1 **Evaluating mate encounter and walking dispersal dynamics of termites using posture**
2 **tracking and behavioral simulation**
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4 **Nobuaki Mizumoto**
5 Department of Entomology & Plant Pathology, Auburn University, Auburn, AL, 36849, USA
6 nzm0095@auburn.edu
7 ORCID: 0000-0002-6731-8684

8
9 **Abstract**

10 Several termite species are problematic to human society as urban structural pests. Although
11 mature termite colonies with thousands to millions of individuals damage human properties, all
12 these colonies must start from a mating encounter of a female and a male. After seasonal
13 dispersal flights, the termite dealates walk to search for a mating partner and a potential nest site.
14 This very initial phase of the termite colony cycle plays an essential role in dispersal ability, initial
15 infestation, and invasion success; yet, the searching dynamics and success of these walking
16 termites are poorly understood across the environmental factors. In this study, I investigate mate-
17 searching and post-pairing dispersal behavior in *Coptotermes formosanus*, one of the most
18 damaging subterranean termites, by reanalyzing observations in the experimental arena with the
19 deep-learning posture tracking approach. I estimated that termites can walk about 23 m on
20 average and disperse up to 18.74 m on maximum within 15 minutes, with nest-searching tandem
21 pairs expected to disperse more than mate-searching single termites because of the movement
22 coordination. The simulations parameterized by termite observations quantified that urban light
23 attraction greatly contributed to the pairing success of termites, even with the low termite
24 population density. Thus, in the urban context, termites can effectively find a partner near the light,
25 and then tandem coordination helps them disperse from the encounter place. Comparative
26 quantitative behavioral studies across species may predict movement characteristics relating to
27 the invasive and pest status in termite diversity.

28
29 **Keywords**
30 Alate behavior, colony foundation, nest establishment, movement ecology, urban entomology,
31 light pollution, courtship, Formosan subterranean termite
32

Introduction

Among more than 3,000 species of diversity, some termites are serious structural pests, causing damage of $40 billion annually across the world as of 2010 (Rust and Su, 2012). Invasive termite species, especially, have a substantial impact, e.g., *Coptotermes formosanus* is listed as one of the top 10 costliest invasive species (Cuthbert et al., 2022). Termite studies have traditionally focused on the mature colonies, as structural damage to buildings arises only after colonies reach the developed stage (Gordon et al., 2022; Su and Scheffrahn, 1998) (Figure 1). However, even though the mature colony is made up of millions of individuals, all colonies of termites begin with a monogamous mating pair of a female and a male (Nutting, 1969) (Figure 1) with a few exceptions (Perdereau et al., 2015). Such a mate-pairing stage is highly mobile and can be a determinant of initial infestation, population dynamics, and invasion success. Yet, this critical stage has been understudied compared to the mature colonies. In this study, I explore the mate-finding and dispersal dynamics of a termite, *Coptotermes formosanus* Shiraki (Blattodea: Heterotermitidae), especially focusing on their walking behaviors.

In a season of the year, a large number of alates (winged reproductive individuals) fly off from their parental colony nests (Figure 1). There are three immediate tasks for the alates: 1) disperse from their original place, 2) find a mating partner, and 3) find a nest-site to start a colony. This information on *C. formosanus* is well summarized in a chapter of a book on this species (Chouvenc, 2023), where dispersal flight is relatively well-described. The dispersal flight of *C. formosanus* initiates in dusk (late twilight) and continues 15 minutes to an hour (Chouvenc, 2023). Alates of *C. formosanus* show a variable ability to disperse by flight. Direct observation tracked up to 460 m dispersal (Ikehara, 1966), and extensive mark recapture efforts show that they can disperse 621 m on average and up to 1,300 m (Messenger and Mullins, 2005; Mullins et al., 2015), while genotyping alates and surrounding colonies suggests alates dispersed 20-510 m away (Simms and Husseneder, 2009). Collectively, these indicate that alates of *C. formosanus* have a decent ability to disperse and expand their distribution ranges and thus are useful for the distribution surveys. However, as a socially monogamous insect, females and males of *C. formosanus* have to find a partner after dispersion and shedding their wings. Contrary to social Hymenoptera, all important mating processes happen during walking, i.e., finding a mating partner, engaging in pairing courtship, and finding a nest site. Thus, it is essential to quantitatively estimate the dynamics after shedding their wings to evaluate their success after dispersion.

After landing on the ground and shedding their wings, both females and males engage in a mate search by walking. This mate search is assumed to be a random search (Mizumoto and Dobata, 2019), indicating that termites do not know where their partner is until they encounter it, because *C. formosanus* termites do not rely on vision (Mizumoto and Bourguignon, 2022) or long-distance attracting chemicals (Chouvenc et al., 2020; Raina et al., 2003) for locating a partner. Before encountering a partner, both females and males actively move to search for a partner to maximize the searching areas (Mizumoto and Dobata, 2019). Once encountered, a pair of a female and a male performs tandem running behavior, with the leader female and the follower male coordinating motion, while searching for a suitable nest site. In tandem running, a female leader determines the course of the movement (Mizumoto et al., 2021; Valentini et al., 2020), while the follower male maintains contact with his antennae and pulps to maintain the coordination (Mizumoto and Reiter, 2025; Raina et al., 2003). In case of accidental separation between partners, a female leader pauses to wait for the partner, and a male follower engages in a restricted search, which is an effective reunion strategy for the strayed partner (Mizumoto et al., 2020; Mizumoto and Dobata, 2019). Encounters of the same sex may result in tandem runs (Mizumoto et al., 2024a), but it is rarer than other species (Mizumoto et al., 2022). Therefore, on the ground, termites dynamically alternate mate search and nest search until they settle in an available and suitable space for colony foundation (Chouvenc, 2023; Su et al., 1989). These observations provide important behavioral rules used by termite dealates. However, the dispersion-encounter dynamics of dealates remains unknown, e.g., how far termites can travel

84 after shedding their wings or the effective density required for mate searchers to encounter their
85 partner.
86   In this study, I open this research direction by reanalyzing termite searching strategies studied
87 in a previous study and building a behavioral simulation. Especially, Mizumoto and Dobata 2019
88 studied the movement patterns of termite dealates in both *Coptotermes formosanus* and
89 *Reticulitermes speratus* to investigate their mate searching strategies. This study obtained the
90 movement trajectories of termite dealates in a petri dish arena, by tracking their body centers with
91 a background subtraction technique, i.e., UMATracker (Yamanaka and Takeuchi, 2018). Since
92 then, more video tracking tools have become available, where there are many advancements in
93 deep-learning-based posture tracking. In this study, by updating the analysis, I reanalyze the
94 same video with one of these advanced tools, i.e., SLEAP (Pereira et al., 2022) to track termite
95 movements by body parts. Then, using posture information, I attempted to unwrap the termite
96 movements in a dish to the approximate open space, to grasp their dispersal abilities by walking.
97 Furthermore, by using the movement parameters of termites, I developed a mate searching
98 simulation and tested the effect of density and urban lights on mating encounter dynamics.
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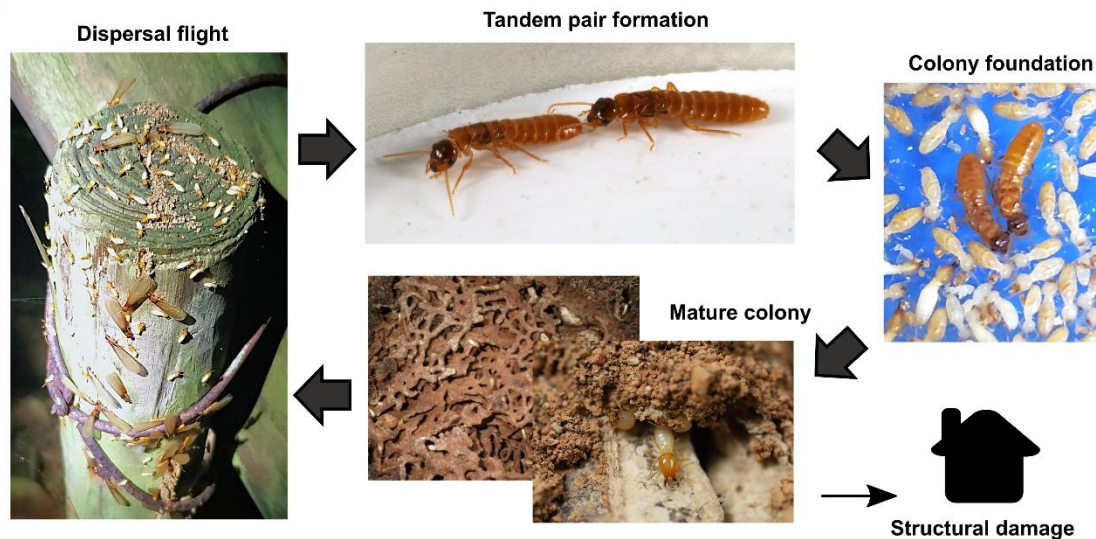
100
101 **Figure 1.** Life cycle of subterranean termites, as an example of *Coptotermes formosanus*.
102   In a season of the year, many alates (winged individuals) fly to disperse. After dispersal,
103   females and males look for a mating partner. Encountered pair performs a tandem run to
104   seek a nest site for colony foundation. The established colony grows into the mature
105   colony, which produces alates again. Among these, only mature colonies can damage
106   human property with a large number of colony members.
107

Methods

Behavioral data

110   I used the videos obtained in a previous study (Mizumoto and Dobata, 2019). In this study,
111 experiments with *C. formosanus* were performed to study the adaptive mate search strategy used
112 in termites. Alates were collected using light trapping, or from 2 colonies of *C. formosanus* with
113 nesting wood in Wakayama, Japan, in June 2017. After dispersal flights in the lab, termites that
114 shed their wings were used for the observations. Observations were performed in a Petri dish (Ø
115 = 145 mm) filled with moistened plaster. They observed termites in two different conditions; in
116 single searching experiments, they introduced a female or a male to the experimental arena and
117 recorded their movement for 30 minutes, while in tandem running observations, they introduced
118 one female and one male together to the arena and recorded for 60 minutes. A total of 22 single
119 females, 21 single males, and 20 tandem running pairs were observed.

120   All videos were analyzed using SLEAP v 1.4.0 (Pereira et al., 2022) to estimate the movement
121   of body parts of each individual. The model was based on that developed for *C. formosanus* in a
122   previous study (Mizumoto and Reiter, 2025), with a 17-node skeleton: antenna tips (LR), antenna
123   middle (LR), antenna base (LR), head (middle of mouth parts), head-pronotum boundary,
124   pronotum-mesonotum boundary, metanotum-abdomen boundary, abdomen-tip, fore legs (LR),
125   mid legs (LR), and hind legs (LR). I only used the data of the head and the abdomen-tip for
126   movement analysis. Due to the video quality, the detection accuracy of legs or antennae was very
127   low, but including these improved the tracking accuracy of the head and abdomen-tips. I trained
128   a U-Net-based model with a multi-animal top-down approach, with a receptive field size of 76
129   pixels for the centroid and 316 pixels for the centered instance, on Nvidia GeForce RTX 4090,
130   where augmentation is done by rotating images from -180 to 180 degrees. The video analysis
131   was performed for tandem running and single termites separately because of the setup difference
132   between these two experiments, where I finished tandem running first and then used the model
133   developed for tandem running to develop the model for single termites. I labeled 65 frames from
134   15 videos in tandem running, while 61 frames from 25 videos in single termites. While tracking
135   after the inference, I used the instance similarity method with the greedy matching method. All
136   pose estimation data were converted to HDF5 files for further analysis. I used Python to format
137   all HDF5 files for further analysis and converted them into FEATHER files for analysis in R (R
138   Core Team, 2024). We employed a linear interpolation method to address missing values in the
139   dataset. After scaling all data from pixels to mm, we used a median filter with a kernel size of 5 to
140   reduce noise. All analyses were performed after downsampling at 5 FPS.
141   From the trajectories, I obtained several kinetic variables as follows. First, I determined the
142   body center as the middle position between the head and the abdomen tip. Displacements of
143   body center positions were computed for every frame to obtain the instantaneous movement
144   speed. The change of the movement speed (acceleration/deceleration) and movement direction
145   were also computed using the displacements. Independent of the movement direction, I also
146   computed termite heading directions as the vector from the abdomen tip to the head. For tandem
147   running observations, we defined tandem running as a state where the distance between the
148   female abdomen tip and the male head is shorter than 3.1 mm (Mizumoto and Reiter, 2025),
149   where short separation or short running (< 1 sec) were smoothed. Then we analyzed movement
150   patterns only during tandem running behavior to compare with single-dealates.
151
152   *Unwrapping movements in a dish to open space*
153   In the dish arena, termite movements are bounded by the arena wall, making it impossible to
154   investigate their dispersal behavior (Nagaya et al., 2017). In this study, however, to grasp the
155   dispersal ability by walking in termite dealates, I converted the movement trajectories recorded in
156   a circular dish into the approximated open-space movements by applying a series of corrections
157   to movements bounded by a constrained space. The conversions addressed two main artifacts:
158   wall-following behavior and mismatches between heading and movement directions caused by
159   the dish walls. Note that these conversions do not completely reflect their motion in the open
160   space; instead, I aimed to approximate how far termites could disperse if there were no
161   boundaries in a dish (Figure S1-3).
162   First, termites in a dish often exhibit wall-following behavior, moving along the perimeter of the
163   dish in a smooth and curved trajectory (Miramontes et al., 2014; Paiva et al., 2020; Shimoji et al.,
164   2019). I assume that termite movements were biased due to the wall, and termites would maintain
165   their heading direction rather than curving along a dish wall in an open space. Thus, I considered
166   that termites are forced to turn at angles that require them to rotate along the wall. To correct this,
167   I converted the x-y coordinates into polar coordinates relative to the center of the arena. I
168   searched for sequences of frames, where termites moved for more than 10 mm in the same
169   direction of angular coordinates. For each of these events, I obtained how many angles the termite

170 rotated and then adjusted the trajectory by rotating positions to extend the path outward,
171 unwrapping the wall-following sequences (Figure 2A).
172   Second, near the wall, termite movements are often bounded by the wall, creating many
173 discrepancies between the heading direction (direction from the abdomen tip to the head) and the
174 actual movement direction. I fixed all these discrepancies near the wall (defined as the outer half
175 region in area) by rotating the trajectory around the previous location to align with the heading
176 direction. This assumes that the termite attempts to move forward along its body axis without
177 redirection arising from the dish or tracking artifacts (Figure 2B).
178
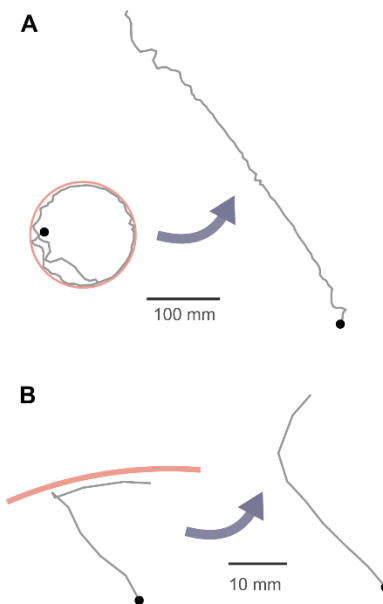
Figure 2. Unwrapping trajectories in a dish to open space. (A) Correction of the
wall-bound rotating motions. The path circulating around the dish was unwrapped
by rotating positions to extend the path outward. (B) Fixing the discrepancy
between heading directions and movement directions. Using posture tracking
datasets, the movement directions were replaced by heading directions to mimic
the movements in an open space.

Statistical analysis

188   I used a series of linear mixed models (LMMs) to compare the speed, change of speed
189 (acceleration/deceleration), and turning patterns, using R functions lmer() in the package 'lme4'
190 (Bates and Maechler, 2015) and lme() in 'nlme' (Pinheiro, 2011). I used the likelihood ratio (type
191 II) test to examine the statistical significance of each explanatory variable. First, I investigated the
192 relationship between instantaneous speed and speed change in the next moment, using an LMM,
193 where speed change was the objective variable, while speed, single or tandem leader (hereafter
194 units in this section), and their interaction were fixed variables. The video ID that is nested within
195 the original colony was included as a random effect (random intercept). Second, I compared the
196 instantaneous speed between units using a similar LMM with instantaneous speed as the
197 objective variable, units as fixed variables, and the video ID nested within the original colony as
198 a random intercept. In addition, to compare whether the variability in these parameters differed
199 between units, I fit two LMMs: the first included only random intercepts (the video ID that is nested
200 within the original colony), and the second assumed that the variance could be variable between
201 units in addition to the random effect. The fittings of these two models were compared using the
202 likelihood ratio test. I also compared the traveled distance between units using an LMM with

203 traveled distance as the objective variable, units as fixed variables, and colony as a random effect.
204 The traveled distance was obtained by computing the mean step length per 0.2 seconds and
205 summing up for 15 minutes for the aid of interpretation.
206   Next, I investigated the dispersal patterns of the trajectories unwrapped from the bounded
207 space to the open space. As for tandem running observations, I focused on each tandem running
208 event rather than each video, as the latter included both tandem running and separations. First,
209 for each trajectory, I extracted how far termites dispersed at 15-minute time points and compared
210 them between units using a similar LMM as above. I also computed the mean squared
211 displacement (MSD) to investigate the diffusive properties of the unwrapped trajectories. The
212 MSD is the mean of the squared distance that an organism travels from its starting location to
213 another point during a given delay time, τ. The MSD is proportional to the time to the power of α,
214 MSD $\sim \tau^{\alpha}$, where α characterizes the behavior of diffusive processes. In normal diffusion, as is
215 the case with Brownian motion, the MSD increases linearly with time ($\alpha = 1$), while $\alpha < 1$ indicates
216 subdiffusive and $\alpha > 1$ indicates superdiffusive processes. MSDs were obtained in the entire range
217 of each trajectory, using the function computeMSD() in the package 'flowcatchR' (Marini, 2017).
218 Then, to obtain the diffusion properties, I examined the relationship between MSD and τ using a
219 log-log transformation. Fitting was restricted to a subset of datasets (0.2, 0.4, 0.6, 0.8, 1, 2, 4, 6,
220 …, 1000) to avoid the oversampling at the larger τ. The fitting was performed by an LMM with
221 each trajectory identity included as a random slope. The slope α obtained from this regression
222 corresponds to the scaling exponent, which characterizes the diffusion regime (e.g., subdiffusive,
223 diffusive, or superdiffusive).
224
225 **Results**
226   In both single dealates and tandem leaders, moving speed and change in speed were
227 obviously correlated, where termites speed up after the slower movements, while they slow down
228 after the fast movements (Figure 3AB). The slopes of the response regressions were different
229 between singles and leaders (LMM, interaction: $\chi^2_1 = 28.18$, $P < 0.001$), with singles changing
230 their speed more sensitively than tandem leaders (slope, single: -0.184, leader: -0.176). There
231 was no difference in mean speed between singles and leaders (LMM, $\chi^2_1 = 1.2$, $P = 0.273$).
232 However, the data distributions clearly showed that both speed and change in speed are more
233 variable (wider distribution) in single dealates than tandem leaders (Figure 3AB). When
234 comparing the models with and without variability between single and leaders, the model allowing
235 different variances provided a much better fit to the data, with leader speed being less variable
236 than single dealate speed ($\chi^2_1 = 17010.06$, $P < 0.001$). The same was true for the change in speed
237 ($\chi^2_1 = 21499.91$, $P < 0.001$).
238   Similarly, turning patterns also differ between single dealates and tandem leaders. Again, data
239 distribution clearly showed the wider distribution in single dealates compared to tandem leaders
240 (Figure 3CD), which is supported by comparing models with and without variable variance of
241 angles between singles and leaders ($\chi^2_1 = 27673.09$, $P < 0.001$). Also, interestingly, the
242 relationship between instantaneous speed and turning was different between single dealates and
243 tandem leaders. In single dealates, turning angles became more variable according to the
244 movement speed (Figure 3C). On the other hand, tandem leaders decreased turning angles when
245 they are constantly moving (S.D. of turning angles achieved a local minimum around 3.8
246 mm/0.2sec, Figure 3D).
247
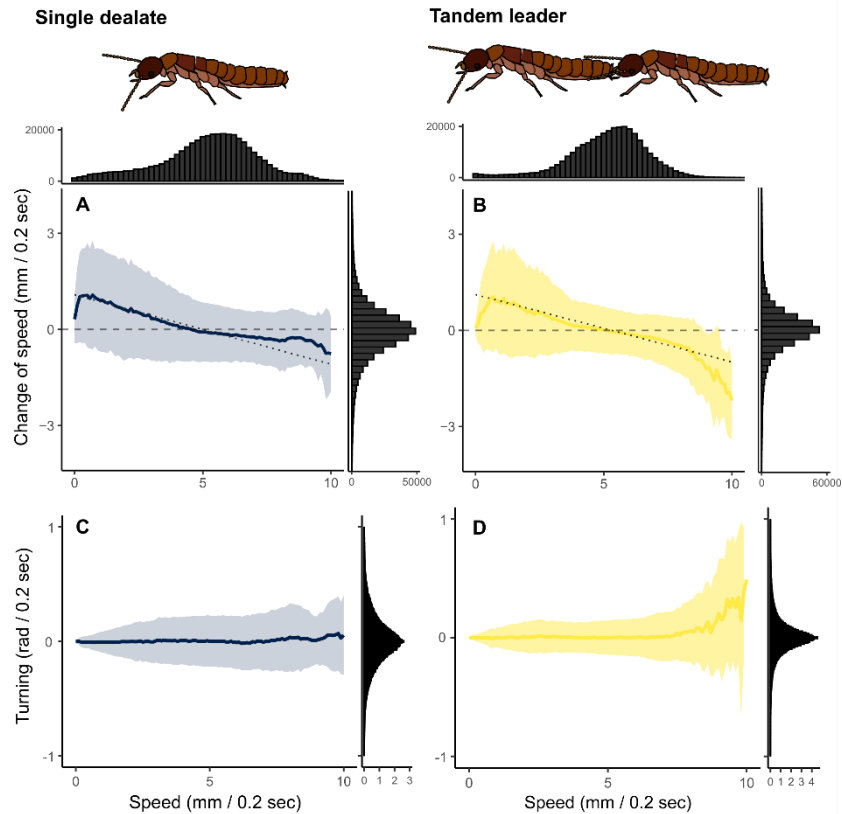
Figure 3. Movement parameters for termite dealates. The lines and colored area indicate the Mean ± S.D., which was calculated by binning the speed by 0.1. For the change of speed (acceleration/deceleration), the dashed regression lines by LMM were drawn. The histogram of each kinetic parameter was also shown.

During the observations, termites kept moving on the petri-dish arena despite the bounded space. There was no significant difference in traveled distance between single dealates and tandem leaders (χ^2_2 = 1.52, P = 0.469, Figure 4A). Notably, termites walked about 23 ± 4.2 m (mean ± S.D.) in 15 minutes on average. The unwrapping procedure extended the movement trajectories to an open space (Figure 4CD, Figures S1-3). Within the first 15 minutes, tandem running dispersed further distances than single individuals (χ^2_1 = 5.03, P = 0.025, Figure 4B), where, on average, single individuals dispersed 6.5 ± 3.7 m from the starting point, while the tandem leader dispersed 9.6 ± 4.8 m.

The MSD showed that tandem leader movements were more diffusive than single termites (Figure 4CD). The diffusive exponent α was estimated to be 1.65 (with S.D. of 0.12 by the random slope, LMM) for single termites, while 1.80 (with S.D. of 0.12 by the random slope, LMM) in tandem leaders. In either case, the trajectories showed the superdiffusive properties as observed in arthropods in (pseudo-) open spaces (Johnson et al., 1992; Mizumoto et al., 2024b; Nagaya et al., 2017; Seuront and Stanley, 2014).
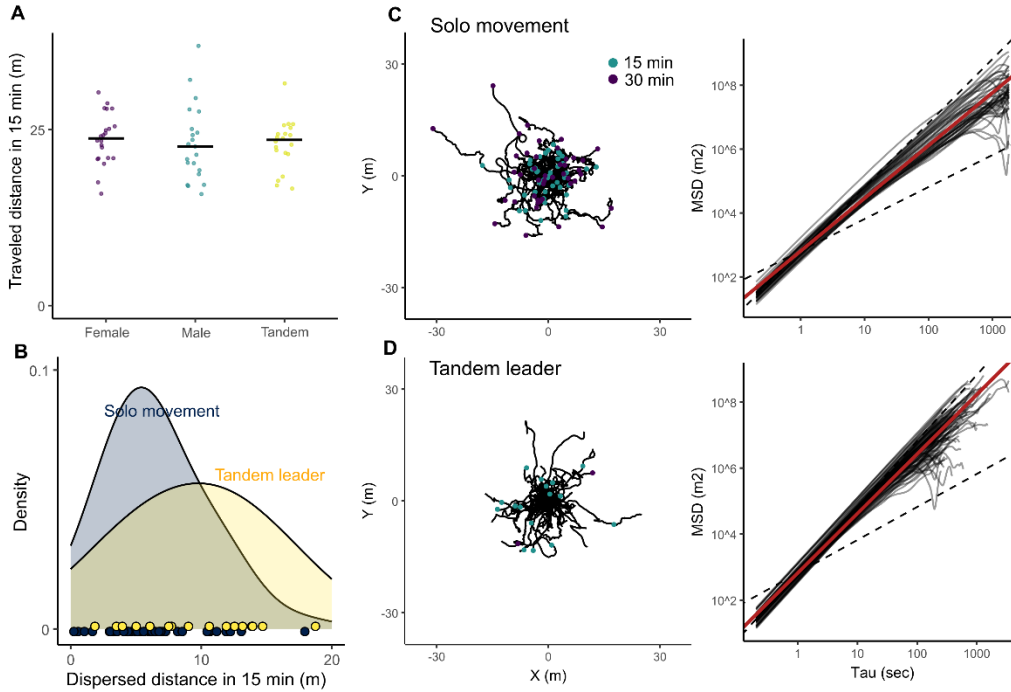
269
270 **Figure 4.** Dispersion patterns of termite dealates. (A) The comparison of traveled
271 distance between different dealate units. The traveled distance for 15 minutes was
272 obtained from the mean traveled distance in 0.2 seconds for each individual. (B) The
273 distribution of dispersed distances from the starting point after 15 minutes in the
274 unwrapped trajectories. Unwrapped trajectories and mean square displacements in
275 (C) single individuals and (D) tandem leaders. Red regression lines are generated
276 using LMM. Data of females and males are pooled in (B-C).

277
278 **Simulations**
279   I used an individual-based model to examine the mating encounter dynamics of termites with
280 the estimated movements in the open space. Termites search for a mating partner in a periodic
281 boundary condition of size L_{area} x L_{area}. There are two different scenarios for mate search (Figure
282 5A): i) without light, where all individuals are randomly located in the area, ii) with light, where all
283 individuals are attracted by light before shedding their wings, and thus start from the concentrated
284 area with size L_{light} x L_{light}. In each condition, females and males walked until they encountered
285 another individual of the opposite sex. When the distance between the centers of a female and a
286 male became smaller than φ (= 10 mm), they were regarded as having encountered (Mizumoto
287 and Dobata, 2019).
288   Individuals perform correlated random walks in terms of both speed and turning angles. The
289 current individual movement speed is correlated with the previous speed as the acceleration
290 correlates with the speed (Figure 3), which is determined as follows:
291 $$v_t = b - av_{t-1} + \epsilon, \quad \epsilon \sim \text{Laplace}(0, \sigma),$$
292 where parameter values were obtained by fitting the empirical datasets of solo individuals, a = -
293 0.184, b = 0.910, σ = 0.628. Turning angles also followed a Laplace distribution with scale
294 parameter σ = 0.164. I used Laplace distribution instead of common angular distributions, such
295 as wrapped Cauchy or von Mises distributions, because the distribution of empirically observed
296 turning angles was skewed towards the center (Figure 3), where the Laplace distribution showed
297 a better fit than others.
298   In the simulation, one timestep corresponds to 0.2 seconds, consistent with the frequency of
299 data analysis of 5 FPS. The simulation lasted for 30 minutes (9,000 steps), and the number of

pairs produced was recorded for every frame. I set the initial number of individuals as 100, 1,000, and 10,000, corresponding to small, middle, and large swarming events (Chouvenc et al., 2017; Higa and Tamashiro, 1983; Sugio, 2019). The whole area size L_{area} was 30 m, and the alates are attracted to the area with L_{light} = 3 m. The simulation program was implemented in C++ as functions and executed in R, using a package Rcpp (Eddelbuettel and Balamuta, 2018). The results of the sensitivity analysis of these parameters are in the supplementary materials (Figure S4).

The simulation results clearly showed the Allee effects on the termite mating encounters as observed in a termite (Kusaka and Matsuura, 2017). In higher density conditions, more termites could encounter a mating partner, and light trapping greatly increased the mating encounter probability by increasing the local termite densities (Figure 5B, S4). With the empirically observed walking abilities of *C. formosanus*, 100 randomly located termites in a 30x30 m area are desperate to find a mating partner only by random search. However, with increased density, dealates of *C. formosanus* could find a partner sufficiently only through random search. On the other hand, even with a limited number of termites available in the population (e.g., 100), light trapping can increase the local density and result in a higher encounter probability than the condition without light but with a larger population (Figure 5).
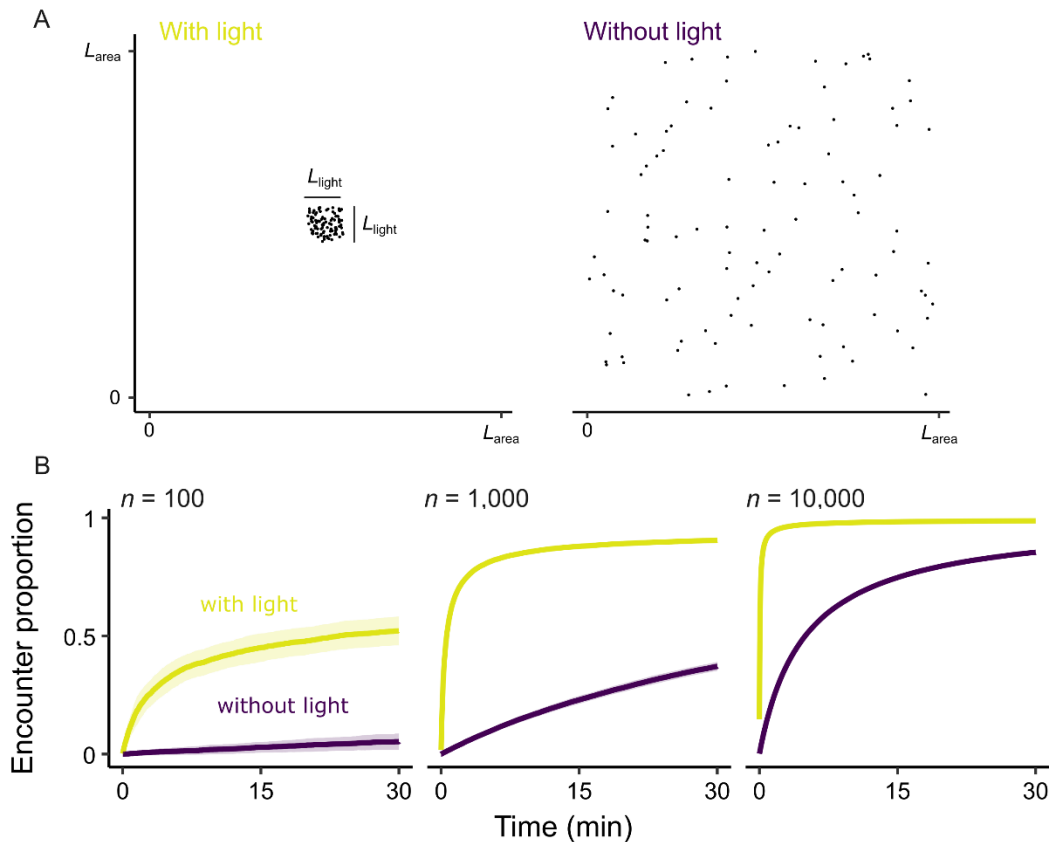
Figure 5. Termite movement simulations. (A) Two different initial searching conditions. Without light, termites are located randomly across the entire area, while with light, termites are located in a specific area. In both situations, the area of L_{area} x L_{area} is a periodic boundary condition. (B) The results of the simulation with L_{area} = 30 m and L_{light} = 3 m. See Figure S4 for other parameter combinations.

Discussion

In termite dealates, walking to search for a mating partner and a suitable nest site is an essential first task after dispersal. The comparison shows that the movement of tandem running pairs (nest site searching) is more diffusive and more stable than the movement of single termites (mate searching). The moving speed of tandem leaders is less variable than that of single termites, and the turning angles are also less variable (Figure 3). Such a stable and more straight motion by tandem leaders resulted in dispersing more distances from the initial points, even though the total travel distance was not different from single termites (Figure 4). This difference between single termites and tandem leaders makes sense from both ultimate and proximate points of view. Ultimately, a more dispersed motion of tandem running leaders allows them to get apart from the place where they encountered. Mate searching behavior is mutual search, where both females and males search for each other, and even slow-moving or pausing behavior can achieve a higher encounter rate for one sex (Foffi et al., 2025; Mizumoto et al., 2017; Mizumoto and Dobata, 2018; Reynolds, 2006). On the other hand, in nest-site search, the advantage of moving a greater distance will be higher than in mate search, as the nest-site does not move to find a site searcher. Furthermore, if termite mate searchers are clumped in one location, dispersing from there may be advantageous, as encountering another mate searcher can lead to the interruption of tandem running (Mizumoto et al., 2020).

Proximately, more stable and straight motion of tandem running may be the consequence of movement coordination. In tandem running behaviors, leaders and followers coordinate their motion. Especially, leaders slow down and followers speed up with more distance between partners, while leaders speed up and followers slow down with less distance (Mizumoto and Bourguignon, 2022; Mizumoto and Reiter, 2025; Valentini et al., 2020), where similar speed controls can be observed in ant tandem running (Franks and Richardson, 2006) or different types of movement coordination (e.g., fish (Schaerf et al., 2021)). Also, to maintain contact between leaders and followers, the possible movement directions of leaders may have been limited compared to when they are alone, because sharp turns by leaders often result in the interruption of tandem running (Mizumoto et al., 2020; Valentini et al., 2020). In this sense, even though tandem running is a simple movement coordination, cooperation between partners can, in turn, affect the pair-level movement patterns.

Artificial light, especially in urban areas, is generally harmful to nocturnal flying insects (Owens et al., 2020), e.g., by trapping insects near the light source for a long period and eliminating the time window for other essential activities (Kasai and Hironaka, 2024). However, *C. formosanus* termites (and several other species) could be in a unique position that can use artificial light in a beneficial way, because termites change their response to the light in a short time frame. With wings, alates are attracted by lights as in other nocturnal insects, but once they shed their wings near the light source, dealates turn to show negative phototaxis (Chouvenc, 2023; Ferreira and Scheffrahn, 2011; Ohmura et al., 2014). Thus, termites will not be trapped by light for a long period, and their tandem running behavior is not affected by light (Mizumoto and Bourguignon, 2022). Previous studies suggest that urban lights should have contributed to their successful invasion processes (Chouvenc, 2025), which is indirectly supported by the fact that the diurnal flight species, *C. testaceus*, is not as invasive as *C. formosanus* or *C. gestroi* (Scheffrahn et al., 2015). The simulation also quantitatively support this idea by demonstrating that *C. formosanus* can enjoy the benefits of urban light, with empirically observed walking abilities of termites (Figure 5 S4), e.g., 100 termites / 30x30 m^2 is too low density for termites to find a partner through random search, but light traps can inflate the encounter rate more than the level of 10 times density in the same area. This can make even the small swarming events fruitful for termites (Chouvenc et al., 2017; Higa and Tamashiro, 1983; Sugio, 2019), as well as the nest establishment in the invasion frontier, which is usually limited by the population size, promising.

Note that the unwrapping method used in this study is not a perfect approximation of the movement in an open space, but the aim is to grasp the dispersal ability of *C. formosanus* termites by walking. The unwrapped trajectories still have several artifacts. For example, termites

377   sometimes show 180° turns while following the wall. This can be interpreted that termites try to
378   turn in some direction but are bounded by the wall, resulting in 180°. It is impossible to know the
379   termite's intention; thus, these turns appear as sharp directional changes in the unwrapped
380   trajectories (Figures S1-3). Also, the wall itself could affect the behavior of insects (Scharf et al.,
381   2024). However, except for several artifacts, I consider that the effect of bounded space on termite
382   behaviors is minimal, especially in mate-or nest-searching termite dealates. Different from other
383   solitary insects, the time for termites to search for a partner or nest is very short, i.e., up to a few
384   hours (Chouvenc, 2023) or until they die (Mizumoto et al., 2024b, 2016). At this stage, searching
385   is the only task termites engage in, and dealates keep moving during the observation period
386   (Figure 4B), which is consistent with the field observations. Still, further studies will be required to
387   better estimate the termite dispersal ability on their feet, including mark recapture on termite
388   dealates (Mullins et al., 2015), or collecting termites using a nest site trap in the field environments
389   (Nkunika, 1988; Su et al., 1989). Caution will be required when applying the methods used here
390   to other taxonomic groups than termites, but this can also potentially provide insight into other
391   walking-based movements of pest insects, which is common in urban entomology (Socha and
392   Zemek, 2003; Suchy and Lewis, 2011).
393   In general, mate pairing is the phrase that has had little attention in the termite life cycles.
394   However, this phrase is a critical starting point of the colony foundation, and actually has a wide
395   diversity across species (Mizumoto et al., 2022; Nutting, 1969). High density is clearly important
396   for *Coptotermes* species that use random encounters as a primary method of the pairing process,
397   but this is not always the case in other invasive pest species (Evans et al., 2013), especially in
398   Kalotermitidae. For example, *Cryptotermes brevis* and *Incisitermes minor* are two major drywood
399   pest species in the US and are regarded as invasive species. Both of these exhibit tandem running
400   courtship behavior, but the density is much smaller than that of *Coptotermes* termites, and *I. minor*
401   disperses during the day (Harvey, 1934; Minnick, 1973). Furthermore, e.g., *Cryptotermes*
402   *domesticus* completely lacks tandem running behaviors (Huang et al., 2007), which should have
403   a distinct pairing process for colony foundation. These drywood termites are one-piece nesting
404   termites that do not move to other nesting materials according to colony development (Abe, 1987).
405   Thus, nest-site selection is a main determinant of their later colony success, and locating a
406   suitable nest site should be critical for initial infestation prevention. Yet, the information on mate-
407   pairing and nest-site selection in termites is critically lacking in both pest and non-pest species.
408   Future building comparative information will be helpful to predict the spread patterns of termites
409   in urban areas.
410

The datasets and codes generated during the current study are available at GitHub, https://github.com/nobuaki-mzmt/DealateDiffusion. The accepted version will be deposited in Zenodo to obtain DOI.

Ethics approval
This study did not require ethical approval as it involved only the analysis of previously published data. No new data were collected from human or animal subjects.

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591   Supplement materials for
592   **Evaluating mate encounter and walking dispersal dynamics of termites using posture**
593   **tracking and behavioral simulation**
594
595   **Nobuaki Mizumoto**
596   Department of Entomology & Plant Pathology, Auburn University, Auburn, AL, 36849, USA
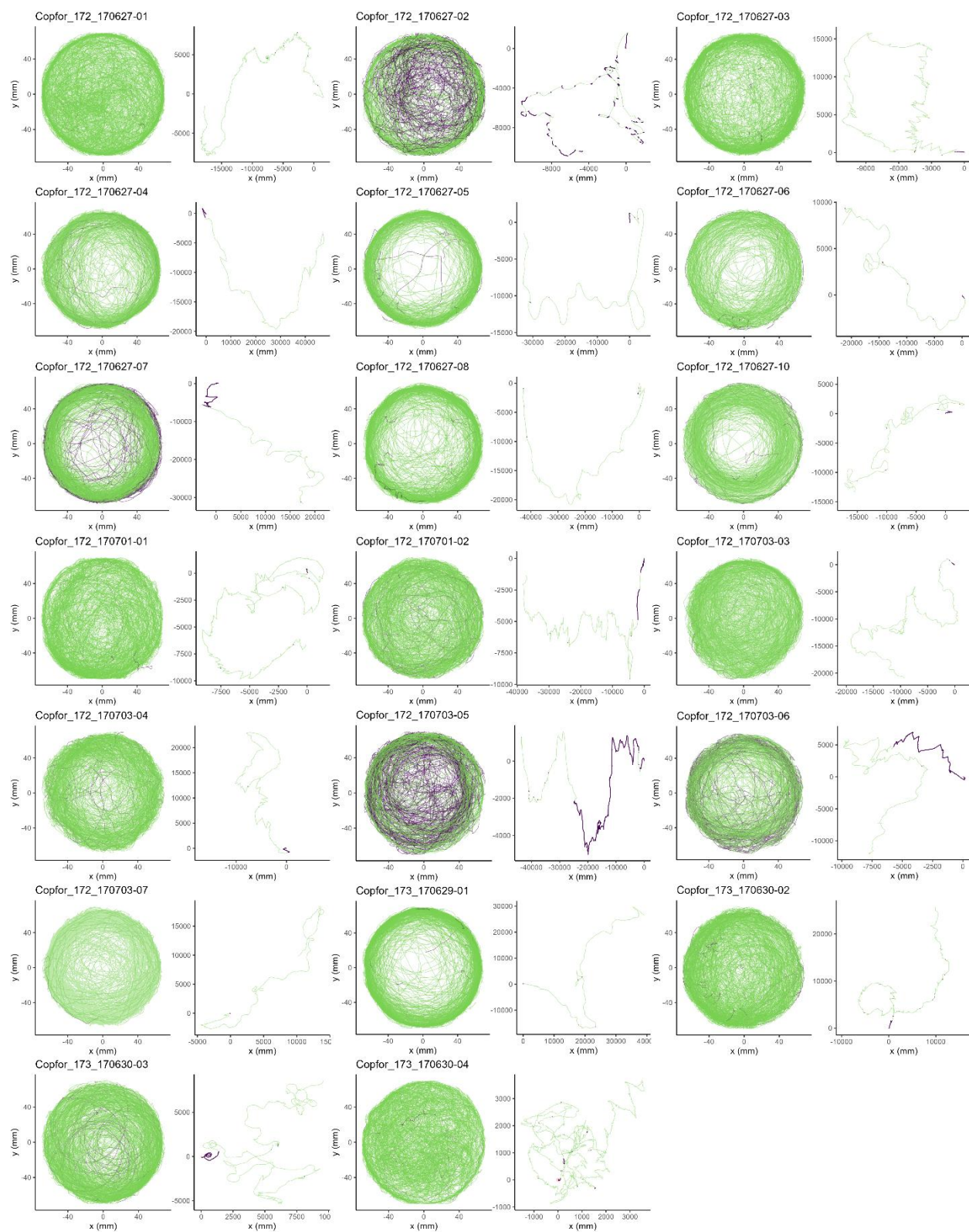597   nzm0095@auburn.edu
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599   **Figure S1-S4**
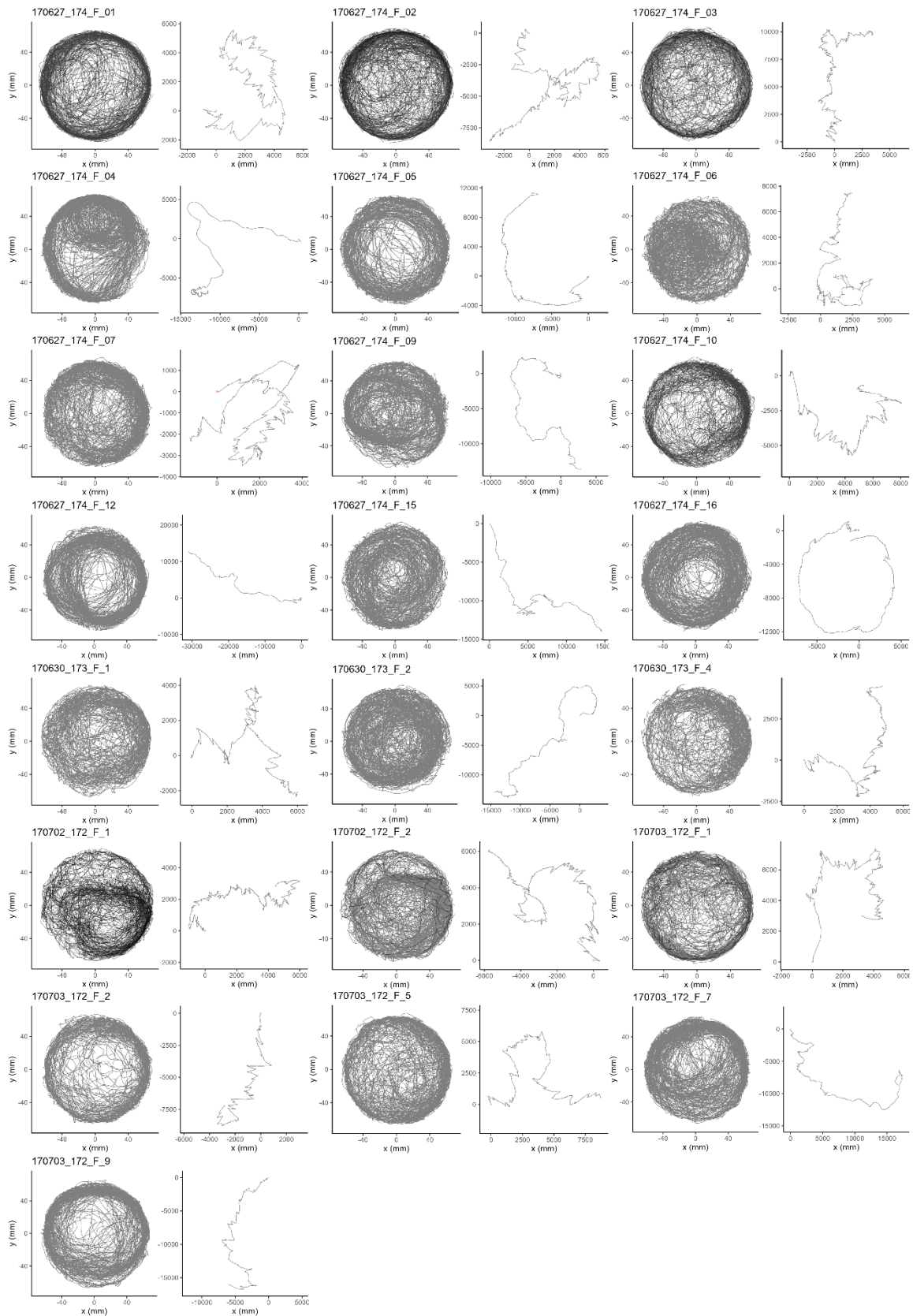
600
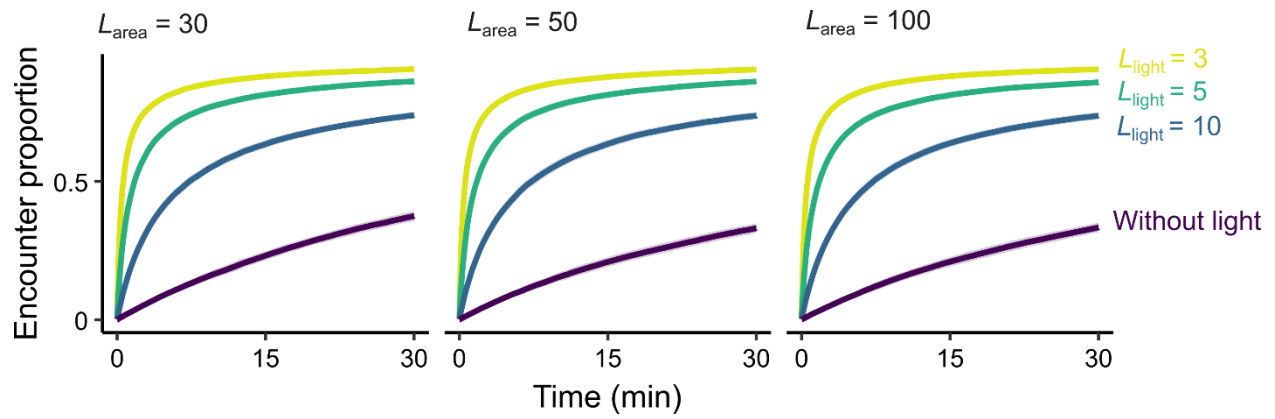601 **Figure S1**. Original and unwrapped trajectories of single females.
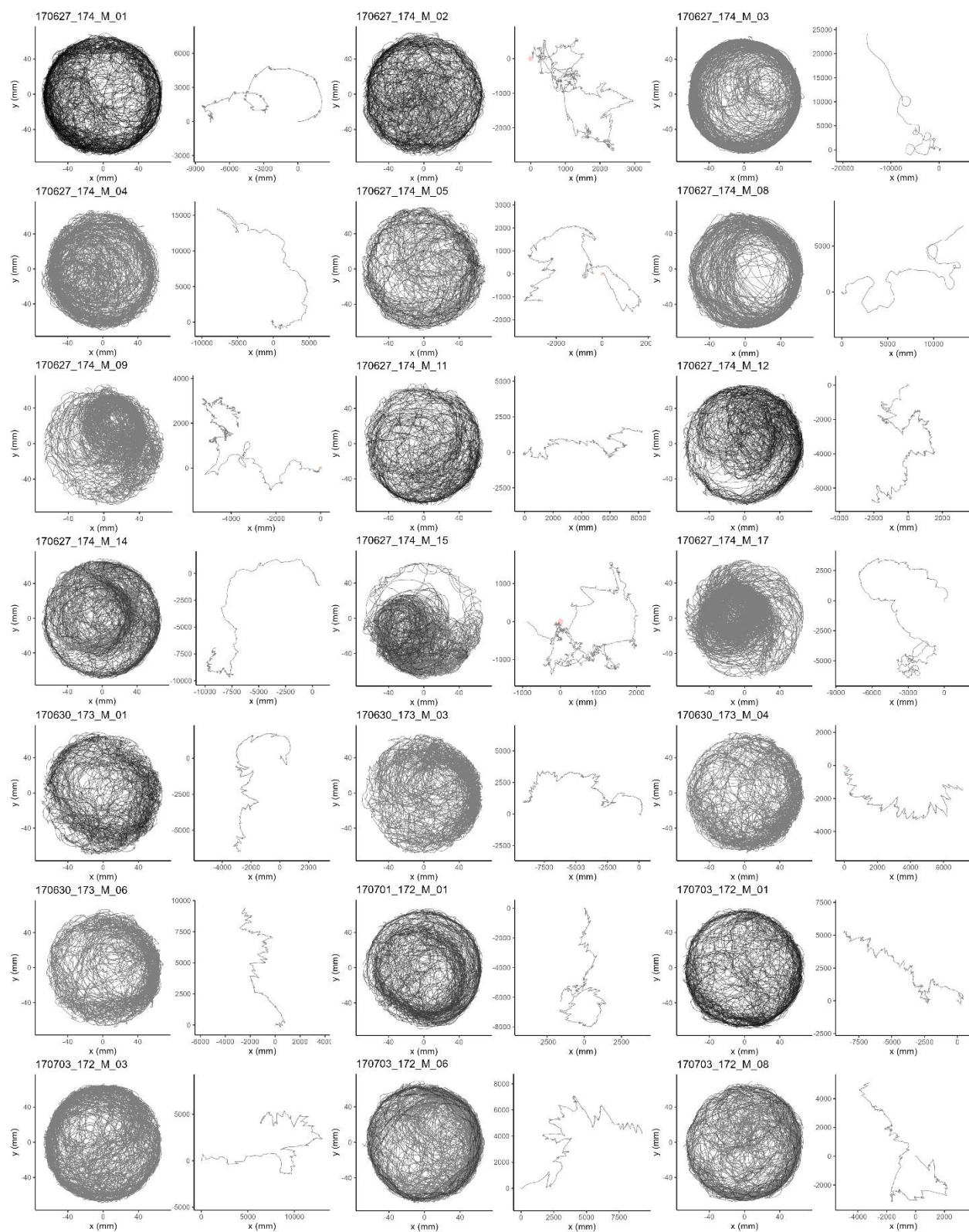
Figure S2. Original and unwrapped trajectories of single males.

Figure S3. Original and unwrapped trajectories of tandem running pairs. Green is for tandem running, while purple is for separation.

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609 **Figure S4**. The results of the sensitivity analysis of the parameters L_{area} and L_{light}
610 when $n = 1,000$.