPad Software, Inc., San Diego, California, USA), unless otherwise specified. The resulting data were analyzed conservatively using non-parametric, paired, or unpaired, two-tailed t-tests, or regression analyses.

Results

LIGHT VERSUS DARK

Time-to-trail-formation with light was significantly shorter than when the foraging workers were challenged in complete darkness (Fig. 1) (*X* ± SE; 6.2 ± 0.7 and 45.9 ± 4.3 mins, respectively; 2-tailed paired t-test, $t = 10.3139$, df = 19, $P = 0.0001$, N = 10). Six of 10 complete darkness replicates were stopped at 60 mins after the start of the experiment because the ants were unable to form a discernable trail within that time.

EFFECT OF VISUAL CUES

Time-to-trail-formation was compared between a bioassay set-up with a single light source and two different sets of visual cues. There

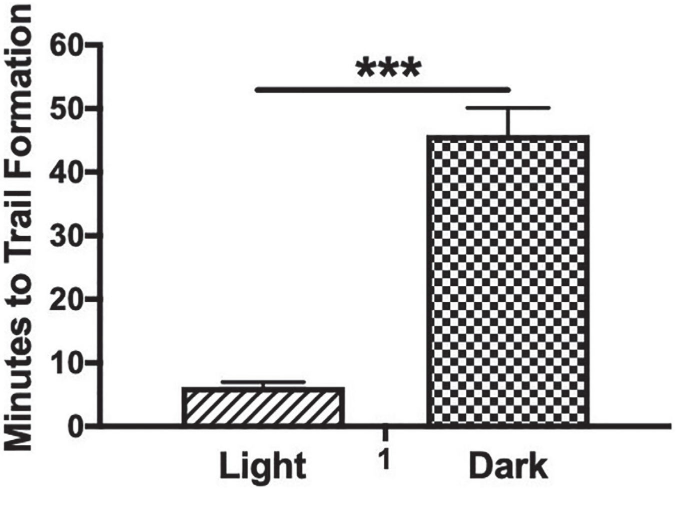

Fig. 1. Effect of light on the time-to-trail-formation by the red imported fire ant, *Solenopsis invicta*. The time-to-trail-formation is shown for a single light source in a light sealed room versus the same room with no light. Bars represent mean time-to-trail-formation + standard error, ***$P < 0.0001$.

was no difference in time-to-trail-formation between light with natural cues versus light with artificial cues (*X* ± SE; 4.4 ± 0.6 and 3.7 ± 0.6 mins, respectively; 2-tailed paired t-test, $t = -1.615$, df = 9, $P = 0.1408$, N = 10).

FIXED VERSUS ROTATING LIGHT

Confirmation of the importance of a fixed light source was obtained when the time-to-trail-formation experiment was carried out with a light source that A) changed sequentially to 1 of 4 symmetrically placed light sources at a rate of 1 rpm, compared with B) a single light source that was moved in a circle planar to the bioassay tray in 90° increments at 1 rpm. Changing the position of the light while workers attempted to form a trail back to their nest resulted in significant delays in trail formation, regardless of the way the light movement was accomplished (Fig 2). When 4 lights were sequentially turned on and off the time-to-trail formation was significantly slower than with a fixed light source (*X* ± SE; fixed, 10.5 ± 2.2 and rotating, 54.7 ± 3.5 mins; 2-tailed paired t-test, $t = -44.277$, df = 9, $P = 0.0001$, N = 10). By inference the timed rotation of a single light (*X* ± SE; rotating, 56.0 ± 3.2 mins and fixed 6.15 ± 1.7 mins, N = 6) also resulted in slower time-to-trail formation compared with a fixed light source (see Fig. 2). There were 8 of 10 replicates with the 4 light system and 4 of 6 replicates for the moving single light that did not form a trail after 60 mins. At 60 mins the light rotations were stopped with a light on (now fixed). The foraging workers quickly developed a discernable trail (X ± SE; 5.0 ± 1.4 mins, N = 12). For 10 of these replicates, after the pheromone trail was established, re-activation of the rotating light regime had no discernable effect on the trail (N = 10).

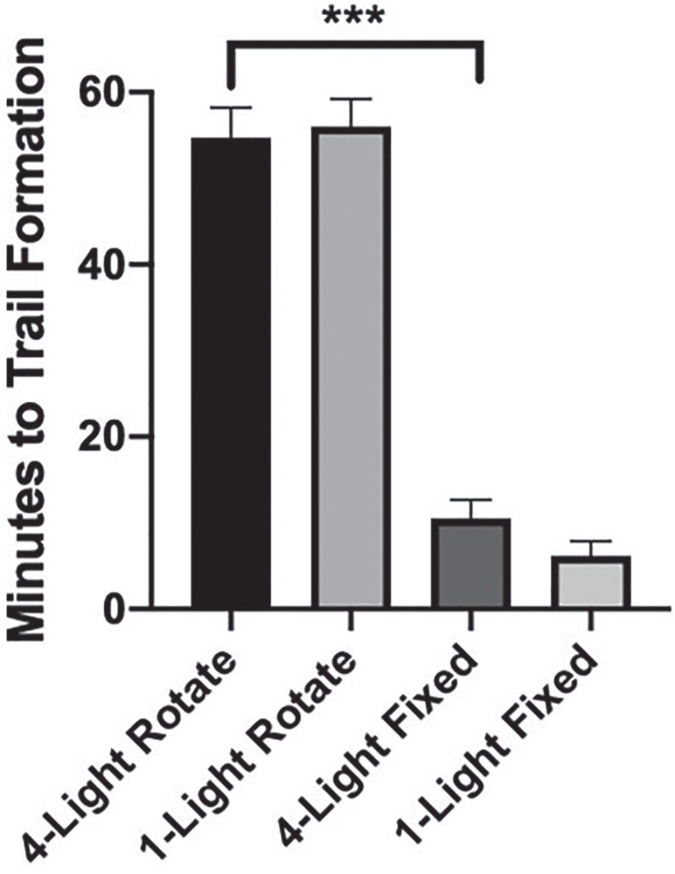

Fig. 2. The importance of a fixed light source to foraging red imported fire ants, *Solenopsis invicta*. Time-to-trail-formation was recorded with a light source that changed sequentially to 1 of 4 symmetrically placed light sources or a single light source that was moved in a circle planar to the colony tray in 90° increments at 1 rpm. Bars represent mean time-to-trail-formation + standard error, ***$P < 0.0001$. By inference, the mean time-to-trail-formation for the single light rotation was longer than the fixed light control.

EFFECT OF LIGHT INTENSITY

Figure 1 illustrates the importance of light for foraging fire ants to find their way home after finding resources. Here we determined the sensitivity of fire ants to light intensity. The time-to-trail-formation was not affected by light intensity down to 1 lux (Fig. 3). The 22 lux mean + SE time-to trail-formation was greater (by inspection) than the results for the 3 other light intensities. The time-to-trail-formation for 22 lux versus the time-to-trail-formation in the dark was significantly different (2-tailed paired t-test, $t = 6.803$, df = 5, $P < 0.0001$, N = 6). By inference all light intensities evaluated were different from the time-to-trail-formation in the dark.

EFFECT OF COLOR

Time-to-trail-formation with standard white light was only significantly less than the result for red light and by inference dark (no light) conditions (Fig. 4) (*X* ± SE; 12.6 ± 2.0 versus 30.5 ± 7.1 mins, respectively; unpaired t-test, $t = 2.442$, df = 18, $P = 0.0251$, N = 10). By inference the time-to-trail-formation with white light is significantly shorter than for dark (no light) conditions. Time-to-trail-formation using red light was not significantly different from complete darkness (black, Fig. 4; *X* ± SE; 30.5 ± 7.1 versus 46.3 ± 4.8 mins, respectively; unpaired t-test, $t = 1.853$, df = 18, $P = 0.0803$, N = 10). However, the ants were significantly faster in trail formation with yellow light than in the dark (X ± SE; 27.1 ± 7.7 versus 46.3.5 ± 4.8 mins, respectively; unpaired t-test, $t = 2.113$, df = 18, $P = 0.0488$, N = 10) and by inference, time-to-trail-formation was also faster than in the dark when the light color was blue or white. The mean values for time-to-trail-formation increased with increasing light wavelength (approximate expected wavelength), e.g., 24.0, 27.1, and 30.5 mins for blue ~ 475 nm, yellow ~ 570 nm, and red ~ 650 nm, respectively. Comparison of the 3 color wavelengths evaluated (yellow,

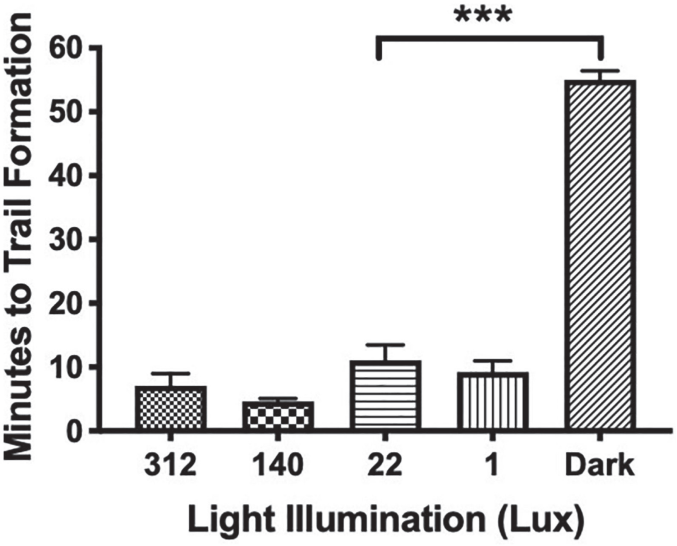

Fig. 3. The effect of illumination intensity on time-to-trail-formation is shown for workers of red imported fire ant, *Solenopsis invicta*. The time-to-trail-formation (mean + standard error, N = 6) of the 22 Lux light intensity was significantly shorter than the time-to-trail-formation in the dark. The 3 other light intensities evaluated had lower mean and SE values than the 22 Lux intensity. Therefore, by inference, time-to-trail-formation for light intensities, 312, 140, and 1 Lux were also shorter than the time-to-trail-formation in the dark. ***$P < 0.0001$.

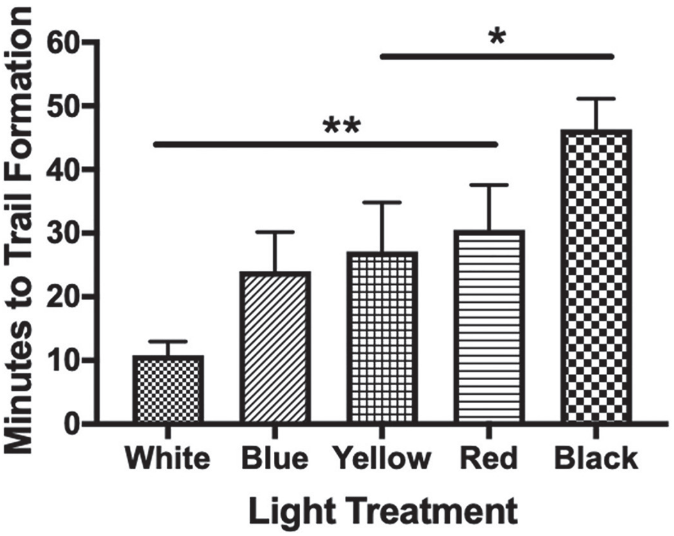

Fig. 4. The effect of white, blue, yellow, and red light, as well as total darkness (black) on time-to-trail-formation of workers of red imported fire ant, *Solenopsis invicta* (mean + standard error). Results for time-to-trail-formation in yellow light were significantly faster than for black (dark) and by inference white and blue are also faster than black. Time-to-trail-formation under white light was significantly different from red and by inference white was also faster than black. Red and black time-to-trail-formation results were not significantly different. $*P < 0.01$ and $**P < 0.001$.

blue, and red) versus their mean time-to-trail formation resulted in a significant correlation (linear regression: $R^2 = 0.9942$; $Y = 0.03700X + 6.293$; slope significantly non-zero; $P = 0.0484$). Six of 10 replicates in the dark were truncated at 60 min because the ants were not able to form a trail. The 6 truncated replicates were distributed as follows: the red treatment had 2, the yellow had 3, the blue had 1, and the white had zero.

Discussion

The foraging behavior of ants was proposed to be a combination of hunting for resources, homing, and path building (Li et al. 2014), and that the movement of foraging workers was not random but deterministic. Decades ago, Wilson (1962a, 1962b) showed that foraging fire ant workers move about their territory in irregular looping paths and when a food source is found the foraging worker carries the food material on a direct path back to its nest, or if the food is too big to carry back, the foraging worker lays a chemical trail directly to its nest and recruits workers to follow the trail back to the food source. Vander Meer et al. (1981) determined that Z,E--farnesene, produced by worker Dufour's glands, was responsible for trail following activity; however, the recruitment of additional workers from the nest was chemically more complex (Vander Meer et al. 1988; Vander Meer et al. 1990). The chemical trail continues to be re-enforced by returning workers; however, as the food source diminishes, fewer foraging workers are stimulated to reinforce the trail, and ultimately the volatile recruitment pheromone disappears.

The pheromone trail explains the trail formation but not how the foragers orient directly back to their nest once food is found. The results of our study show that without a fixed light source, time-to-trail-formation back to the colony was significantly delayed or did not occur within the 60 mins of our experiment. This confirms that foraging workers are dependent on a light source to gather information during their foraging activities that enable them to directly return to their colony. Indeed, fire ant foraging workers form a relatively direct trail back to their colony within minutes of finding the food source. Other studies have shown that fire ants had a sensitivity to light, but these were related to already trailing ants (Marak & Wolken 1965) or workers carrying dead ants to the refuse pile (Howard & Tschinkel 1976). The positive correlation between light and successful worker homing back to their colony suggests that the irregular worker looping foraging activity described by Wilson (1962a, 1962b) plays a role in updating the foraging worker's position relative to their nest. Additional experimentation is needed to test this supposition.

There was no difference in time-to-trail-formation between 4 fixed light intensities, even at low light (1 Lux), thus demonstrating that foraging worker homing efficiency is consistent from dawn to dusk, and longer if the moon is visible. We have not evaluated fire ant worker sensitivity to plane polarized light, which is capable of penetrating cloud cover, and has been shown to expand the foraging capabilities of *Cataglyphis* desert ants (Lebhardt & Ronacher 2014; Wehner et al. 2016). Bees and wasps also use polarized light in navigation (Zeil et al. 2014). Most insects are blind to red wavelengths of light (Owens & Lewis 2018), thus in the laboratory we often put red cellophane over nest cells to simulate darkness and induce the ants to stay in the cell. The action spectrum of fire ant workers toward a range of visible light wavelengths showed activity in the near red area (610 nm) but not at 650 nm (red) (Marak & Wolken 1965). Our results similarly showed that the time-to-trail formation was negatively correlated with increasing wavelength and that red light was not significantly different from no light (dark).

Within the 60 mins of our experiments, trail formation was delayed or did not happen when the light was rotated, but not with a fixed light. This suggests that within the fire ant temporal/spatial activities the sun acts as a fixed light source. Unlike some ant species (Rosengren 1977), our experiments suggest that visual cues in the presence of a light source, are not used in fire ant orientation, as the time-to-trail-formation with 2 unique sets of visual cues were not different.

Fire ants, as well as many other ant species, are competent at nocturnal foraging in complete darkness (Kidd & Apperson 1984; Porter & Tschinkel 1987). Under these circumstances, it had been difficult to understand the homing mechanism (Cosens & Toussaint 1985). However, Anderson and Vander Meer (1993) discovered that fire ants are sensitive to the earth's geomagnetic field in complete darkness and that reversing the earth's magnetic field significantly influenced the time-to-trail-formation. Later studies isolated magnetite from fire ants and confirmed the ability of *Solenopsis* species to detect the earth's magnetic field (Slowik & Thorvilson 1996; Slowik et al. 1997a, 1997b; Esquivel et al. 1999; Abracado et al. 2005). Other ant genera also were demonstrated to detect the earth's magnetic field (Çamlitepe & Stradling 1995; Jander & Jander 1998; Acosta-Avalos et al. 1999; Acosta et al. 2001; Banks & Srygley 2003; Çamlitepe et al. 2005). Magnetic field orientation for fire ant workers could only be demonstrated under complete darkness, as we have shown here, workers are highly sensitive to light.

Insects that search for food from a central nest, as is the case for many social insects including fire ants, must search widely for resources; yet keep track of their location relative to their nest location (Rosengren & Fortelius 1986; Salo & Rosengren 2001). It is well known that celestial orientation (the sun, polarized light, and the moon), and terrestrial landmarks can be important visual cues (Rosengren 1977). Other ant species have been shown to use olfactory and environmental cues, long term stored vector information (Beugnon et al. 2005), and skyline panorama (Fukushi 2001). Additional research is needed to determine if fire ant workers are sensitive to polarized light, which is capable of penetrating clouds and would expand the weather conditions supported by light as an orientation mechanism.

Fire ants have populations up to 120 mounds/ha, with each colony possibly containing 200,000 workers and living up to 6 yrs. Thus, its territory is likely continuously being marked with colony specific odors, including pheromones, that could contribute to a foraging worker's finding its way back to the colony, as suggested by Steck (2012) and referred to as olfactory landmarks. In our experiments the tray surfaces were washed with hexane prior to use, so they started free of ant markings; however, an hour was given to allow test colony workers to settle into their new environment. It is likely that during this time colony odors are passively put on the tray surface. As with visual cues, whatever chemistry is on the tray surface had less impact on worker foraging than did the light stimuli.

Desert ants, e.g., *Cataglyphis* spp., forage individually or in tandem to food sources and have been the focal group for the study of homing mechanisms in ants (Wehner 1999; Collett & Collett 2006). Solitary desert ants can even use vision to navigate when pulling prey backward to the nest (Schwarz et al. 2017). Graham and Philippides (2017) developed a conceptual model to rationalize the robust navigational capabilities of desert ants that include behavioral strategies, visual mechanisms, and neural hardware.

The fire ant has evolved at least 2 mechanisms to find its way back to the nest. The sensitivity of the ants to light demonstrated in this study suggests that light tracking works for most situations. The exception would be in near-to-total darkness where sensitivity to geomagnetism could be utilized. Underground foraging is under appreciated but supported by the fire ant workers getting a significant amount of carbohydrates from underground resources (Tennant & Porter 1991). This is another situation where geomagnetic sensitivity or unknown mechanisms could be used.

The strong fire ant trail formation interference when light positions change suggests potential applications. For example, in greenhouse situations powerful lights, strategically placed and programmed to periodically turn on and off could interfere with fire ant foraging, possibly even in daylight and eliminate or impede ant recruitment. Small area specialty crops may be another area that would benefit from non-insecticide inhibition of fire ant homing/recruitment.

This research advances our understanding of the fire ant recruitment system, identifies areas of research that need action, and suggests possible ways to use these discoveries to mitigate the impact of fire ants in particular agricultural situations.

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