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Short title: Mullins et al.: Termite flight dispersal

Dispersal Flights of the Formosan Subterranean Termite (Isoptera: Rhinotermitidae)

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ABSTRACT

The Formosan subterranean termite, *Coptotermes formosanus* Shiraki, is a pest of major economic concern. This termite is particularly known for its tendency to establish populations in non-endemic areas via maritime vessels as well as human-aided transport of infested materials. The natural spread of this species after new introductions occurs in part by dispersal flights originating from mature colonies. Dispersal flight activity is also the primary variable for the evaluation of area-wide management programs. Few studies exist describing the dynamics and distribution of a typical dispersal flight for this species. The present study used data collected by mark-recapture of *C. formosanus* alates over 12 individual evenings of dispersal flights in the New Orleans French Quarter. In this study, we documented that the majority of alates flew ≤250 m from their parent colonies in the general direction of perceived artificial light. A new record of a 1300 m dispersal flight was recorded. Spatial analysis showed that the primary factor influencing the direction of flight was not wind direction, but the direction of perceived artificial light.

KEY WORDS: area wide management, invasive species, IPM, modeling, nuptial flight, reinvasion, swarm, urban pests.

Introduction

Long-distance dispersal of pest termites is commonly carried out by human-aided transport of infested goods as well as dispersal flights of alates originating from ships infested with termites into new ports (Hochmair and Schefrahn 2010, Scheffrahn et al. 2009, Scheffrahn and Crowe 2011). While native to southeastern China (Kistner 1985), *Coptotermes formosanus* Shiraki is one such termite that has been transported to numerous temperate and subtropical regions around the world. Its current distribution tends to be bounded between ≈35° north and south of the equator, and is a pest of major economic importance wherever it occurs (Su 2003).

Mature colonies of *C. formosanus* produce winged reproductive alates which undergo nuptial flights at dusk typically between April and June in the northern hemisphere (Higa and Tamashiro 1983). Following the nuptial flight, alates shed their wings, pair off with potential mates, tunnel into the ground and found new colonies. Once a colony is founded, territory tends to expand as the colony population grows. It is generally believed that a newly founded colony reaches maturity and begins developing alates four to six years following its foundation (Chouvenc and Su 2014, Nutting 1969). Thus this species has two methods of expanding its range once introduced into a new area; that of nuptial flights by air, and the slower in-ground expansion of established, mature colonies (Mullins et al. 2011). These modes of colony spread also pertain to re-invasion scenarios following area-wide approaches to subterranean termite control (Husseneder et al. 2007, Messenger et al. 2005). Once a target area is treated for termites, if treatment stops the treated area is subject to re-invasion by alates flying into the area from outside of the treatment zone, as well as the in-ground expansion of young colonies that perhaps evaded treatment (Mullins et al. 2011). An understanding of the dynamics of alate dispersal is important because it can lead to accurate estimates of the size and scope of newly discovered infestations, as well as estimating the growth of populations following introduction to non-endemic areas (Hochmair and Scheffrahn 2010, Hochmair et al. 2013, Tonini et al. 2013). Alate capture counts are regularly used as an evaluation variable for the outcome of area-wide control programs (Lax and Osbrink, 2003, Su et al. 2004, Lax et al. 2007). A better understanding of flight distributions would lend to a more accurate interpretation of these capture rates by allowing investigators to better account for the possibility of termites flying in from outside the test area.

Mark-recapture and genetic fingerprinting has been used in subterranean termite studies to monitor and track the range and spread of in-ground colonies (Lai et al. 1983, Su and Scheffrahn, 1988, Messenger and Su, 2005, Messenger et al. 2005, Vargo et al. 2006, Forschler 1994). However, little is known of the dynamics of aerial dispersal of alates. Many authors have stated that alates exit the nest, and then fly to the closest light source before landing on the ground and dropping their wings (Nutting 1969, Higa and Tamashiro 1983, Jones et al. 1988, Raina et al. 2003). Studies evaluating flight speed and distance of *Reticulitermes flavipes* (Kollar) Resulted in a maximum measured flight distance of 458.3m (Shelton et al. 2006). However, in the only mark-recapture study on alates of *C. formosanus*, three alates were recorded to fly between 771 m and 892 m, bypassing many light sources along the way (Messenger and Mullins 2005). According to a separate study, eight captured alates were genetically linked to known in-ground colonies between 20 m and 510 m away (Simms and Husseneder 2009). Based on field observations of an observed dispersal flight on the campus of Ryukyu University in Japan, Ikehara (1966) proposed an estimated dispersal "plume" of descending alates, originating from a building and extending into an adjacent field in a teardrop shape downwind from the dispersal flight origin. The height of the flights were estimated at 14 m, the distance between 0-460 m, and with a width of >150 m. Ikehara (1966) also stated that the alates seemed to fly randomly in different directions; however the majority tended to follow the direction of the slow (2.2 m/s) wind. While Ikehara (1966) reported more than just distance records, his observations were based on a single dispersal flight, and since no marking was done, they represent at best an estimation of a single dispersal flight event under one set of environmental variables (such as wind direction, wind speed, and intensity of artificial lights).

The primary objectives of this study are to define the distribution of dispersal flights for *C. formosanus* and to investigate environmental factors that may influence their distribution.

Materials and Methods

In the weeks proceeding the dispersal flight season of 2004 and 2005, the French Quarter of New Orleans was scouted for signs of flight preparation behavior of *C. formosanus* as described by Leong et al. (1983). Mud tubing and flight slits, consistent with pre-flight behavior, were located on trees and landscape timbers along the southeast border of the French quarter. These flight slits are narrow openings excavated by termites in galleries within the trunk and penetrating the surface of infested trees. They are typically covered with mud until the commencement of dispersal flights, when the mud is removed by workers, allowing alates in galleries within the tree to exit the colony. The geographic location of the test area, known as the Riverwalk, was chosen because of the lack of treated structures, and accessibility to trees and landscape timbers. Further evidence of impending flights included the presence of moist mud, and small perforations in the mud with soldier termites protruding their antennae from within. Over the course of two dispersal flight seasons (Spring 2004 and Spring 2005), six such flight origins were located from which alates emerged. In 2004, alates emerged from three separate locations, over six separate evenings. In 2005, alates emerged from six locations, over six separate evenings. Two of the locations were identical to the previous year (Fig.1). Alates often emerged from the same location on multiple evenings.

The potential dispersal flight origin sites were monitored most evenings during the month of May when dispersal flights were most likely to occur. Microclimatic data were recorded every ~10 min at each site using a hand-held weather station (Kestrel 4000, Nielsen-Kellerman, Boothwyn, PA). On evenings when dispersal flights were observed from more than one dispersal flight origin, the environmental readings were taken by other employees of the New Orleans Mosquito, Termite & Rodent Control Board. Data recorded included wind speed, direction, temperature, atmospheric pressure, and humidity. In addition to the microclimatic data, general meteorological data were provided for the evenings from a nearby NOAA National Climatic Data Center weather station (NCDC 2014).

When a dispersal flight was imminent, worker termites quickly removed the mud coverings over flight slits in infested trees; alates then walked out of the slits, and began flying. Fluorescent visible powders (Shannon Luminous Materials, Inc., Santa Ana, CA) were used to mark the alates. Different colors were used for each dispersal flight origin. The powders were applied to the alates by creating a light plume of dust with a handheld commercial duster (J.E. Eaton & Co. Inc., Twinsburg, OH). Alates were marked by either flying through a plume of powder, or walking across powder which had accumulated on the substrate prior to flight.

Marked alates were recaptured on 445 glue board traps (20.7 cm×10.2 cm, TRAPPER LTD, Bell Laboratories, Inc., Madison, WI) affixed to streetlights in a grid throughout the French Quarter (Fig. 2). These glue board traps were monitored and replaced twice per week in cooperation with the U.S. Department of Agriculture's Agricultural Research Service (USDA-ARS), the New Orleans Mosquito, Termite & Rodent Control Board, and the Louisiana State University (LSU) AgCenter (Guillot et al. 2005). Care was taken to not mark alates with the same color until all traps had been removed and replaced. All traps were carefully examined under an ultraviolet black light for the presence of alates marked with the fluorescing powders.

Because the distribution of glue-board traps was not symmetrical in all directions around a dispersal flight origin, an expected distribution of flight directions was made based on the distribution of glue-board traps (Fig. 3). Assuming more termites would be captured in the direction of a higher number and more nearby traps, the expected recapture distribution among 45 degree directional wedges of each origin site was modeled based on a linear distance decay function. More specifically, the number of traps in each of the eight directional wedges around the origins were identified, then weighted by inverse distance from the origin, i.e. $\frac{D-d}{D}$. Where D= the maximum observed flight distance, and d= the observed distance from the dispersal flight origin. The calculated values were summed up to give a weighted measure of traps in each directional wedge. These distribution maps serve as a control in order to assess how observed recaptures deviate from expected distributions. The assumption for the distributions in Fig. 3 is that each trap has the same chance to catch a termite, where it is further assumed that the chance decreases with distance from the dispersal flight origin.

Spatial data was analyzed using ESRI's ArcGIS 10 software. Measuring illuminance proved difficult, as the perception of illuminance would change as a flying termite moves away from its point of origin. Light blocked by buildings becomes visible, and distant lights fade or grow in relation to the termite as it flies. In addition, the 900 m x 900 m ground resolution of

NOAA satellite images taken at night was not high enough to derive reliable directional illuminance values for the test area. Because road data, more specifically TIGER/Line road data, are available in vector data format allowing to compute accurate road densities for small cell sizes, and streetlights are a major source of light in the French Quarter at night, road density was used as a proxy for the amount of light emitted in a given area. In addition to more precise resolution, using road density as a proxy was also useful since it is stable, while streetlight location and functionality were prone to change between the time of recapture and data analysis, road data has remained static for decades. In order verify the relationship between road density and amount of light emitted, the correlation between those two variables was computed for 69,834 900 m x 900 m pixels around New Orleans, which amounted to $r=0.63$ (Pearson Correlation, $p<0.01$). In order to construct a model of perceived illuminance in the French Quarter, a 300 m x 300 m grid was centered on the Artillery Dutch elm dispersal flight origin, and the distance of each cell from the dispersal flight origin was computed in ArcGIS. Once the grid was established in the software, 45 degree wedges were created radiating from the dispersal flight origin up to a 4 km radius centered on cardinal directions (N, E, S, W) and intermediate directions (NE, SE, SW, NW). Each 300 m x 300 m grid cell was assigned to its intersecting wedge (Fig. 4). Perceived illuminance for each cell was computed as $\frac{A\rho}{D^2}1000$. Where A is equal to the cell area, ρ is equal to the road density, and D is equal to the distance from the dispersal flight origin. This formula takes into account that illuminance decreases with the squared distance from the light source. Illuminance values for each wedge were then summarized into a circular diagram of perceived illuminance (Fig. 4). This model is based on the simplifying assumptions that the observer, i.e. alates, perceived emitted light from above, and that the view towards grid cells is not blocked. This model was computed only for one dispersal flight origin, as the result is applicable to the entire French Quarter.

Results

Dispersal flight origins & flight initiation:

In May 2004 flight slits were discovered on a live oak tree (*Quercus virginiana* Mill). The flight slits were located approximately 3 m high in the crotch at the base of a bifurcation in the trunk. This tree was located in Artillery Park, a small park across Decatur Street and adjacent to Jackson Square (Fig. 1). While monitoring this tree for flight activity throughout May and June, 2004, two additional dispersal flight origins were discovered in the immediate vicinity. Alates were observed emerging from a single flight slit 1 m from the base of a nearby Dutch elm tree (*Ulmus sp.*). In addition to this tree, Alates emerged from the mulch and soil of a nearby planter. These three dispersal flight origins were named “Artillery oak,” “Artillery Dutch elm,” and “Artillery planter” (Fig. 1). Alates emerged and were marked blue on six separate evenings from the Artillery oak origin May 15, 18, and 27 2004, May 14, 16 and June 1, 2005. Alates emerged and were marked yellow on four separate evenings from the Artillery Dutch elm origin on May 10 and 15 2004, as well as May 16 and 24, 2005. Alates emerged and were marked red on four evenings from the Artillery planter origin May 11, 13, 15 and 18 2004. No alates were observed emerging from this site in 2005.

During the dispersal flight season of 2005, the study was expanded, and three new sites were added. All three were located southeast of the Artillery park site, and were named by the type of tree and nearby landmarks. The “Statue maple” tree (*Acer sp.*) had flight slits approximately 1 m from its base. Alates emerged from this origin and were marked orange May 16, 22, and June 5, 2005. The “Sculpture oak” site was a water oak tree (*Q. nigra* Linnaeus). Flight slits were discovered approximately 7 m from the base. Alates emerged and were marked red on May 22, 24, and June 5 2005. The color red was re-assigned due to the lack of dispersal flights originating from the Artillery planter origin in 2005. The “Natchez cypress” dispersal flight origin was a cypress tree (*Taxodium distichum* Rich). Flight slits were located approximately 1.5 m from the base. Alates emerged and were marked green on May 25, and June 5, 2005.

Flight distance:

Over the course of this study a total of 804 marked alates were recaptured on the glue-board traps. The greatest distance travelled by an individual alate was 1300 m between the sculpture oak origin, and a trap at the northern corner of the French Quarter (Fig. 5). Although this is a new flight distance record, it is important to note that the vast majority (>90%) of alates were recovered ≤250 meters away from the origin (Fig. 6a). The three source points located in Artillery Park had the shortest flight distances (Fig 1, Fig. 6b,c,d). Flight distances increase as dispersal flight source origins are located further from the Artillery Park/Jackson Square area towards the south. The southernmost dispersal flight origin (sculpture oak) had the longest flight distances (Median=534m, Mean=621m) (Fig. 6f).

Flight direction:

In general, termites tended to fly in a northwestern direction away from the river and into the French Quarter. Termites starting from the Artillery planter dispersal flight origin were the westernmost oriented, (Azimuth=302 deg from north). Termites starting from the sculpture oak origin were the northernmost oriented (Azimuth=348 deg from north). Artillery oak was the only dispersal flight origin where a few termites flew in a southeastern direction toward the river (Figs. 1,5b,7b). With the exception of the sculpture oak origin, the observed flight direction did not follow the expected flight directions based on trap locations (Figs. 3, 7) indicating that alate flight direction is not entirely random. With the exception of the Artillery Dutch elm origin, wind direction did not play a significant role in predicting the direction of termite flight (Fig. 7). With a few exceptions, termites did not fly upwind; however, they didn't necessarily follow the direction of the wind either.

The perceived illuminance model shows that most light is perceived inland from the directions between southwest and north, while there is much less perceived light radiation in the direction of the river (Fig. 4b). This is consistent with the recapture of alates generally occurring in the direction of perceived light (Fig. 7).

Discussion

The lack of a clear, consistent relationship between wind vectors and direction of termite distribution is surprising. Leong et al. (1983) stated that dispersal flights would not be initiated if winds are greater than 3.7 km/h. This avoidance of high winds may be an explanation for not finding wind as an influential factor in dispersal flight direction. In addition to the fact that termites simply won't initiate a dispersal flight if the wind is too strong, it is also important to consider that wind directions at low elevations tend to vary greatly in highly urbanized areas. Buildings act as wind blocks, and prevailing winds channel between them in different directions. Perhaps if this experiment was performed in a large open field, wind would be a more reliable predictor of termite flight direction. However, in urban areas, using prevailing wind directions as a predictor of where new colonies will be founded from a source infestation could be misleading. In addition to wind direction, other analysis of these data proved inconclusive. These include searching for a relationship between flight distance and windspeed, flight plume area and windspeed, plume area and wind direction, etc… The only conclusive relationship found was that *C. formosanus* alates tended to fly in the direction of the most perceived light (Figs. 4b, 7a-f, 8).

When all the data are pooled, the majority of all alates were recaptured within 250 m from the colony of origin (Fig. 6a). However, when considering each dispersal flight origin separately, there is some variation (Fig. 6b-g). The dispersal flight origin with the highest mean flight distance was Sculpture oak, with a median flight distance of 534 m. This could be accounted for by the fact that it was the highest in elevation (7 m from the ground). Thus giving the alates a higher starting point, and resulting in a longer nuptial flight.

The maximum flight distance of 1300 m recorded in this study is much farther than Messenger and Mullins (2005) and is a new record for this species. It is important to point out that this flight represented the maximum distance measurable by our methods. If additional glue-board traps had been placed outside the test area, further distances would likely have been observed. While this new record is notable, our results showed that flight distances of over 250 m were relatively rare. In the instance of a newly reported infestation of this species, it is safe to say that within the first 8-12 years (2x the age of a mature colony) following introduction to a non-endemic area; the airborne natural spread will be limited to 250m from the point of origin, and in the general direction of perceived light. This is because termites flying further than 250m will be much less likely to find a mate. However, in a large established population of *C.*

formosanus, such as the city of New Orleans, alates that fly further than the normal constraints could play an important role in outbreeding, reducing homozygosity of the population (Husseneder et al. 2007, Vargo et al. 2006). The further a termite flies, the less likely it is to find a mate; however, the chance of finding an unrelated mate greatly increases if the area is populated by other colonies. On the other hand, if an alate does not fly far it may find a mate but that mate is much more likely to be a sibling nestmate, and inbreeding can result in the expression of recessive, deleterious alleles (Husseneder et al. 2007).

One potential problem with this method of recapture is that it is destructive in nature. Once a termite is caught, it is incapable of flying farther. This perhaps skewed the distribution, and a “true” representation of a dispersal flight is farther than reported here. This is particularly true for the three dispersal flight origins located in Artillery Park. These dispersal flight origins had the lowest median flight distances (Fig. 7b,c,d). The highest concentration of glue-board traps in the French Quarter was located in Jackson Square, adjacent to Artillery Park. While this high concentration of traps was accounted for in the data analysis, it did not account for the large numbers of termites recaptured in Jackson Square that were incapable of further flight once ensnared in the trap.

When observing the flying termites from the ground it became clear that termites do not stop at the first artificial light source, then land, detach their wings, and seek a mate. Rather, a marked individual can be observed heading to the nearest light, briefly flying about, and then moving on to another light without landing, and so on. When observing a large dispersal flight “swarm” around a single street light, it could be tempting to think that all the alates in that swarm came from nearby; however, this study shows that this is not necessarily the case. The termites in this study regularly flew more than 50-250 m, bypassing many streetlights along the way. The sex of the recaptured alates was not determined so it is unknown which sex tended to fly further during each dispersal flight event.

This study took into account three extrinsic variables affecting the flight distribution of *C. formosanus* alates. While the only one showing a conclusive effect on flight was perceived light direction, it is quite likely that other variables are at work. These could include synergistic interactions of environmental conditions as well as variables intrinsic to each colony.

Acknowledgments

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Figure captions:

Figure 1:

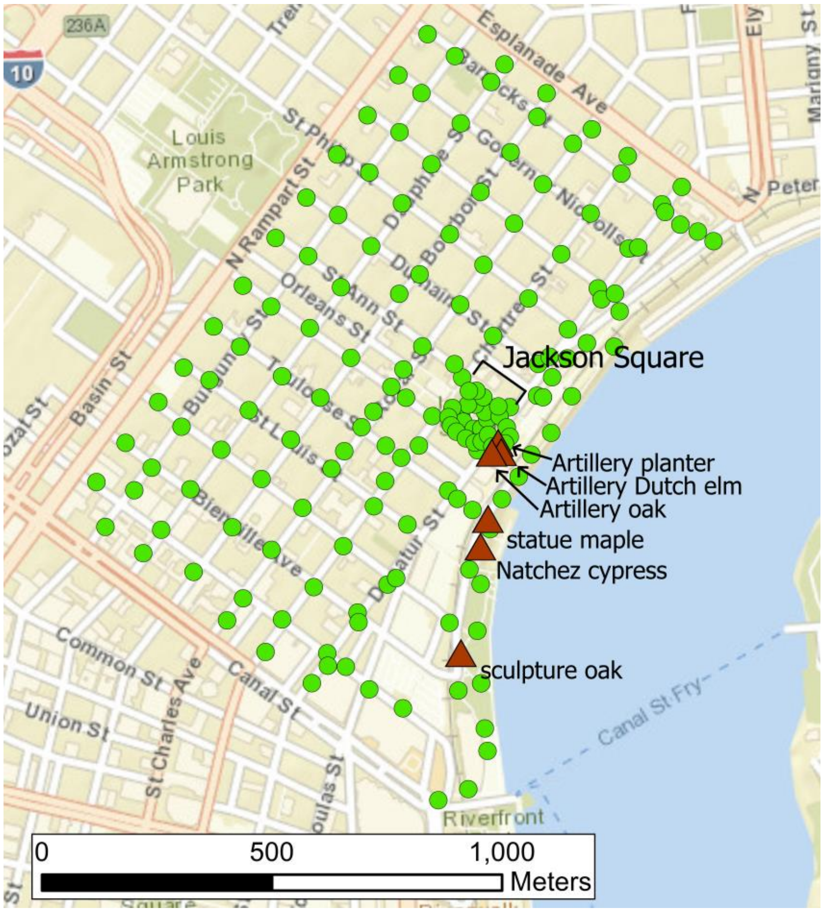

Fig. 1. The French Quarter in New Orleans, LA. The location of Jackson Square is indicated and its proximity to six *C. formosanus* dispersal flight origins. Dots indicate the locations of 445 glue-board traps affixed to streetlights throughout the test area.

Figure 2:

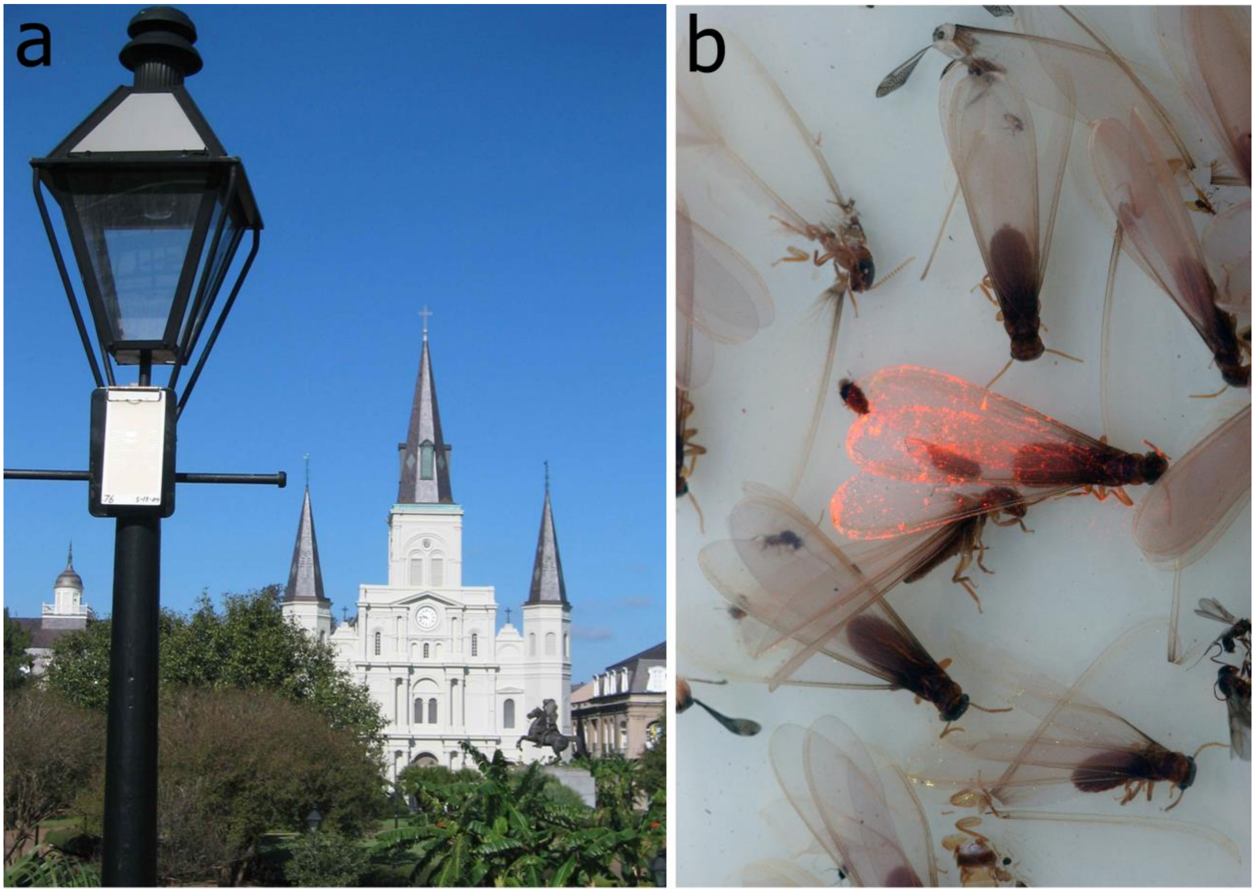

Fig. 2. Recapture of marked *Coptotermes formosanus* alates. (a) A glue-board trap affixed to a streetlight in the New Orleans French Quarter. Alates attracted to the light during evening dispersal flights would become ensnared by the glue-board. (b) A trapped alate marked with red fluorescent visible powder on its wings, legs, and antennae.

Figure 3:

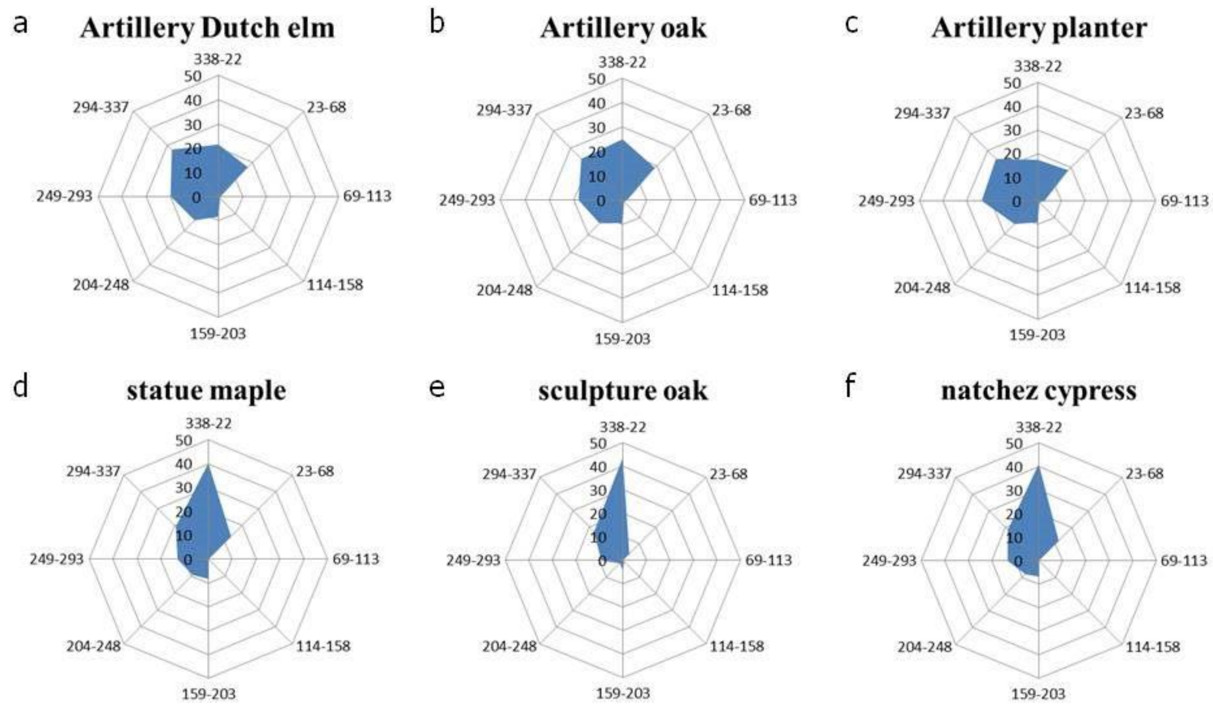

Fig. 3. Distribution of six expected flight recaptures in cardinal and intermediate directions based on the spatial distribution of traps around six different *C. formosanus* dispersal flight origins for 45 degree wedges. Outside numbers indicate the azimuth range for each wedge in degrees (with the azimuth being an angle counted in clockwise direction from north), and inside numbers express a weighted measure of traps within each directional wedge.

Figure 4:

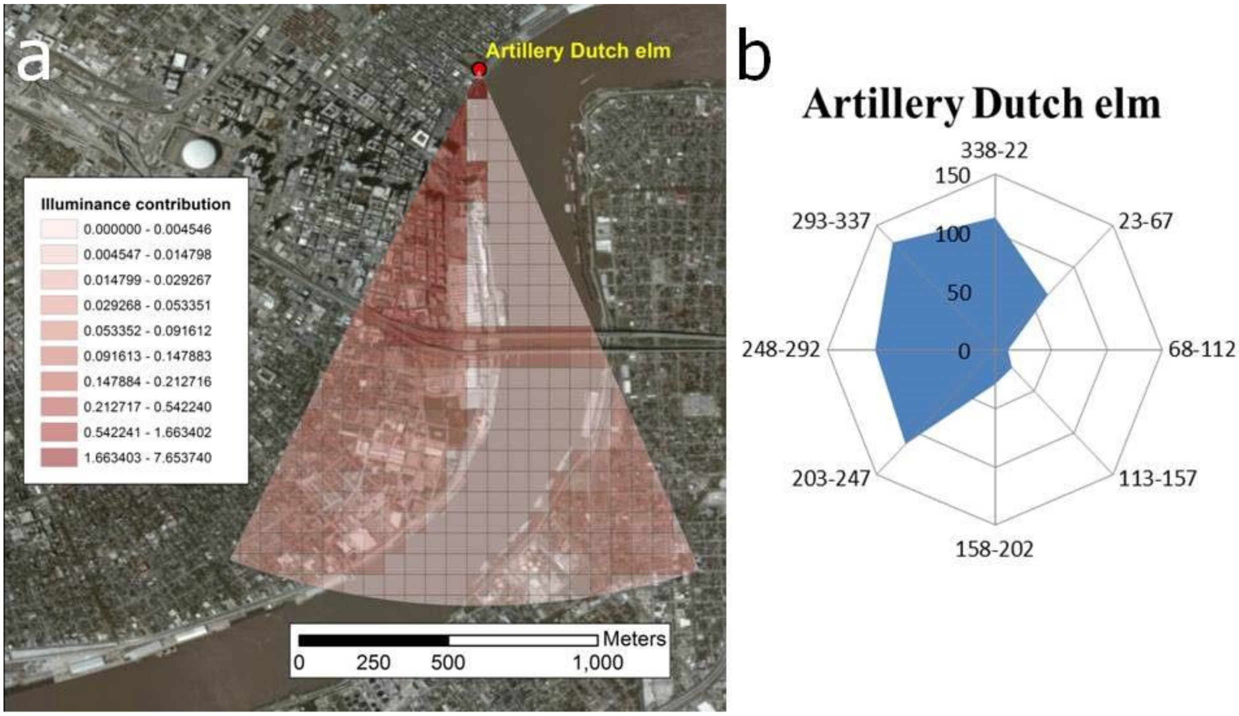

Fig. 4. A model of predicted light radiation as perceived by a flying *C. formosanus* alate in the New Orleans French Quarter. (a) An example of the 45 degree wedge around the southern direction transposed over a 300m by 300m grid centered on a dispersal flight origin. Perceived illuminance for each cell was computed as $\frac{A\rho}{D^2}1000$. Where A is equal to the cell area, ρ is equal to the road density, and D is equal to the distance from the dispersal flight origin. The model was calculated for only one dispersal flight origin (Artillery dutch elm) because it is a broad model that is applicable to all dispersal flight origins in this study.

Figure 5:

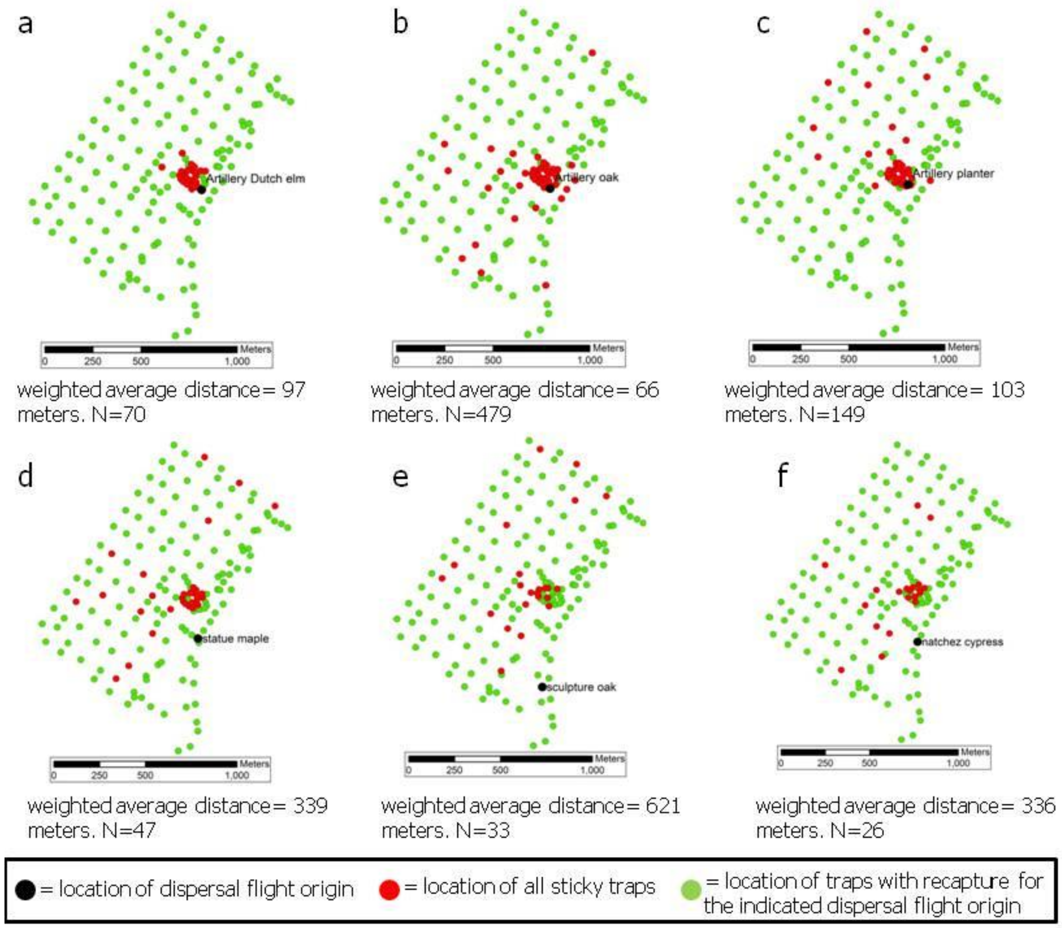

Fig. 5. Locations of all six *C. formosanus* dispersal flight origins in the New Orleans French Quarter. All glue-board trap locations as well as recapture locations are indicated.

Figure 6:

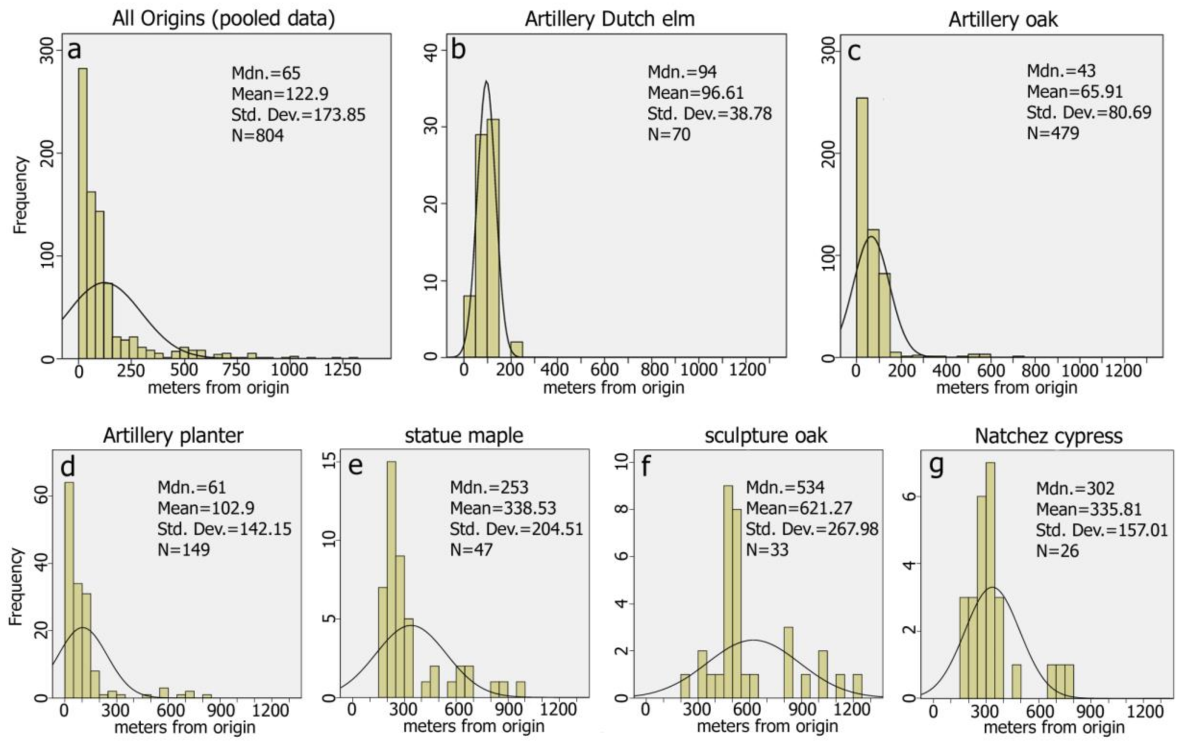

Fig. 6. Flight distances of recaptured *C. formosanus* alates, including histograms and descriptive statistics of (a) all data pooled and (b-g) separated by dispersal flight origin.

Figure 7:

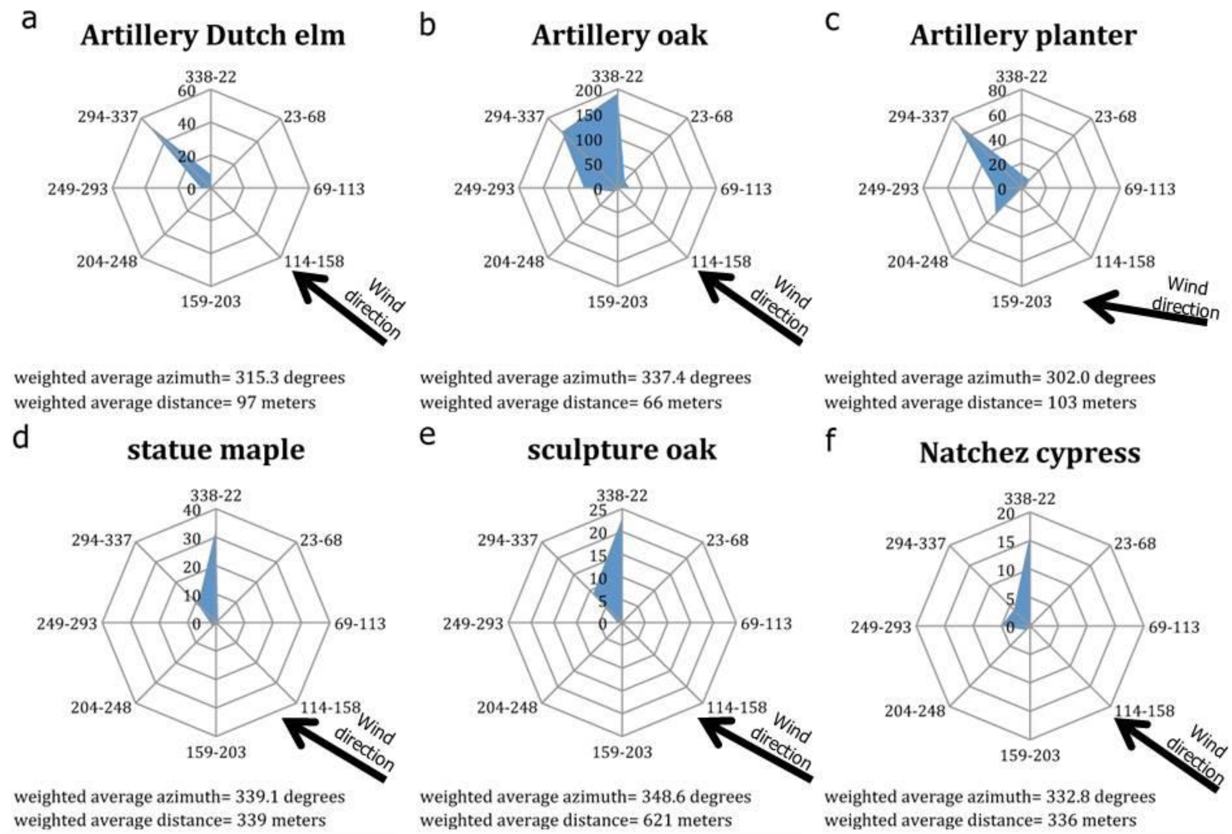

Fig. 7. Distribution of six observed flight recaptures in cardinal and intermediate directions around six different *C. formosanus* dispersal flight origins. Average wind directions are indicated, showing that the termites did not tend to fly directly downwind from the dispersal flight origin.