

Light alters activity but do not disturb tandem coordination of termite mating pairs

Running title: Visual cue for termite tandem

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Abstract

Group-living animals coordinate their movements via local interactions, which can be mediated by visual, tactile, and chemical communication channels. Termite mating pairs form tandems with one male following one female in a synchronized way to explore the environment and search for a nesting site. Imagoes are the only developmental stage with compound eyes in termites, but the role of vision during tandem run remains unknown. Here, we investigate the movements during tandem runs of two termite species, *Coptotermes formosanus*, which swarms during the night, and *Reticulitermes speratus*, which swarms during the day. We performed the experiments with light and in complete darkness. We found that females and males of both species adjust their speed to each other to form a stable tandem and reunite efficiently upon separation, with or without light. However, the activity was dependent on illuminated conditions in the diurnal *R. speratus*, where termites were more active with light. On the other hand, the nocturnal *C. formosanus* was mostly insensitive to light environments, with termites being slightly more active in darkness. Our results suggest that termites can use light as an environmental cue to start forming mating pairs but not as means to locate mates or coordinate their movements.

Keywords: circadian rhythm, mate search, phototaxis, social insects, tandem run

Introduction

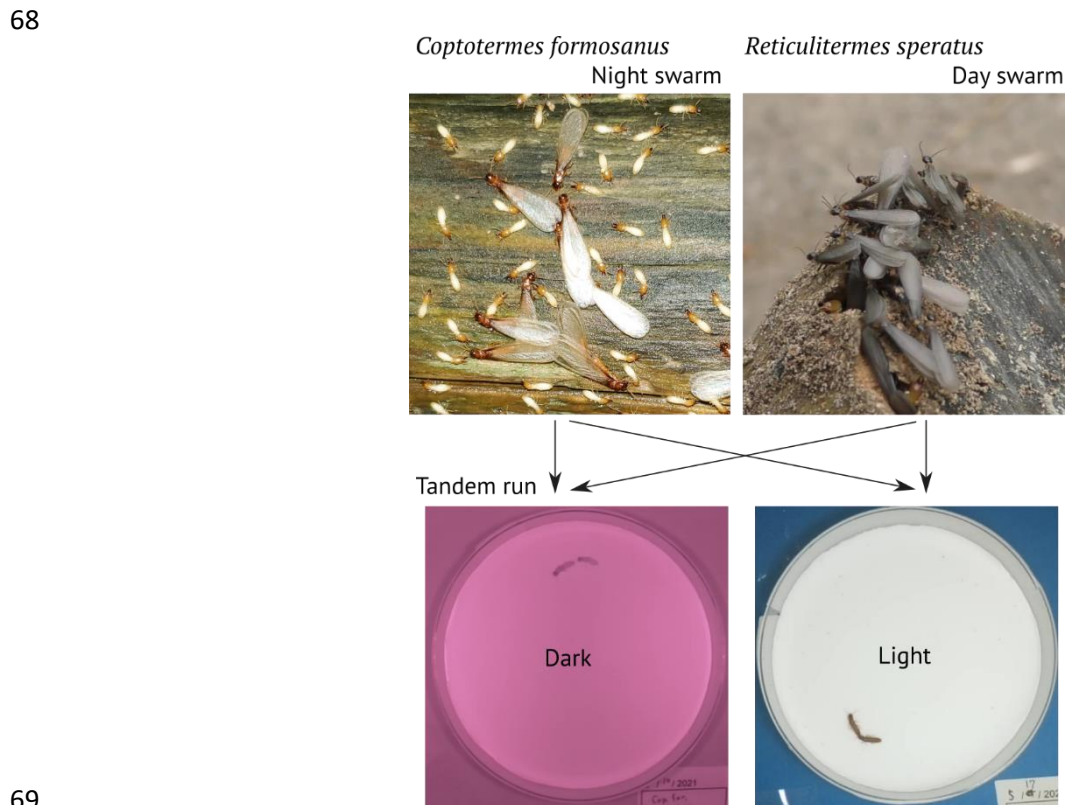
Groups of animals coordinate their movements through social interactions (Camazine *et al.*, 2001; Couzin & Krause, 2003). Social interactions are mediated by a variety of communication channels. Vision plays an essential role in the coordination of movements in groups composed of individuals changing their relative positions dynamically and interacting with multiple individuals remotely (Kowalko *et al.*, 2013), such as fish schools and bird flocks (Ballerini *et al.*, 2008; Collignon *et al.*, 2016; Bastien & Romanczuk, 2020). On the other hand, many insects or invertebrates coordinate their motion by moving in files, such as procession observed in caterpillar, sawfly larvae, or lobster (Weinstein & Maelzer, 1997; Fitzgerald, 2003; Radwański *et al.*, 2009), and tandem running behavior in ants and termites (Nutting, 1969; Moglich *et al.*, 1974). When groups of animals move in files, individuals primarily interact with the few individuals directly in front or behind them. In such groups, interindividual interactions are usually mediated by chemical and tactile communication cues, not by visual cues. However, the potential role played by visual cues to form files has rarely been investigated.

Mating tandem pairs formed by termite alate imagoes before colony foundation are simple cases of files. They form after swarming events, as females and males walk around, searching for a mating partner. Upon encountering an individual of the opposite sex, females and males engage in a tandem run, with one following the other (Nutting, 1969). This tandem running behavior can be observed in 64 species among 72 species of termites with records, and leader-follower role is fixed in Neoisoptera with female being leader and male being follower (Mizumoto *et al.*, 2022). During tandem runs, interactions are one-directional: females decide the speed and course of movements and males follow (Valentini *et al.*, 2020). When mating pairs get separated, females pause while males walk around, facilitating reunion (Mizumoto & Dobata, 2019; Mizumoto *et al.*, 2020). The communication

47 between females and males is mainly mediated by chemical and tactile cues (Nutting, 1969). The leading females
 48 release short-range sex pheromones to guide males (Bordereau & Pasteels, 2011; Sillam-Dussès, 2011), while
 49 males touch female abdomens with their antennae and mouthparts, confirming their continued presence (Nutting,
 50 1969; Raina *et al.*, 2003). Alate imagoes are the only termite caste endowed with compound eyes (Chang *et al.*,
 51 2005; Maekawa *et al.*, 2008); however, the role of vision during mating pair formation and coordination remains
 52 unclear.

53 Vision can be used by mating termites in different ways. First, termites may use vision to determine partners'
 54 location, and males may use vision to track the motion of females and keep them in sight during tandem runs. We
 55 reason that if vision is used by mating pairs, complete darkness should hinder tandem formation or reunion upon
 56 separation. Second, termites may also use vision as a cue to initiate swarming and form mating pairs, which they
 57 are known to perform at a specific time of the day (Nutting, 1969). In this case, the unusual light intensity would
 58 result in lower rates of mating pair formation (Mizumoto *et al.*, 2017), without necessarily affecting the
 59 coordination of mating pairs.

60 In this study, we tested these hypotheses by examining the effect of illuminated conditions on the
 61 movement patterns of alate imagoes in two species of subterranean termites, *Coptotermes formosanus* (Shiraki) and
 62 *Reticulitermes speratus* (Kolbe). The former initiates swarming events and forms mating pairs after sunset and thus
 63 under dark or dim light conditions (Sugio, 2019). In this case, vision would not be used for pair coordination, but
 64 light may disrupt communication and interactions between mating pairs, as observed in the case of light pollution
 65 by artificial light at night (Owens *et al.*, 2020). On the other hand, the latter swarms and form mating pairs around
 66 noon on the sunny day and thus under the daylight (Takematsu, 1999) (Fig. 1). Thus, termites may use vision for
 67 tandem pairing, with dark conditions hindering communications.



69
 70 **Figure 1.** Experimental scheme. We used two species, *Coptotermes formosanus*, which performs pairing
 71 during night time (~2 hours after sunset), and *Reticulitermes speratus*, which performs pairing during
 72 daytime (around noon). We observed their movements in a Petri-dish arena (90 mm diameter) in the
 73 dark (IR LED) and with light.
 74

Material and Methods

Termites

We used two termite species, *C. formosanus* and *R. speratus*, the former swarms during night and the latter swarms during day. Alates of *C. formosanus* has larger eyes than *R. speratus* (compound eye diameter: ~0.4 mm in *C. formosanus* (Chang *et al.*, 2005), ~0.2 mm in *R. speratus* (Takematsu, 1999); number of ommatidia: 300-400 in *C. formosanus* (Chang *et al.*, 2005), 110 in *R. speratus* (Maekawa *et al.*, 2008)). This is consistent with the pattern observed in many other insect species (Land, 1997), including alates of ants, where night-flying species has larger eyes compared with day-flying species (Moser *et al.*, 2004). Note that *C. formosanus* has larger body size than *R. speratus* (body length: ~10 mm for *C. formosanus* and ~7 mm for *R. speratus*), and thus further comparative studies will be required to test if *C. formosanus* has larger eye size relative to their body size than *R. speratus*. Both species are known to respond to the light. Alates of *C. formosanus* strongly respond to the light with wavelength of 350-400 nm (Ohmura *et al.*, 2014), and they show a strong positive phototaxis behavior (Ohmura *et al.*, 2014). In *R. speratus*, there is no data on alates, but workers, which are usually less sensitive than alates, respond to the light with wavelength of < 550 nm.

We collected alates of *C. formosanus* using light traps during dispersal flight in Okinawa, Japan, in May 2021. Because *C. formosanus* shows synchronized flight among colonies within the same area, it is presumed that alates were originated from multiple colonies. Alate sampling was performed over a period of six days.

We collected wood pieces containing seven colony fragments of *R. speratus* in Kagoshima (RA-RB), Miyazaki (RC-RD), and Fukui (RE-RG) prefectures, Japan. Sampling was performed in March 2021, one month before the swarming season. At the time of sampling, the colony fragments contained numerous large nymphs, which undertook imaginal molts in the lab. Colony fragments were kept in the lab at 22°C until alate imagoes ready to swarm emerged. They were then moved to a 27°C incubator to induce swarming. Alates coming out of the nests were sampled for experiments.

Experimental setup

For both species, alates were separated individually more than 30 minutes before the experiments. We used individuals that shed their wings on their own as tandem running behavior happens after termites shed their wings. All experiments were performed between 12:00 – 24:00 in *R. speratus* and 21:00 – 2:00 in *C. formosanus* within the 12 hours following swarming events. Note that the time of the day could be different from natural swarming events in *R. speratus* for some observations. However, we kept colonies under dark conditions for ~ 1 month before the experiments. In this condition, previous studies showed that alates of *Reticulitermes* termites show circadian rhythm by taking swarming as a starting point (Mizumoto *et al.*, 2017). Individuals within the colony do not show endogenous activity rhythm (Fuchikawa *et al.*, 2012).

To investigate the role of vision in termite movement coordination, we observed the movements of termite tandem runs and single female and male individuals under artificial light and in the dark. Experimental arenas consisted of a petri dish (ϕ = 90 mm) covered with a layer of moistened plaster that was polished before each trial (Fig. 1). Arenas were placed in an acrylic cube box (200 mm) on which a Raspberry Pi Camera Module was mounted. The camera modules were connected to the Raspberry Pi 4 Computer Model B. Videos were recorded using RPi-Cam-Web-Interface (<https://elinux.org/RPi-Cam-Web-Interface>) at 25 frames per second for 30 minutes. We extracted the coordinates of moving termites from each video using the video-tracking system UMATracker (Yamanaka & Takeuchi, 2018). A white LED light (440 lm) was mounted next to the camera module, resulting in ~1,000 lux for the experiments performed under artificial light conditions (corresponding to the daylight condition). As termites respond to light with >0.6 lux, our light condition was strong enough for termites to respond (Ohmura *et al.*, 2014). For the experiments performed in darkness conditions, termites were observed under infrared light. For *C. formosanus*, we observed 25 and 26 tandem pairs in the dark and with light, respectively. For *R. speratus*, we observed 30 tandem pairs in each illuminated condition (5 for col RA and RC-RF, 7 for RB, and 3 for RG). In *R. speratus*, pairing females and males were from the same original colony. Note that there is no nestmate preference or avoidance in tandem running behavior of *R. speratus* (Mizumoto *et al.*, 2022). We also

observed single individuals, to confirm how the light environments affect the movement activity of termites. For *C. formosanus*, we observed 25 females and 26 males in the dark and 26 females and 25 males under artificial light. And for *R. speratus*, we observed 34 females (5 for col RA and RC-RF, 6 for RB, and 3 for RG) and 33 males (5 for col RA -RF and 3 for RG) in the dark and 35 females and 35 males (5 for col RA and RC-RF, 7 for RB and 3 for RG) under artificial light. Individuals were introduced to the arena by dropping them from above the arena. In tandem experiments, we introduced both females and males at the same time. Each individual was used only once. All observations were performed in incubators maintained at 27°C.

Analyses of termite tandem coordination

All data analyses were performed using R v4.0.2 (R Core Team, 2020). We examined the movement coordination during tandem runs. Each termite individual was considered in one of three states: (a) tandem running, (b) interacting with nestmates in ways other than tandem running, and (c) searching (Mizumoto & Dobata, 2019; Mizumoto *et al.*, 2020, 2021). We automatically classified the state of each termite individual based on a time sequence. We defined female and male individuals as interacting (or tandem running) when the distance between their centroids was smaller than 7 mm for *R. speratus* and smaller than 10 mm for *C. formosanus*. This distance slightly exceeds termite body length with antennae, thence slightly exceeds the distance between a female and a male performing tandem run, during which both individuals have physical contact (Mizumoto & Dobata, 2019). An interacting pair was considered to be performing a tandem run when the interaction lasted for more than 10 seconds and both individuals moved more than 50 mm while interacting. The absence of contact between tandem run partners for less than 3 seconds was not regarded as a separation event unless the distance between individuals was >14 mm or 20 mm for *R. speratus* and *C. formosanus*, respectively (Mizumoto *et al.*, 2020). Following separation, we considered individuals engaged in searching until they interacted again.

Based on the criteria described above, we measured the duration of tandem runs and the time required for a female and a male to re-encounter upon separation. We compared tandem duration and separation duration between experiments performed in the dark and under artificial light, for each species separately. We carried out a mixed-effects Cox model using the `coxme()` function implemented in the `coxme` package (Therneau, 2015), with illuminated condition as a fixed effect and source colony (*R. speratus*) or sampling date (*C. formosanus*) as a random effect within which video ID was nested. A likelihood ratio test was carried out to determine the statistical significance of the explanatory variable (type II test). Observations interrupted as the end of the video was reached were included by treating them as right-censored data.

During tandem runs, the leader and the follower adjust their speeds to coordinate their motion (Franks & Richardson, 2006; Valentini *et al.*, 2020). We investigated whether illuminated conditions influence this speed regulation for tandem maintenance. We examined the relationship between acceleration and inter-individual distances, in the dark and under artificial light, using a linear mixed effect model (LMM), with inter-individual distances as fixed effect and source as random effects within which video id was nested. Furthermore, females pause while males move upon separation, facilitating reunion (Mizumoto & Dobata, 2019; Mizumoto *et al.*, 2020). We compared the mean speed during each tandem and separation event using LMM with tandem-separation schemes as fixed effect and source colony as random effects within which video id was nested. All analyses were performed for each sex and illuminated condition separately.

Comparisons of movement patterns

We examined how illuminated conditions affect termite movement patterns during tandem runs and random searches without partners. Animal movement patterns can be described by speed, sinuosity, and pausing patterns (Bartumeus & Levin, 2008). Thus, we measured moving speed, pausing duration, and trajectory sinuosity for each individual. We compared the distance of individuals in two successive frames taken at 0.2 second intervals and found that it followed a bimodal distribution, with two peaks around 0 and 3.5 mm for *R. speratus*, and 0 and 4.7 mm for *C. formosanus*. The two peaks represent individuals pausing and moving, respectively. We set a threshold for moving and pausing individuals as the value representing the second peak multiplied by 0.2 ($3.5 \text{ mm} \times 0.2 =$

0.70 mm for *R. speratus*; $4.7 \text{ mm} \times 0.2 = 0.94 \text{ mm}$ for *C. formosanus* (Mizumoto & Dobata, 2019)). When the distance of one individual in two successive frames was smaller or equal to the threshold value, the individual was considered to be pausing. On the contrary, when the distance was larger than the threshold value, the individual was considered in movement. We used the mean value of instantaneous speed during motion as a measure of speed. The use of other speed measures, including mean and median of all displacements and median during motion, did not change our results. For pausing duration, we calculated the proportion of displacements defined as pauses among all displacements. The sinuosity of the trajectory was measured as the variance of the turn angles calculated as the magnitude of changes in the direction of motion between two successive frames.

We compared three parameters of movement patterns (speed, pause duration, and sinuosity) between illuminated conditions and searching units (females, males, and tandem runs). For tandem runs, we used female motion as a representative. We performed LMM treating illuminated conditions and searching units as fixed effects and source colony (*R. speratus*) or collected date (*C. formosanus*) as random effects. Note that we did not include interaction between illuminated conditions and searching units in our final analysis as it was not significant. The likelihood ratio test was used to determine the statistical significance of the explanatory variable (type II test). Note that some variables did not always follow normal distributions, but LMM is robust against violations of distribution assumptions (Schielzeth *et al.*, 2020).

Ethical Note

No permits or licenses were required for this study. We followed OIST Animal Experimental Regulations and the ASAB/ABS Guidelines for the treatment of animals in behavioral research and teaching. Only flying alates were collected in *Coptotermes formosanus*. We needed to collect nesting logs for *Reticulitermes speratus* as it is difficult to locate the natural swarming. However, these sub nests did not contain reproductive, and the rest of the colony was used for another experiment or maintained in the lab. Termites were tagged with a dot of paint on the abdomen during observation. These tags did not alter their behavior, as a previous study showed that termites could normally survive > 2 years with tags (Mizumoto *et al.*, 2016).

Results

There was no significant difference in the proportion of pairs forming tandem runs with and without light (Fisher's exact test, $P > 0.05$; *C. formosanus*: 23/25 without light and 25/26 with light; *R. speratus*: 28/32 without light and 32/32 with light). The duration of tandem runs did not differ under light and darkness conditions in both species (mixed-effects Cox model; *C. formosanus*: $\chi^2_1 = 0.182$, $P = 0.670$; *R. speratus*: $\chi^2_1 = 1.220$, $P = 0.269$; Figure 2A-B). During tandem runs, females and males coordinated by adjusting their speed regardless of the illuminated conditions (Fig. 2C-F). When the distance between females and males increased, the leading females slowed down while the following males accelerated, catching up with the females (LMM; $\chi^2_1 > 4,500$, $P < 0.001$ for all, estimate slope < 0 for females, > 0 for males; Fig. 2C-F).

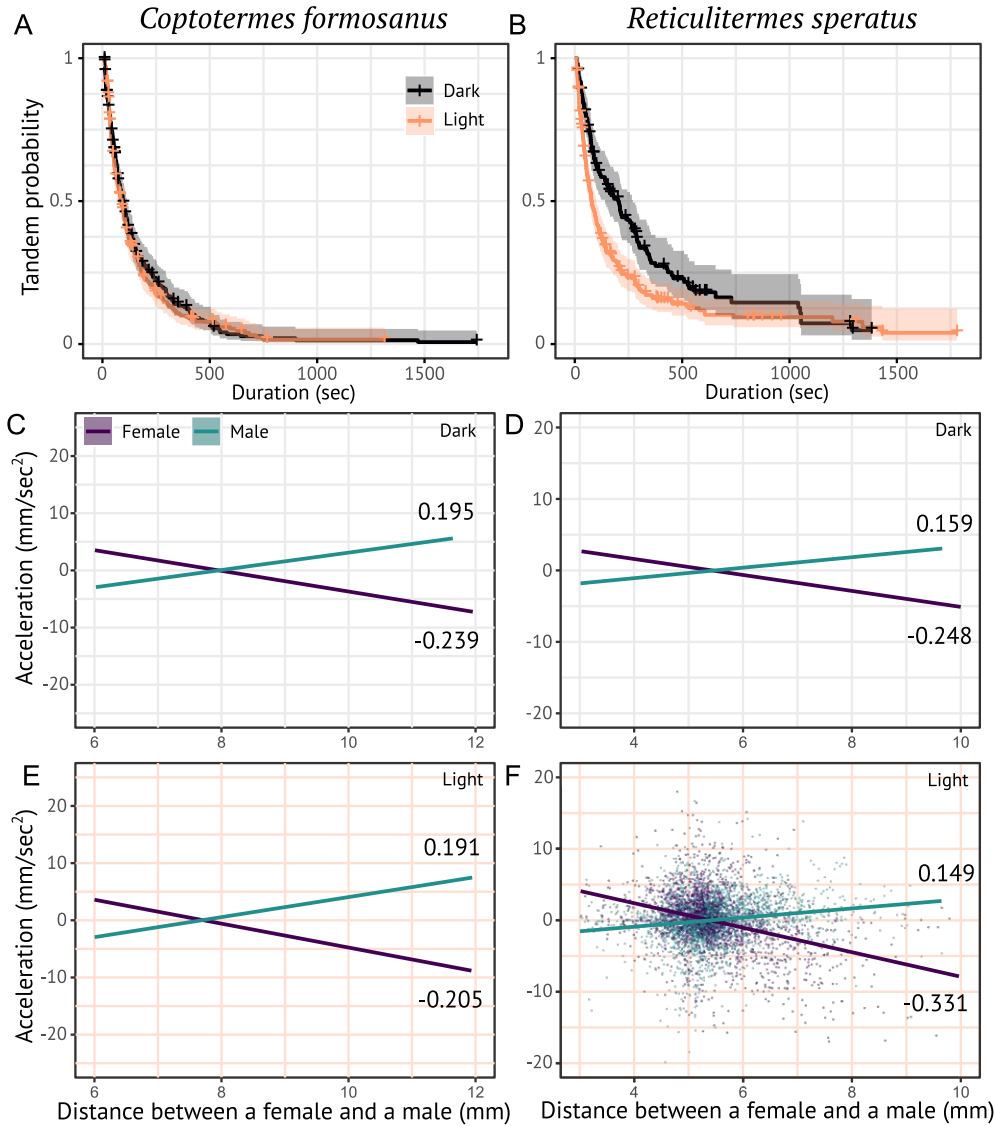


Figure 2. Movement coordination by termite tandem pairs in *C. formosanus* (left: A, C, E) and *R. speratus* (right: B, D, F). (A-B) Comparison of the duration of tandem running until separation under light and dark conditions. Kaplan-Meier survival curves were generated for each treatment, and Y-axis is the probability of tandem run (1 indicates all pairs are engaging in tandems, and 0 indicates all pairs are separated). There were no significant differences between the two illuminated conditions (mixed effect Cox model, $P > 0.05$). The symbol “+” indicates the end of observations. The shaded regions show 95% confidence intervals. (C-F) Acceleration by females and males during tandem run in response to their distances in the pairs under dark (C-D) and light (E-F) conditions. Plots show 5,000 randomly sampled data points. Lines indicate linear regressions. The number next to the regression lines are estimated slopes.

The time required for pairs to re-establish contact upon separation was similar under light and darkness conditions (mixed-effects Cox model; *C. formosanus*: $\chi^2_1 = 1.927$, $P = 0.165$; *R. speratus*: $\chi^2_1 = 1.854$, $P = 0.173$; Figure 3A-B). After separation of tandem runs, males of both species moved faster than females under both illuminated conditions (Fig. 3C-D).

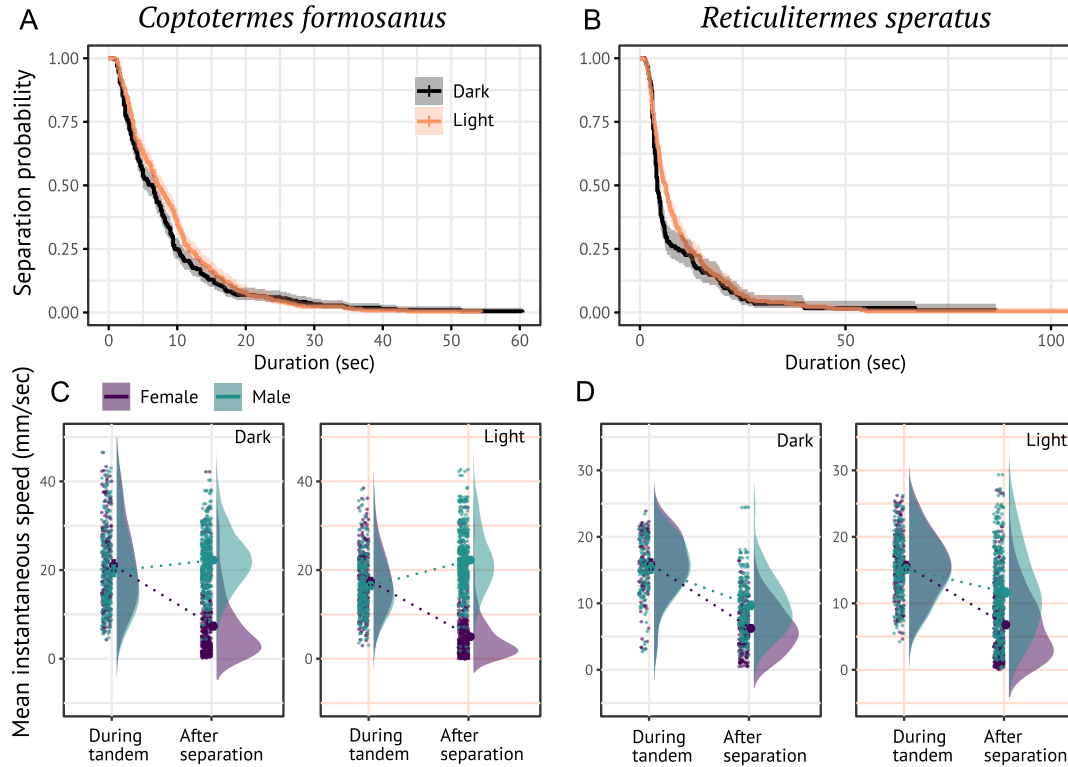


Figure 3. Reunion process after separation of tandem runs in *C. formosanus* (left: AC) and *R. speratus* (right: BD). (A-B) Comparison of the duration of searching until re-encounter after separation in the dark and under artificial light. Kaplan-Meier survival curves were generated for each treatment, and Y-axis is the probability of separation (1 indicates all pairs are separated, and 0 indicates all pairs are reunited). We found no significant differences between illuminated conditions (mixed effect Cox model, $P > 0.05$). (C-D) Instantaneous speed of females and males during tandem runs and after separation. Error bars indicate 95% confidence intervals.

The movements of the species mating during night, *C. formosanus*, was independent of illuminated condition (Speed: $\chi^2_1 = 3.154$, $P = 0.076$; Pause duration: $\chi^2_1 = 3.611$, $P = 0.057$; Fig. 4A, C), while *R. speratus*, the species with diurnal mating, moved more actively and faster under light condition (Speed: $\chi^2_1 = 7.468$, $P = 0.006$; Pause duration: $\chi^2_1 = 10.523$, $P = 0.001$; Fig. 4B, D). In contrast, sinuosity was not affected by the illuminated condition in both species (*C. formosanus*: $\chi^2_1 = 0.820$, $P = 0.365$; *R. speratus*: $\chi^2_1 = 0.999$, $P = 0.312$; Fig. 4E-F). These parameters for movement pattern were variable among comparisons. In *C. formosanus*, males were more active and faster than females and tandem runs (Speed: $\chi^2_2 = 10.910$, $P = 0.004$, Pause duration: $\chi^2_2 = 46.042$, $P < 0.001$, Sinuosity: $\chi^2_2 = 2.239$, $P = 0.327$; Fig. 4A, C, E), while in *R. speratus*, tandem runs were more active than single male and female individuals, and males performed more sinuous motion (Speed: $\chi^2_2 = 5.318$, $P = 0.070$, Pause duration: $\chi^2_2 = 22.473$, $P < 0.001$, Sinuosity: $\chi^2_2 = 6.585$, $P = 0.037$; Fig. 4B, D, F).

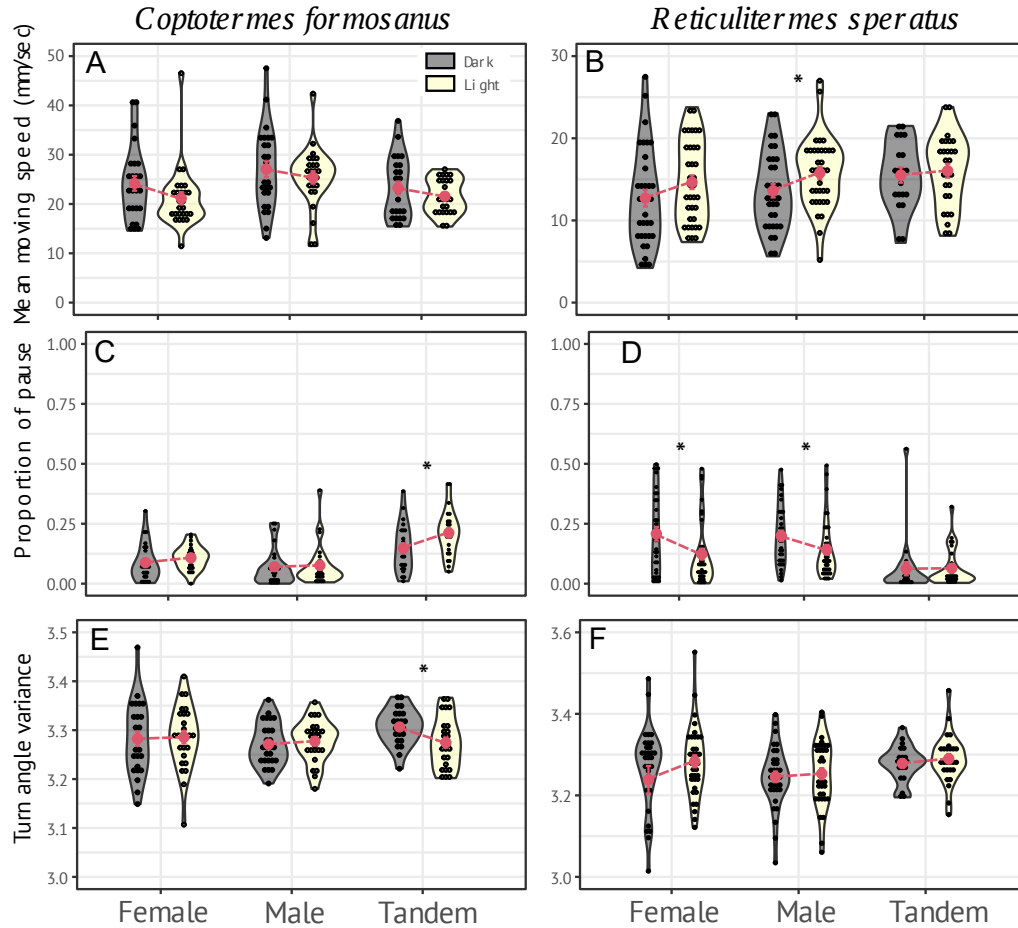


Figure 4. Effect of illuminated conditions on termite movement patterns, moving speed (A-B), pausing duration (C-D), and sinuosity (E-F). Red points and error bars indicate mean \pm 95% confidence intervals. * indicates statistical significance (LMM to compare between illuminated conditions for each sex/species separately).

Discussion

The formation of tandem runs was independent of illuminated conditions in both studied termite species. During tandem runs, females and males coordinated their motion with each other by adjusting their speed without using any visual information (Fig. 2), indicating that, like for ant tandem runs (Franklin *et al.*, 2011), following males do not visually track the motion of leading females. Following the breaks up of tandem formation, separated females and males could re-establish connection with each other under both dark and light conditions (Fig. 3). Thus, the dealates of the two species we studied engage in a blind search for a mating partner after separation, contradicting previous interpretations of another termite species reunion process (Sen-Sarma, 1962). Note that our study focused on communication at a closed distance, and further studies will be required to confirm if termites use visions to locate mating partners from a long distance. These results suggest that interindividual communication during movement coordination is mediated by tactile and chemical cues, not by visual cues.

Termite activity is sensitive to illuminated conditions. Termites engaged in mate searching more intensively by moving longer and faster under the light environments that reflect the species' natural situation. In *R. speratus*, swarming events occur during daytime (Takematsu, 1999), which is in line with our observations that individuals were more active under light conditions (Fig. 4B, D). In contrast, swarming events of *C. formosanus* take place after sunset, where individuals tend to be more (but not significantly) active in the dark (Fig. 4A, C). The activity pattern

of *C. formosanus* was not as clear as that of *R. speratus*, possibly because night is often under dim light rather than complete darkness (O'Carroll & Warrant, 2017), and *C. formosanus* may adapt to dim light environments rather than complete darkness. These results indicate that mate searching behavior can be affected by the surrounding light environments (Nutting, 1969; Mizumoto *et al.*, 2017). Such decreased mating activity in abnormal light environments is also observed in other insects, such as fruit moths (Li *et al.*, 2019) and olive flies (Kokkari *et al.*, 2017). Interestingly, despite decreased movement activity, tandem runs occurred normally under different light environments. Thus, once two individuals form a mating pair, they do not use visual cues anymore.

The visual acuity of termite dealates may not be good enough to track the partner's motion while tandem running. Termite imagoes are the only stage that possesses compound eyes. Although there is no anatomical data to estimate the acuity of termites, small insects often have low visual acuity and usually visually interact at short distances and on high contrast backgrounds (Land, 1997; Caves *et al.*, 2018). Although tandems are maintained within a few millimeters, termites do not have conspicuous coloration in their body, which may hinder the use of visual cues for communications. Instead, the primary function of compound eyes is phototaxis, which has been widely observed in termite alates (Williams, 1959; Ferreira & Scheffrahn, 2011; Ohmura *et al.*, 2014). Although eye-less workers also show phototactic behaviors (Cabrera & Rust, 1996; Park & Raina, 2005; Siderhurst *et al.*, 2006), developed compound eyes presumably improve sensitivity (Randel & Jékely, 2016). Thus, termites appear to use vision to orient themselves, which can be important information during flying dispersal or determining where to found a colony.

In summary, for single file movement coordination, like tandem runs or processions, individuals do not rely on vision for interindividual interactions but for collecting global information. For example, ants do not use vision for leader-follower communications but potentially for navigation during tandem runs (McLeman *et al.*, 2002; Franklin *et al.*, 2011; Bowens *et al.*, 2013; Mukhopadhyay & Sumana, 2021). In social caterpillars, chemical and tactile stimuli are involved in forming processions, but the visual cue is important for group orientation (Fitzgerald, 2003; Uemura *et al.*, 2021). In addition, even blind animals form single file movements (Radwański *et al.*, 2009; Vannier *et al.*, 2019). Here we confirm that termites do not use visual information for pair movement coordination but for synchronizing pairing time window. Such evolutionary convergence of communication mechanisms for single file movements suggests that visual information is unsuitable for interindividual interactions in a closed distance; instead, the benefit of chemical and tactical cues is predominant.

Data accessibility

All data that support the findings of this study and source codes for analyzing them are available at Zenodo, DOI: 10.5281/zenodo.7323333.

Authors' contributions

Nobuaki Mizumoto: Conceptualization, Data Curation, Formal Analysis, Funding Acquisition, Investigation, Methodology, Resources, Validation, Visualization, Writing-Original Draft Preparation. Thomas Bourguignon: Project Administration, Supervision, Writing-Review & Editing.

Competing interests

The authors declare no competing interest.

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