

1 **Termite males enhance mating encounters by changing speed according to density**

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24 **Keywords**

25 Mate search; Movement ecology; Random search; Sexual selection; Social insects; Tandem runs

26
27 **Abstract (< 350 words)**

28 1. Search theory predicts that animals evolve efficient movement patterns to enhance encounter
29 rates with specific targets. The optimal movements vary with the surrounding environments,
30 which may explain the observation that animals often switch their movement patterns
31 depending on conditions. However, the effectiveness of behavioral change during search is rarely
32 evaluated because it is difficult to examine the actual encounter dynamics.

33 2. Here we studied how partner-seeking termites update their search strategies depending on the
34 local densities of potential mates. After a dispersal flight, termites drop their wings and walk to
35 search for a mate; when a female and a male meet, they form a female-led tandem pair and
36 search for a favorable nesting site. If a pair is separated, they have two search options: reunite
37 with their stray partner, or seek a new partner. We hypothesized that the density of individuals
38 affects separation-reunion dynamics and thus the optimal search strategy.

39 3. We observed the searching process across different densities and found that termite pairs were
40 often separated but obtained a new partner quickly at high mate density. After separation, while
41 females consistently slowed down, males increased their speed according to the density. Under
42 high mate density, separated males obtained a partner earlier than females, who do not change
43 movement with density.

44 4. Our data-based simulations confirmed that the observed behavioral change by males contributes
45 to enhancing encounters. Males at very low mate densities did best to move slowly and thereby
46 reduce the risk of missing their stray partner, who is the only available mate. On the other hand,
47 males that experienced high mate densities did better in mating encounters by moving fast
48 because the risk of isolation is low, and they must compete with other males to find a partner.

49 5. These results demonstrate that termite males adaptively update their search strategy depending
50 on conditions. Understanding the encounter dynamics experienced by animals is key to
51 connecting empirical work to the idealized search processes of theoretical studies.

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53 **Introduction**

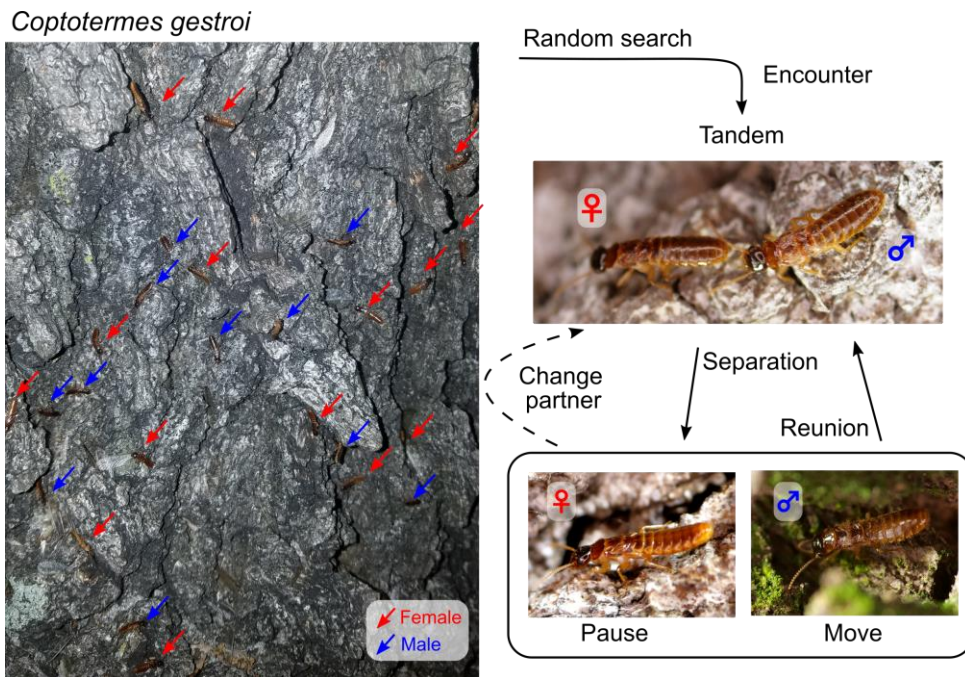
54 Animals move to search for food, nest sites, and mates, which is essential for their survival and
55 reproduction (Bell, 1990; Nathan et al., 2008). Search theory predicts that animals engage in random
56 search when locations of targets are uncertain, and they evolve efficient movement patterns to
57 enhance encounter rates with specific targets (Bartumeus, Da Luz, Viswanathan, & Catalan, 2005;
58 Viswanathan, Luz, Raposo, & Stanley, 2011). Simulation studies of random search have proved that
59 there is no universal solution to any search problems; instead, search efficiency of movement
60 patterns strongly depends on the information available to searchers and on environmental
61 conditions (Abe & Shimada, 2015; Ferreira, Raposo, Viswanathan, & Da Luz, 2012; Reynolds &
62 Bartumeus, 2009). Supporting this idea, animals often change their movement patterns according to
63 conditions. Studies analyzing GPS data of wildlife suggest that animals do not use a single search
64 strategy but alternate between different movement patterns (e.g., Brownian walk and Lévy walk) in
65 areas with different resource distributions (Auger-Méthé et al., 2016; Humphries et al., 2010; Sims,
66 Humphries, Bradford, & Bruce, 2012). Laboratory experiments manipulating the availability of
67 targets have also demonstrated that animals change their movement patterns according to their
68 situation (Bartumeus, Peters, Pueyo, Marrase, & Catalan, 2003; Cloyed & Dell, 2019; Mizumoto &
69 Dobata, 2019). Thus, condition-dependent behavioral change is critical to connecting search theory
70 to empirical animal movements.

71 Among factors that affect the searching process, the density of targets is fundamental. For
72 example, predators searching for food commonly increase search effort by moving slowly and
73 sinuously within patches with high resource densities, a behavior referred to as area-restricted search
74 (Banks, 1957; Murdie & Hassell, 1973; Weimerskirch, Pinaud, Pawlowski, & Bost, 2007). In mate
75 search, the density of females and males will change both the availability of targets and the
76 abundance of competitors, which can substantially affect the selective pressure on searching
77 strategies (Berec, Kramer, Bernhauerová, & Drake, 2018; Kokko & Rankin, 2006; Mizumoto, Abe, &
78 Dobata, 2017). Some studies have found that mate searchers move faster and more actively in high
79 densities of conspecifics than in low densities (DeRivera, Backwell, Christy, & Vehrencamp, 2003;
80 Holwell, Allen, Goudie, Duckett, & Painting, 2016; Jirotkul, 1999). Moreover, in some species, it has
81 been demonstrated that sexual selection favors high male locomotion activity during mate search
82 (Able, 1999). This behavioral change can be adaptive by overcoming competitors when multiple
83 potential mates are available. However, behavioral change during mate search is rarely evaluated in
84 terms of encounter efficiency, because of the difficulty of examining the actual encounter dynamics.

85 Here we study the encounter dynamics of partner-seeking termites across different densities.
86 During swarming season, mature termite colonies synchronously produce large quantities of alates
87 (winged imagos) that fly off in a large swarm and disperse (Mullins et al., 2015). Dispersed alates shed
88 their wings and walk in search of a mating partner (Nutting, 1969; Vargo & Husseneder, 2009). Both
89 females and males are poorly informed because they search in a completely unfamiliar environment,
90 and pairing pheromones emitted by females work only within short distances or on contact in some
91 species (Bordereau & Pasteels, 2011; Sillam-Dussès, 2011). Successfully encountered couples
92 perform tandem runs to seek a suitable nest site and found a colony. In tandem runs, a leading
93 female decides the course of movement, and a male follows the female by maintaining almost
94 contact with her back (Valentini, Mizumoto, Pratt, Pavlic, & Walker, 2020). As the pairing process is
95 extremely limited in time, termites should optimize their search patterns to increase the chance of
96 encounter before all potential mates progressively become unavailable. Both females and males
97 explore wide areas to enhance random encounters before pairing, while if the pair gets separated, the
98 leading female pauses and the following male moves, which enhances reunion rates (Mizumoto &
99 Dobata, 2019). We hypothesize that this reunion process will be profoundly affected by the density of
100 individuals (Fig. 1). In low-density conditions, the lost partner is the only likely nearby mate, hence
101 each termite should move in a way that facilitates reunion. Under high densities, separated
102 individuals can search either for the stray partner or for a new partner, which will change their
103 optimal movement pattern.

104 The termite, *Coptotermes gestroi* (Wasmann, 1896) (Blattodea, Rhinotermitidae), experiences a
 105 variety of densities in natural conditions. In this species, newly dispersed females and males often
 106 gather on a tree trunk (Fig. 1), where the abundance of individuals can widely change depending on
 107 the day, ranging from ~1 to ~10,000 individuals/m² (Chouvenc, Helmick, & Su, 2015; Chouvenc,
 108 Scheffrahn, Mullins, & Su, 2017). Because of this life-history trait, we expect that they have evolved
 109 to change their search behavior with density. Furthermore, as the pairing pheromone of *Coptotermes*
 110 termites has low volatility and primarily works upon contact (Chouvenc, Sillam-Dussès, & Robert,
 111 2020; Raina et al., 2003), *C. gestroi* is expected to rely on random search rather than long-distance
 112 navigation during mate search. In this study, we test how density affects pair-forming dynamics and
 113 individual searching behavior in *C. gestroi*. We found that males change their walking speed when a
 114 pair gets separated, depending on the potential mate density they experience. Using data-based
 115 simulations, we confirm that termite males update movement patterns adaptively during mate
 116 search.

117



118 **Figure 1.** Mate search scheme of a termite, *Coptotermes gestroi*. In the mating season, alates fly
 119 off in large swarms at dusk and then land to aggregate on a tree trunk. They shed their wings
 120 and walk to search for a mating partner. Encountered pairs perform tandem running, but pairs
 121 are often accidentally separated. A separated female temporarily pauses while a male moves to
 122 facilitate re-encounters. At the same time, they also have the option to encounter a new
 123 partner to initiate another tandem pair, especially under high-density conditions.

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125
 126 **1. Materials and Methods**

127 **2.1 Termites and experimental setup**

128 *C. gestroi* is a critical structural pest species with a substantial economic impact. This species is
 129 native to South East Asia and has been introduced in various parts of the neotropics and subtropics,
 130 including Florida, the Antilles and South America (Chouvenc et al., 2016). We collected alates of *C.*
 131 *gestroi* using a light-trapping system at dusk between March 5th and March 18th in Broward
 132 County (Florida, USA). All collected individuals were brought back to the laboratory and maintained
 133 on wet cardboard at 28°C. We used individuals that shed their wings by themselves and observed
 134 their behaviors within 24 hours after the flight.

135 To observe mate search behavior of termite dealates, we prepared an experimental arena by
 136 filling a petri dish (ø=140mm) with moistened plaster so that the surface of the arena could be
 137 cleaned by scraping off plaster before each trial. The petri dish was covered with a clear lid during

138 observations. A video camera was mounted vertically above the arena, and the camera system was
139 adjusted so that the arena filled the camera frame. We placed different numbers of termites (1, 2, 4,
140 or 8 females and the same number of males) in the experimental arena and recorded their behavior
141 using cameras. We allowed termites to gather information about local density for the first 10 minutes,
142 and then extracted the coordinates of termite movements from each video for the next 10 minutes
143 for data analysis, using the video-tracking system UMATracker (Yamanaka & Takeuchi, 2018). All
144 videos were downsampled to a rate of five frames per second. To help visual identification, we
145 marked females and males with one dot on the abdomen using paint markers of different colors
146 (PX-20; Mitsubishi). We discarded 14 videos of 1 pair because no tandem was observed. We obtained
147 data for 27, 9, 9, and 13 replicates for 1, 2, 4, and 8 pairs, respectively. The number of replicates
148 varied depending on alate availability and time availability. Each individual was used only once
149 within 12 hours after collection. All data analyses were performed using R v3.6.1 (R Core Team,
150 2019).

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152 **2.2 Analysis of termite movements across different densities**

153 During observations, each termite was in one of three states: (i) tandem running, (ii) interacting
154 but not tandem running, and (iii) searching. We automatically classified the states of termites based
155 on a time sequence of coordination of each individual, as follows. We defined a female and a male as
156 interacting (or tandem running) when the distance between their centroids was less than 9.75 mm
157 ($1.3 \times$ mean body length). This distance was chosen to slightly exceed the body length of termites
158 including antennae, because termites in a tandem run are nearly in physical contact (Mizumoto &
159 Dobata, 2019). An interacting pair was considered to be performing a tandem run only if they met the
160 following criteria. First, the interaction needed to last for more than 5 seconds; a very short
161 separation (< 2 seconds) was not regarded as a separation event unless the distance between
162 individuals was greater than 20 mm. Second, both termites needed to move more than 30 mm while
163 interacting. After separation, we considered that individuals engage in separation search until they
164 interact with an individual again for more than 1 second.

165 We obtained the following numbers of observations for the 1-, 2-, 4-, and 8-pair treatments,
166 respectively: 95, 70, 146, and 714 complete tandem events for females (and 95, 68, 130, and 621 for
167 males); 112, 72, 142, and 595 separation events for females (and 112, 68, 146, 668 for males). In
168 multiple pair conditions, the number of tandem and separation events was different between sexes,
169 because interactions with more than two individuals sometimes happened. We first compared the
170 duration of tandem running among treatments. We used the Cox proportional hazard model, with
171 the number of termites, sex, and their interaction treated as fixed effects. The likelihood ratio test
172 was used to determine the statistical significance of each explanatory variable (type II test). Then we
173 used a similar Cox proportional hazard model to examine the duration to find a partner after a
174 separation event. As we found a significant effect of sex ($\chi^2_1 = 37.77$, $P < 0.001$) and no significant
175 effect of the interaction of sex and density ($\chi^2_1 = 1.143$, $P = 0.285$), we compared the duration of
176 separation search between sexes for each density, using log-rank tests after generating Kaplan-Meier
177 survival curves. For these analyses, we removed observations censored by the beginning or the end of
178 the observation period. Note that including censored data in our analysis did not affect the
179 conclusion. We present the analysis without censored data for better visibility of the results.

180 We examined the heading directions of females and males when they separated from their
181 partners, because their relative orientation can significantly affect the chances of reunion (Franks et
182 al., 2010). We measured each termite's orientation as the motion direction from the frame just before
183 the separation to the frame in which separation was detected. Then, for each termite, we measured
184 the angle between its orientation and a straight line connecting the two termites' positions. These
185 angles gave each termite's orientation relative to the location of its former partner. For each sex and
186 density condition, we performed a Rayleigh test to check if the relative orientation is biased.

187 Next, we measured the termites' movement patterns, focusing on a time window that started 5
188 seconds before separation and ended 10 seconds after separation. We used correlated random walks
189 (CRWs) as a framework to measure differences in movement patterns. CRWs account for the angular

190 correlations in animal trajectories coming from local scanning behavior and are widely used to
191 describe insect movements (Bartumeus & Levin, 2008; Kareiva & Shigesada, 1983). CRWs can be
192 described by two parameters: speed and sinuosity. We first examined speed, comparing the mean
193 moving speed among treatments with different numbers of pairs. We arbitrarily restricted
194 measurements to the first 2 seconds after separation, but our conclusions did not change for longer
195 focal durations, at least within 10 seconds. We used linear mixed models (LMM), with the number of
196 pairs (as factorial data) treated as a fixed effect and individual identity included as a random
197 intercept. The likelihood ratio test was used to determine the statistical significance of each
198 explanatory variable (type II test). In cases of significant effects of time, we ran Tukey's post hoc
199 tests. We then investigated the time development of sinuosity (turning patterns) of termite
200 movements within the same time window. We computed the turning angles as the magnitude of
201 changes in the direction of motion from one frame to the next frame. Then, we fit wrapped Cauchy
202 distributions to turning angle data using maximum likelihood estimation methods and took the
203 distribution's scale parameter as the sinuosity (Bartumeus & Levin, 2008; Mizumoto & Dobata, 2019).
204 Depending on the value of the scale parameter, the wrapped Cauchy distribution varies from a
205 uniform distribution (scale parameter = 0, maximum sinuosity Brownian walk) to a delta distribution
206 (scale parameter = 1, minimum sinuosity straight walk). We obtained a 95% confidence interval for
207 each sinuosity value by resampling the permuted turning angle data set 1,000 times.

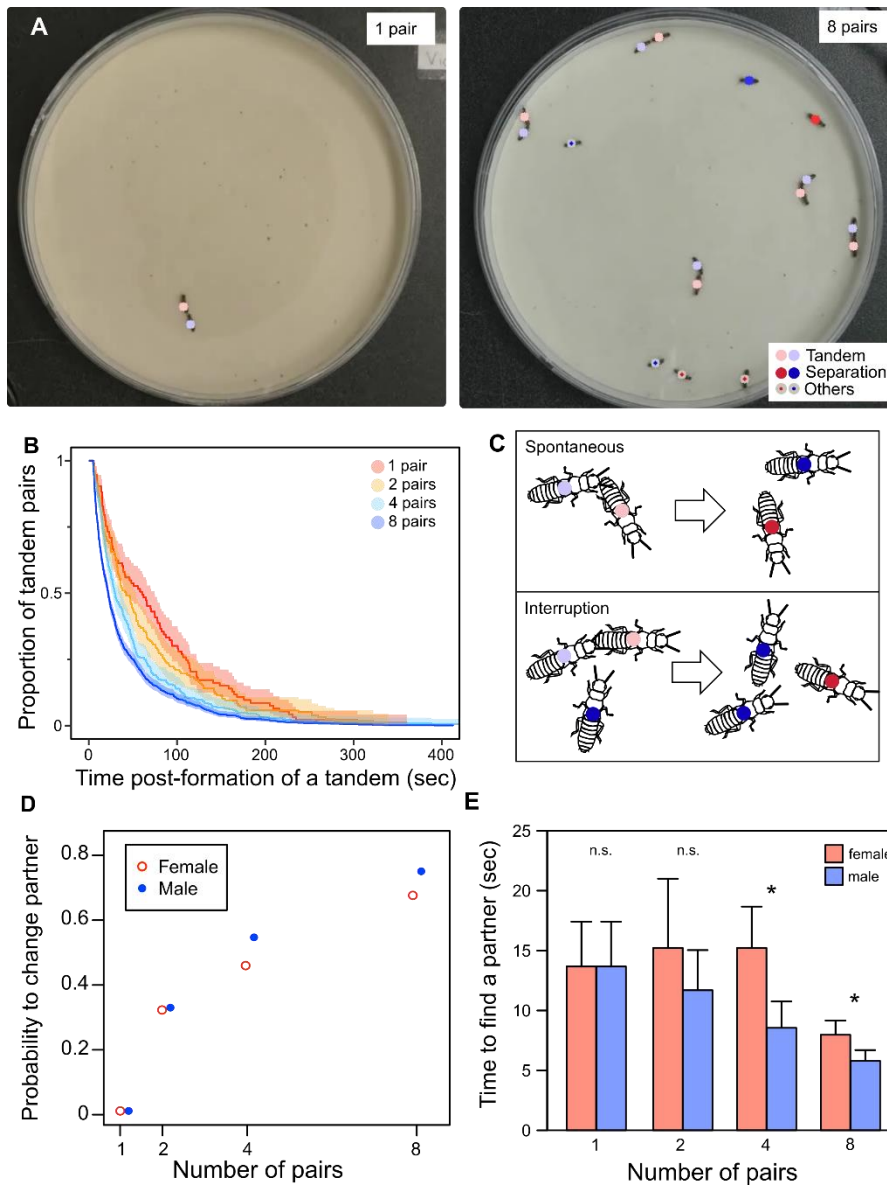
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209 2. Results

210 Termites experienced different dynamics of pair formation across densities (Fig. 2A). As
211 density increased, tandem runs were more frequently interrupted and separated (Fig. 2B; Cox hazard;
212 Pair: LRT, $\chi^2_1 = 81.772$, $P < 0.001$), while the duration of tandem runs was not different between sexes
213 and no interactions were found between density and sex (Cox hazard; Sex: LRT, $\chi^2_1 = 1.098$, $P = 0.295$;
214 Pair:Sex: $\chi^2_1 = 0.093$, $P = 0.76$). The median values for tandem running time were 62.0, 48.8, 30.3, and
215 22.4 seconds for the 1, 2, 4, and 8 pair treatments, respectively. There were two different causes for
216 separation; spontaneous separation and interruption by other termites (Fig. 2C, Video S1, S2). In the
217 case of 1 pair, all separations were spontaneous and presumably accidental as the male lost contact
218 with the female (Video S1). With more termites present, the probability of interruption by a third
219 party increased, explaining the high separation probability at high densities (Video S2). At high
220 density, separated pairs changed partners more frequently (Fig. 2D), and it took longer for separated
221 females to find a partner than for separated males (Fig. 2E; Log-rank tests; 1 pair: $\chi^2_1 = 0$, $P = 1.0$; 2
222 pairs: $\chi^2_1 = 0$, $P = 0.9$; 4 pairs: $\chi^2_1 = 11.7$, $P < 0.001$; 8 pairs: $\chi^2_1 = 19.3$, $P < 0.001$).

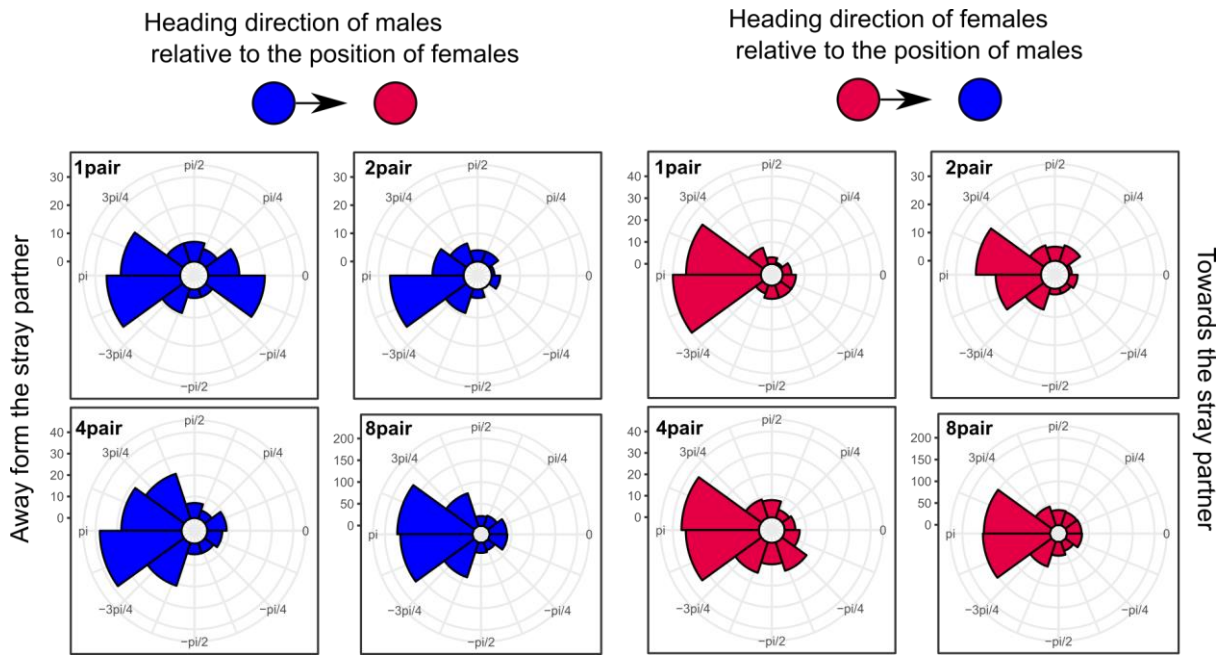
223 When termites separated, their headings relative to their separated partner were not uniformly
224 distributed (Rayleigh test; Males, 1 pair: $\bar{R} = 0.191$, $P = 0.017$; 2 pair: $\bar{R} = 0.562$, $P < 0.001$; 4 pair: \bar{R}
225 = 0.468, $P < 0.001$; 8 pair: $\bar{R} = 0.480$, $P < 0.001$, Females, 1 pair: $\bar{R} = 0.586$, $P < 0.001$; 2 pair: $\bar{R} =$
226 0.519, $P < 0.001$; 4 pair: $\bar{R} = 0.435$, $P < 0.001$; 8 pair: $\bar{R} = 0.440$, $P < 0.001$). The peak of the
227 distribution was near the opposite direction from the separated partner's location, indicating that in
228 most case females and males moved away from each other just after a separation event (Fig. 3).

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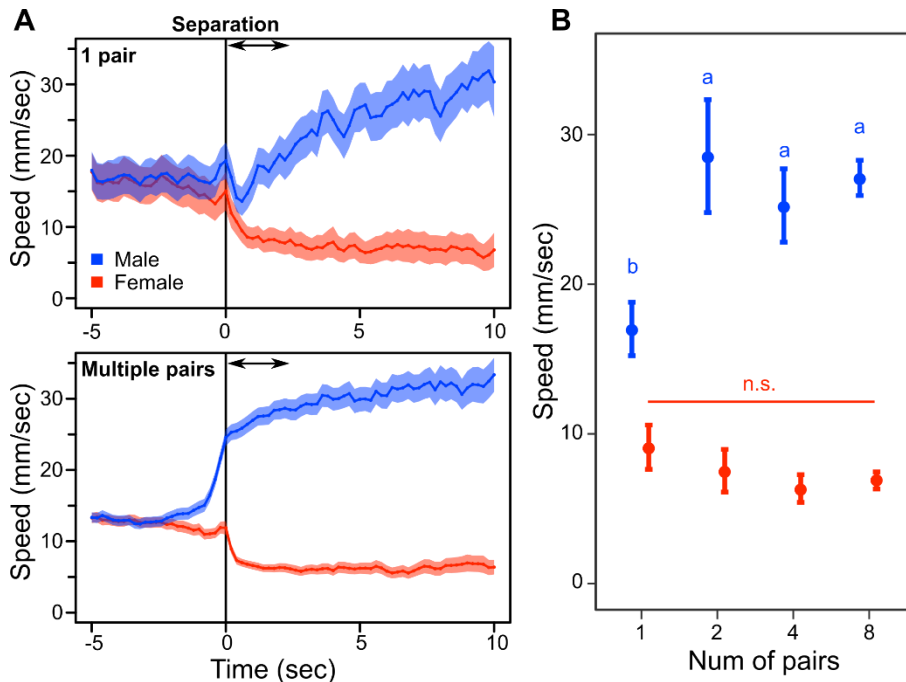
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Figure 2. The dynamics of termite pair formation across different densities. (A) Experimental arena with different numbers of termites. (B) Duration of tandem running until separation across different densities. Tandem pairs were separated sooner with increasing density. Shaded regions indicate 95% confidence intervals. (C) Two types of separation events: spontaneous separation (above) and interruption by another individual (below). In the 1 pair condition, all separations were necessarily spontaneous, while interruption by the third party was common in high-density conditions (Video S1, S2). (D) The probability of changing to a new tandem partner after each separation event. In the 1 pair condition, there was no chance to change partner. (E) Comparison of the time to find a partner after separation. At high density, males found a partner faster than females. Asterisks indicate significant differences between sexes ($P < 0.05$, log-rank test).



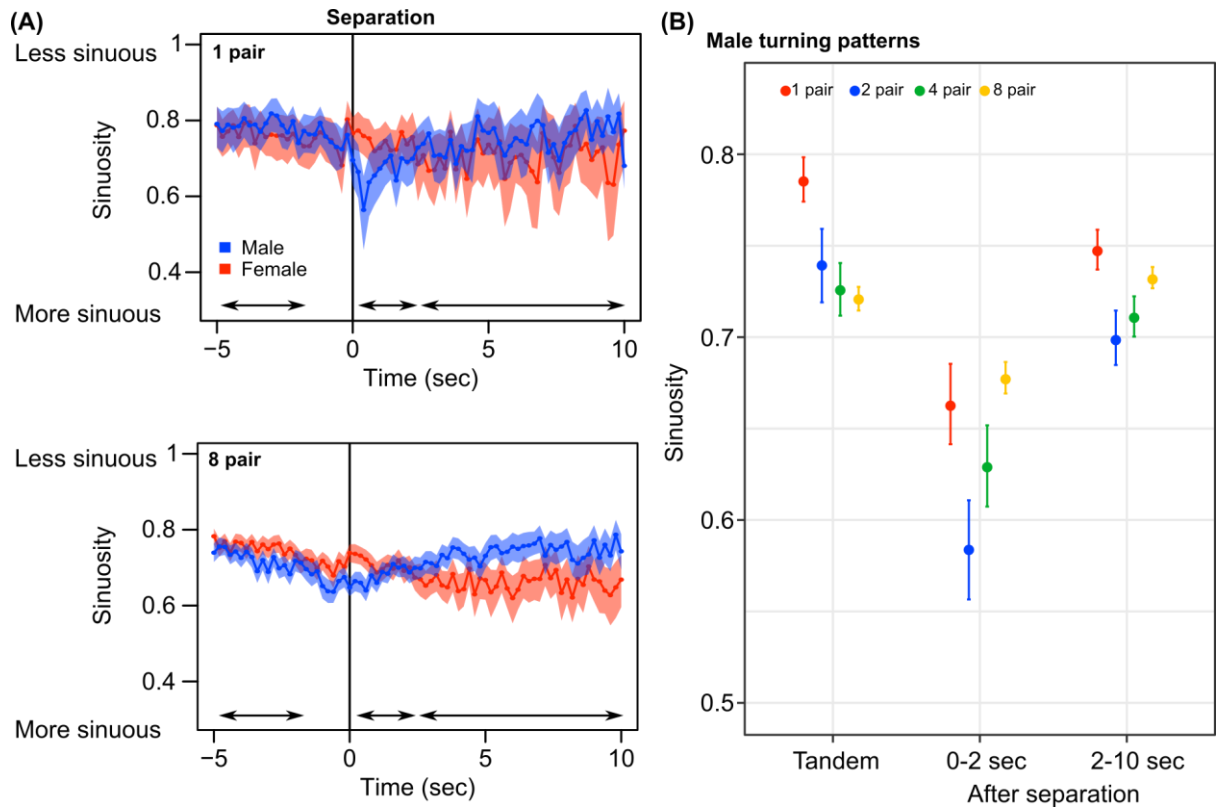
242
 243 **Figure 3.** The distributions of relative orientation to the stray partner after separation. Zero radians
 244 indicates movement toward the stray partner, π radians indicates movement in the opposite
 245 direction.

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 247 After separation, males sped up their movement, while females slowed down (Fig. 4A, Fig. S1),
 248 as reported in two other termite species, *Coptotermes formosanus* and *Reticulitermes speratus*
 249 (Mizumoto and Dobata 2019). However, the acceleration was slower when only a single female and a
 250 male were present (Fig. 4AB, Fig. S1). When we compared the movement speed just after separation,
 251 the speed of males in the 1-pair condition was lower than in the other conditions (Fig. 4B; LMM; $\chi^2_3 =$
 252 14.585, $P = 0.002$). On the other hand, the speed of females just after separation was not different
 253 between conditions (Fig. 4B; LMM; $\chi^2_3 = 0.066$ $P = 0.996$). Also, male movement became more sinuous
 254 just after separation, but soon returned to the lower sinuosity seen before separation (Fig. 5AB, Fig.
 255 S2). When we compared the period just after the separation among different densities, we found that
 256 sinuosity decreased as the density increased from 2 to 8 pairs. However, males in the 1-pair condition
 257 also showed less sinuosity (Fig. 5B).
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Figure 4. Movement speed of termite dealates after separation across different densities. (A) The time development of speed in the 1-pair condition and in the multiple-pair (2, 4, and 8) conditions. Speed was calculated from the distance traveled in 0.2 seconds. Separation timing was determined from the distance to the closest individual, hence termites could change their speed before the separation event was detected. Shaded regions indicate mean \pm 2S.E. (B) Comparison of moving speed during the 2 seconds just after separation. Bars indicate mean \pm 2S.E. Statistical analysis was performed for each sex separately, where different letters indicate a significant difference ($P < 0.05$; LMM with Tukey's test).



271
 272 **Figure 5.** The sinuosity of termite movements across different densities. (A) The time
 273 development of sinuosity in the 1-pair and 8-pair conditions. To obtain the sinuosity, we fit
 274 wrapped Cauchy distributions to turning angle data and estimated the scale parameter. Shaded
 275 regions indicate 95% confidence intervals obtained by resampling the permuted data set. (B)
 276 Comparison of sinuosity across different density conditions and time windows. Bars indicate 95%
 277 confidence intervals obtained by resampling the permuted data set.

279 3. Simulations

280 4.1 Methods

281 We developed an individual-based model to examine how the behavioral changes observed in
 282 males can contribute to mating success. We considered a focal male that has just been separated
 283 from a female, either when no other individuals are available (Fig. 6A), or when additional potential
 284 partners are available (Fig. 6D). Based on our observations of the body orientations of separated
 285 individuals, we assumed that the male and female were heading away from each other in opposite
 286 directions (Fig. 6A, D: arrows). The focal male starts at a distance d ($= 20$ mm) from the separated
 287 female, in a periodic boundary condition of size $= L \times L$. For the condition without other individuals,
 288 we set L as a large value ($= 10,000$ mm) to represent a virtually unbounded surrounding area without
 289 other potential mates. For the high-density condition (corresponding to the 2-, 4-, and 8-pair
 290 conditions), we randomly placed additional females and males ($n = 1, 3,$ and 7), and we set L to 124 to
 291 achieve the same density as the experimental treatment. Two individuals were considered to
 292 encounter each other when the distance between their centers fell below φ , which was set to the
 293 value used above to define tandem running (9.75 mm).

294 Individuals performed a CRW with speed v and sinuosity ρ , which could vary according to sex,
 295 density, and time since separation (Table 1). The value of v was set to the empirically measured mean
 296 speed for the corresponding sex and density. For males, we also assumed that speed depended on
 297 time since separation (< 2 sec or > 2 sec), reflecting empirical observations (Fig. 4A, Table 1). Based
 298 on our behavioral analysis, the length of a time step was set to 0.2 seconds. Thus, each individual
 299 moved $0.2v$ mm in each time step. Values of ρ for different sexes and time windows were set to the
 300 scale parameter of a wrapped Cauchy distribution fitted to corresponding turning angle data (Table
 301 1). We then simulated turning angles by drawing them from a wrapped Cauchy distribution with the

302 appropriate value of ρ . Specifically, we applied the inversion method (Bartumeus & Levin, 2008), first
 303 generating a uniform random number u ($0 < u \leq 1$) and then deriving the turning angles θ from the
 304 following equation:

$$\theta = 2 \arctan\left(\frac{1 - \rho}{1 + \rho} \tan(\pi(u - 0.5))\right)$$

305 We initiated the simulation with a random bearing angle that fluctuated according to θ . At each step,
 306 the bearing angle was equal to the previous bearing angle plus the deviation θ such that the moving
 307 object takes on a new direction correlated with the previous direction, forming a CRW.

308 We compared the searching efficiency between two different moving speeds observed in the
 309 1-pair (slow at the beginning) and multiple-pair conditions (fast at the beginning) (Fig. 4). In the
 310 high-density condition, non-focal individuals moved with the speed of tandem runs. Each simulation
 311 ran for 300 seconds (= 1500 time steps). We ran 10,000 simulations and measured search efficiency as
 312 the probability for focal individuals to encounter a mating partner. We also measured the time until
 313 encounter. The simulation was implemented in Microsoft Visual Studio C++ 2017.

315

316 **Table 1.** Parameters used in the simulations.

Symbol	Definition	Value(s)	Unit
Environmental parameters			
d	Distance between separated pair	20	mm
L	Size of the searching area	10,000 or 124	mm
φ	Range of encounters	9.75	mm
n	The number of additional females and males	0, 1, 3, 7	
Speed parameters			
v_{m1}	Males after separation (< 2sec)	17.05 ^{*1} , 27.02 ^{*2}	mm/sec
v_{m2}	Males after separation (> 2sec)	29.38	mm/sec
v_f	Females after separation	6.77	mm/sec
v_o	Other individuals for multiple pair conditions	12.88	mm/sec
Sinusosity parameters			
ρ_{m1}	Males after separation (<2 sec)	0.64	
ρ_{m2}	Males after separation (>2 sec)	0.73	
ρ_{f1}	Females after separation (<2 sec)	0.72	
ρ_{f2}	Females after separation (>2 sec)	0.69	
ρ_o	Other individuals for multiple pair conditions	0.78	

317 ^{*1}1-pair condition; ^{*2}Multiple-pair condition. Parameter values for <2 sec and >2 sec were
 318 obtained from empirical observations 0-2 seconds after separation and 2-10 seconds after
 319 separation, respectively.

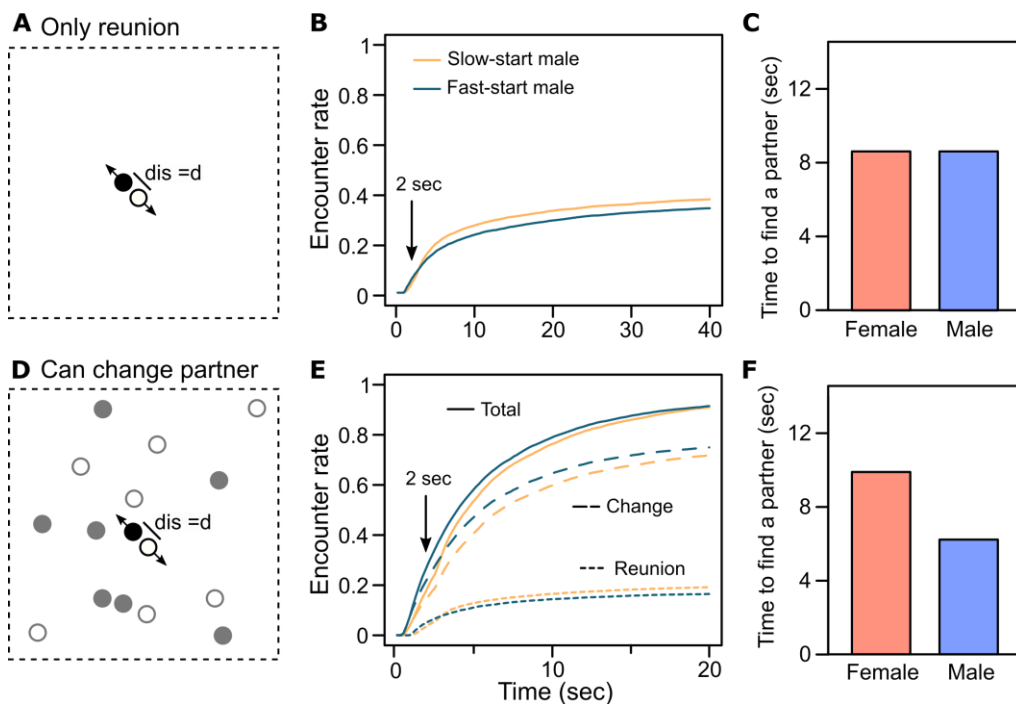
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321 4.2 Results

322 In the condition without any other individuals, males that moved slowly, like those in the 1-pair
 323 experimental condition, achieved higher encounter rates (Fig. 6B). Here, because a male had no other
 324 option than reunion with the stray partner, the time to find a partner was not different between a
 325 separated female and a male (Fig. 6C). Interestingly, there was a time lag for males to enjoy the
 326 advantage of slow movement. When we look at the period just after the separation (0-2 sec),
 327 fast-moving males have slightly higher encounter rates than slow-moving males (Fig. 6B). However,

328 after 2 sec, slow-start males exceed fast-start males even though both move at the same speed (Fig.
 329 6B). This can be interpreted as follows. A fast-start male may quickly encounter the separated female,
 330 but if he does not, he risks moving further away from her. Thus, after 2 seconds, he is likely too far
 331 from the female to have much chance of encountering her. In contrast, a slow-start male can stay
 332 close to the female during the first 2 seconds; when he speeds up after 2 seconds, he can find the
 333 female more efficiently than a fast-start male.

334 On the other hand, under high-density conditions, fast-start males, like those in the
 335 multiple-pairs experimental conditions, achieved higher encounter rates than slow-start males (Fig.
 336 6E). Although the advantage of fast males is more substantial at higher density, this result was
 337 consistent across the different densities tested in the experiments (Fig. S3). In this scenario, there
 338 were two different encounter patterns: reunion with the stray partner and changing to a new partner.
 339 Consistent with the 1-pair case, the reunion rate was higher in slower-moving males (Fig. 6E).
 340 However, faster-moving males obtained a different partner more efficiently, which led to higher
 341 overall encounter rates (Fig. 6E). The simulation also found that males in the high-density condition
 342 obtained a partner faster than females, similar to our experimental results (Fig. 6F).
 343



344 **Figure 6.** Simulated searching efficiency of male movements in two different situations. (A, D) At
 345 low density (A), only a single pair is present, hence reunion is the only way to find a partner after
 346 separation. At high density (D), termites can also change to a new partner. Right after separation,
 347 the female and male are at a short distance (d); in the high-density condition, there are also other
 348 individuals randomly located around them. Dotted squares indicate the periodic boundary
 349 conditions (size $L \times L$). Filled circles indicate males, while open circles indicate females. Focal
 350 individuals are black, while others are grey. Arrows indicate the heading direction at the start of
 351 the simulation. (B, E) Searching efficiency under the respective conditions. Slow-start and
 352 fast-start males move at different speeds in the first 2 sec and then use the same high speed. When
 353 no other pairs are present, slow-start males like those observed in the 1-pair condition achieved
 354 higher encounter rates than fast-start males (B); under high-density conditions, fast-start males
 355 like those observed in the multiple-pair conditions achieved higher encounter rates than
 356 slow-start males (E). (C, F) Time to find a partner for each sex. Without other pairs, there is no
 357 sexual difference (C), while under high density, males obtain a partner faster than females (F).
 358 Model parameters are given in Table 1.
 359
 360

361 4. Discussion

362 In mate search by *C. gestroi*, which aggregate on a tree trunk and search locally, densities of
363 potential mates can vary drastically over time. Within the swarming season, different flight events
364 result in various population densities according to weather conditions and colony readiness
365 (Chouvenc et al., 2017). Even within the same day, the density of potential mate changes according
366 to time. The density is the highest just after the dispersal flight and then decreases as successful
367 tandem pairs isolate themselves for colony foundation. Therefore, density-dependent behavioral
368 change is crucial for mating success. In particular, when a male termite gets separated from his
369 paired female, he needs to adjust search strategy because of a kind of speed/accuracy tradeoff in
370 efforts to find the stray female (Zimmerman, 2011); high speeds may lead to a quick encounter with
371 the stray partner, but they also increase the risk of moving further away from her (Mizumoto &
372 Dobata, 2019). At very low densities of individuals, this risk is so high that males move slower to
373 increase the likelihood of re-encounter with the stray partner. On the other hand, under higher
374 densities, the risk of isolation is diluted because another potential partner may be available even if
375 reunion fails. Our results show that this tradeoff shapes mate search behavior in termites. Our
376 experiments found that males searching when no other potential mates were present moved slower,
377 while males searching at higher densities moved faster (Fig. 4). Data-based simulations confirm that
378 this behavioral change is adaptive; the observed slow movement facilitates reunion, while fast
379 movement leads to higher rates of obtaining a new partner (Fig. 6). Thus, the availability of targets
380 strongly affects mate search strategy and encounter dynamics.

381 In addition to speed, turning patterns may lead to similar effects on encounter dynamics. For
382 example, CRWs with high ρ values lead to straighter movements and should have high search
383 efficiency for new partners (Bartumeus et al., 2005), which is similar to fast movement. Thus, parallel
384 to speed differences, one can expect that males show less sinuous movements at high density. This
385 prediction is partly supported; sinuosity decreased as the density increased among 2-, 4-, and 8-pair
386 conditions (Fig. 5B). On the other hand, males in the 1-pair condition also showed low sinuosity,
387 similar to males at the highest densities. This finding can be interpreted as follows. First, separated
388 females are sometimes found in the heading direction of males in the 1-pair condition, while they are
389 usually in the opposite direction in multiple-pair conditions (Fig. 3). Thus, excessive sinuosity of
390 male movements may decrease encounter efficiency in the 1-pair condition. Second, directional
391 memory (i.e., persistence) may prevent individuals from moving very sinuously after separation
392 (Bardunias & Su, 2009; Turchin, 1998). In the 1-pair condition, individuals showed less sinuous
393 movements even during tandem runs, probably because there are no obstacles in the arena (Fig. 5).
394 Thus, even though males in the 1-pair condition increased their turning angles after separation, their
395 sinuosity can still be smaller than in the 2-pair condition. In fact, males in the 1-pair condition
396 decreased ρ to the same extent as in the 2-pair condition, while decreases in the 4- and 8- pair
397 conditions were smaller.

398 The observation that termite males increase their moving speed at high density after
399 separation also implies a mate competition process. During mate search, the high density of
400 different-sex individuals usually means a high density of same-sex individuals as well. After a
401 tandem run pair get separated, these same-sex individuals may snatch the stray partner before
402 reunion. Thus, males need to find a female sooner than competitors for a successful pairing, which
403 may be another reason why males at high density increased speed at the expense of the likelihood of
404 reunion. Our simulations also demonstrated that the fate of the separated female is affected by the
405 male's movement after separation. If the stray male moved more slowly in the high-density condition,
406 this increased the probability of the female encountering a different male before the stray male found
407 a partner (i.e., 24.16% with a slow-moving male; 22.40% with a fast-moving male). Thus, vigorous
408 males should have an advantage in obtaining a partner when they get separated. This is consistent
409 with previous observations that larger males have a higher chance to obtain a partner when multiple
410 males are present (Husseneder & Simms, 2008; Li, Zou, Lei, & Huang, 2013; Matsuura, Kuno, &
411 Nishida, 2002), although it should be noted that various selective pressures can influence the body
412 size of termite alates other than mate competition (Chouvenc, 2019; Nalepa, 2011). From the mate

413 competition perspective, our results demonstrate that movement pattern is a sexually selected trait
414 in termite mate search (Hartke & Baer, 2011), and vigor of the searching sex reflects both efficient
415 search strategy and effective domination of same-sex competitors.

416 In contrast, females did not change their movement patterns across different densities of
417 individuals and thus achieved lower re-encounter rates compared to males at higher densities (Fig.
418 2E). In additional simulations focusing on females, we predicted that females should also move faster
419 at high mate density to obtain a new partner (Fig. S4). There are two non-exclusive explanations for
420 these contradicting results. First, females of most termite species use pair-bonding pheromones to
421 help males detect them (Bordereau & Pasteels, 2011), where fast movement by females may be
422 disfavored as it decreases detection rate by males (Mizumoto & Dobata, 2018). In *C. gestroi*, which
423 search for a mate at high density (Fig. 1), the importance of attraction pheromone is relatively low
424 compared to other termite species. Actually, the quantity of pheromones produced in the tergal and
425 sternal gland of females is too small for males to locate females even from a short distance (e.g., 75
426 mm) (Chouvenc et al., 2020; Sillam-Dussès, 2011). However, such a chemical signal may still provide
427 some level of information to a searching male, given that a recently-separated female expects to be
428 very close to a male (e.g., < 20 mm). Second, searching animals suffer a fundamental
429 speed-perception tradeoff, where high speeds improve their spreading capacity but reduce perceptual
430 capabilities (Bartumeus et al., 2016; Benhamou, 1992). Because of this tradeoff, individuals moving at
431 high speeds may miss the target upon encounter and require multiple passages before detection. In
432 the case of the termite searching process, not every encounter results in tandem running; sometimes
433 a female and male just pass by each other. Pausing behavior, which is often observed in
434 partner-searchers (Alpern, 1995; Franks et al., 2010; Mizumoto & Dobata, 2019) and ambush
435 predators (Scharf & Ovadia, 2006; Wearmouth et al., 2014), can function to ensure successful
436 encounters.

437 Males in the multiple-pair conditions increase their speed even before separation, while males
438 in the one-pair condition increase speed only after separation (Fig. 3A). This difference may reflect
439 our criterion for separation, which we judged to occur when the distance between the male and
440 female exceeded a threshold ($9.75 \text{ mm} = 1.3 \times \text{body length}$). Thus, males in multiple-pair conditions
441 may be more sensitive to separation and change their behavior even when the distance to the partner
442 is smaller than the threshold. The proximate mechanisms for this behavioral change can be related to
443 the tandem pair's encounters with other individuals, which are more common at high densities and
444 often lead to separation (Fig. 2B, Video S2). First, males may detect the interrupting male upon
445 separation, and the presence of this competitor may be the cue to change their behavior. Second,
446 males can estimate the density of surrounding individuals from the number of separation events they
447 experience. In multiple-pair conditions, frequent interruptions lead males to experience many
448 separation events, which can inform them that conspecific density is high. Thus they become ready
449 to move fast as soon as they detect separation, which they do with greater sensitivity than is captured
450 by our threshold. Similar density estimation mechanisms are also used in other animals. For example,
451 ants use encounter rates to estimate the density of individuals in the nest, an important cue for
452 collective decision making (Pratt, 2005). Given that there is no clear difference in males' moving
453 speed among the 2-, 4-, and 8-pair conditions, termites' density estimation is not quantitative, but
454 rather a binary evaluation of the presence of competitors.

455 In general, availability of resources, including distributions and density of targets, strongly
456 affects optimal search strategy and actual animal movements (Bartumeus et al., 2016; Viswanathan
457 et al., 2011). In both foraging and mate search, searchers increase search effort in areas with a high
458 density of targets; yet interestingly, the types of targets affect the patterns of behavioral change.
459 Foragers often exhibit slow and sinuous movement in high-density areas (Banks, 1957; Murdie &
460 Hassell, 1973; Weimerskirch et al., 2007), which is an efficient random search strategy considering
461 energy intake and perception accuracy (Benhamou, 1992). On the other hand, in this study, we
462 showed that termite males increase their moving speed under a high density of individuals, which is
463 adaptive in increasing encounter rates in a short period. The main difference between foraging and
464 mate search is the value of a target. Foragers collect as many targets as possible given the prevailing

465 costs and benefits (Abe & Shimada, 2015), while termite mate searchers seek only one partner but
466 must do so within a time limit, after which they die (Mizumoto et al., 2017). Clarifying the motivation
467 of searchers, combined with search theory, is key to understanding the movement patterns of
468 animals.

469

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476

477 **Authors' contributions**

478 NM and TC conceived and designed the study. NM performed the experiments. NM and AR collected
479 the data from videos. NM performed data analysis and computer simulations. NM drafted the
480 manuscript. SCP and TC edited the manuscript. All authors gave final approval for publication.

481

482 **Competing Interests**

483 The authors declare no competing interests.

484

485 **Data Availability Statement**

486 Data and source code associated with this manuscript will be available from the Dryad Digital
487 Repository (doi:10.5061/dryad.15dv41ntn).

488

489 **References**

490 Abe, M. S., & Shimada, M. (2015). Lévy walks suboptimal under predation risk. *PLoS Computational*
491 *Biology*, *11*(11), e1004601. doi: 10.1371/journal.pcbi.1004601

492 Able, D. J. (1999). Scramble competition selects for greater tailfin size in male red-spotted newts
493 (Amphibia: Salamandridae). *Behavioral Ecology and Sociobiology*, *46*(6), 423–428. doi:
494 10.1007/s002650050638

495 Alpern, S. (1995). Rendezvous search problem. *SIAM Journal on Control and Optimization*, *33*(3),
496 673–683. doi: 10.1137/S0363012993249195

497 Auger-Méthé, M., Derocher, A. E., DeMars, C. A., Plank, M. J., Codling, E. A., & Lewis, M. A. (2016).
498 Evaluating random search strategies in three mammals from distinct feeding guilds. *Journal of*
499 *Animal Ecology*, *85*(5), 1411–1421. doi: 10.1111/1365-2656.12562

500 Banks, C. J. (1957). The behaviour of individual coccinellid larvae on plants. *The British Journal of*
501 *Animal Behaviour*, *5*(1), 12–24. doi: 10.1016/S0950-5601(57)80039-2

502 Bardunias, P. M., & Su, N.-Y. (2009). Dead reckoning in tunnel propagation of the formosan
503 subterranean termite (Isoptera: Rhinotermitidae). *Annals of the Entomological Society of America*,
504 *102*(1), 158–165. doi: 10.1603/008.102.0118

505 Bartumeus, F., Campos, D., Ryu, W. S., Lloret-Cabot, R., Méndez, V., & Catalan, J. (2016). Foraging
506 success under uncertainty: search tradeoffs and optimal space use. *Ecology Letters*, *19*(11),
507 1299–1313. doi: 10.1111/ele.12660

508 Bartumeus, F., Da Luz, M. G. E., Viswanathan, G. M., & Catalan, J. (2005). Animal search strategies: a
509 quantitative random walk analysis. *Ecology*, *86*(11), 3078–3087. doi: 10.1890/04-1806

- 510 Bartumeus, F., & Levin, S. A. (2008). Fractal reorientation clocks: Linking animal behavior to
511 statistical patterns of search. *Proceedings of the National Academy of Sciences of the United States*
512 *of America*, 105(49), 19072–19077. doi: 10.1073/pnas.0801926105
- 513 Bartumeus, F., Peters, F., Pueyo, S., Marrase, C., & Catalan, J. (2003). Helical Levy walks: Adjusting
514 searching statistics to resource availability in microzooplankton. *Proceedings of the National*
515 *Academy of Sciences of the United States of America*, 100(22), 12771–12775. doi:
516 10.1073/pnas.2137243100
- 517 Bell, W. J. (1990). Searching behavior patterns in insects. *Annual Review of Entomology*, 35(1),
518 447–467. doi: 10.1146/annurev.en.35.010190.002311
- 519 Benhamou, S. (1992). Efficiency of area-concentrated searching behaviour in a continuous patchy
520 environment. *Journal of Theoretical Biology*, 159(1), 67–81. doi: 10.1016/S0022-5193(05)80768-4
- 521 Bercé, L., Kramer, A. M., Bernhauerová, V., & Drake, J. M. (2018). Density-dependent selection on
522 mate search and evolution of Allee effects. *Journal of Animal Ecology*, 87(1), 24–35. doi:
523 10.1111/1365-2656.12662
- 524 Bordereau, C., & Pasteels, J. M. (2011). Pheromones and chemical ecology of dispersal and foraging
525 in termites. In D. E. Bignell, Y. Roisin, & N. Lo (Eds.), *Biology of Termites: A Modern Synthesis* (pp.
526 279–320). doi: 10.1007/978-90-481-3977-4_11
- 527 Chouvenc, T. (2019). The relative importance of queen and king initial weights in termite colony
528 foundation success. *Insectes Sociaux*, 66(2), 177–184. doi: 10.1007/s00040-019-00690-3
- 529 Chouvenc, T., Helmick, E. E., & Su, N.-Y. (2015). Hybridization of two major termite invaders as a
530 consequence of human activity. *PLoS ONE*, 10(3), e0120745. doi: 10.1371/journal.pone.0120745
- 531 Chouvenc, T., Li, H. F., Austin, J., Bordereau, C., Bourguignon, T., Cameron, S. L., ... Su, N.-Y. (2016).
532 Revisiting *Coptotermes* (Isoptera: Rhinotermitidae): A global taxonomic road map for species
533 validity and distribution of an economically important subterranean termite genus. *Systematic*
534 *Entomology*, 41, 299–306. doi: 10.1111/syen.12157
- 535 Chouvenc, T., Scheffrahn, R. H., Mullins, A. J., & Su, N.-Y. (2017). Flight phenology of two
536 *Coptotermes* species (Isoptera: Rhinotermitidae) in southeastern Florida. *Journal of Economic*
537 *Entomology*, 56, 291–312. doi: 10.1093/jee/tox136
- 538 Chouvenc, T., Sillam-Dussès, D., & Robert, A. (2020). Courtship behavior confusion in two
539 subterranean termite species that evolved in allopatry (Blattodea, Rhinotermitidae,
540 *Coptotermes*). *Journal of Chemical Ecology*, 1–14. doi: 10.1007/s10886-020-01178-2
- 541 Cloyd, C. S., & Dell, A. I. (2019). Resource distribution and internal factors interact to govern
542 movement of a freshwater snail. *Proceedings of the Royal Society B: Biological Sciences*, 286(1911).
543 doi: 10.1098/rspb.2019.1610
- 544 DeRivera, C. E., Backwell, P. R. Y., Christy, J. H., & Vehrencamp, S. L. (2003). Density affects female
545 and male mate searching in the fiddler crab, *Uca beebei*. *Behavioral Ecology and Sociobiology*,
546 53(2), 72–83. doi: 10.1007/s00265-002-0555-2
- 547 Ferreira, A. S., Raposo, E. P., Viswanathan, G. M., & Da Luz, M. G. E. (2012). The influence of the
548 environment on Lévy random search efficiency: Fractality and memory effects. *Physica A:*
549 *Statistical Mechanics and Its Applications*, 391(11), 3234–3246. doi: 10.1016/j.physa.2012.01.028

- 550 Franks, N. R., Richardson, T. O., Keir, S., Inge, S. J., Bartumeus, F., & Sendova-Franks, A. B. (2010).
551 Ant search strategies after interrupted tandem runs. *Journal of Experimental Biology*, 213(Pt 10),
552 1697–1708. doi: 10.1242/jeb.087296
- 553 Hartke, T. R., & Baer, B. (2011, November 1). The mating biology of termites: A comparative review.
554 *Animal Behaviour*, Vol. 82, pp. 927–936. doi: 10.1016/j.anbehav.2011.07.022
- 555 Holwell, G. I., Allen, P. J. D., Goudie, F., Duckett, P. E., & Painting, C. J. (2016). Male density
556 influences mate searching speed and copulation duration in millipedes (Polydesmida:
557 *Gigantowales chisholmi*). *Behavioral Ecology and Sociobiology*, 70(8), 1381–1388. doi:
558 10.1007/s00265-016-2145-8
- 559 Humphries, N. E., Queiroz, N., Dyer, J. R. M., Pade, N. G., Musyl, M. K., Schaefer, K. M., ... Sims, D. W.
560 (2010). Environmental context explains Lévy and Brownian movement patterns of marine
561 predators. *Nature*, 465(7301), 1066–1069. doi: 10.1038/nature09116
- 562 Husseneder, C., & Simms, D. M. (2008). Size and heterozygosity influence partner selection in the
563 Formosan subterranean termite. *Behavioral Ecology*, 19(4), 764–773. doi: 10.1093/beheco/arn041
- 564 Jirotkul, M. (1999). Population density influences male-male competition in guppies. *Animal*
565 *Behaviour*, 58(6), 1169–1175. doi: 10.1006/anbe.1999.1248
- 566 Kareiva, P. M., & Shigesada, N. (1983). Analyzing insect movement as a correlated random walk.
567 *Oecologia*, 56(2–3), 234–238. doi: 10.1007/BF00379695
- 568 Kokko, H., & Rankin, D. J. (2006). Lonely hearts or sex in the city? Density-dependent effects in
569 mating systems. *Philosophical Transactions of the Royal Society B: Biological Sciences*, 361(1466),
570 319–334. doi: 10.1098/rstb.2005.1784
- 571 Li, G., Zou, X., Lei, C., & Huang, Q. (2013). Antipredator behavior produced by heterosexual and
572 homosexual tandem running in the termite *Reticulitermes chinensis* (Isoptera: Rhinotermitidae).
573 *Sociobiology*, 60(2), 198–203. doi: DOI: 10.13102/sociobiology.v60i2.198-203
- 574 Matsuura, K., Kuno, E., & Nishida, T. (2002). Homosexual tandem running as selfish herd in
575 *Reticulitermes speratus*: novel antipredatory behavior in termites. *Journal of Theoretical Biology*,
576 214(1), 63–70. doi: 10.1006/jtbi.2001.2447
- 577 Mizumoto, N., Abe, M. S., & Dobata, S. (2017). Optimizing mating encounters by sexually dimorphic
578 movements. *Journal of The Royal Society Interface*, 14, 20170086. doi: 10.1098/rsif.2017.0086
- 579 Mizumoto, N., & Dobata, S. (2018). The optimal movement patterns for mating encounters with
580 sexually asymmetric detection ranges. *Scientific Reports*, 8(1), 3356. doi:
581 10.1038/s41598-018-21437-3
- 582 Mizumoto, N., & Dobata, S. (2019). Adaptive switch to sexually dimorphic movements by
583 partner-seeking termites. *Science Advances*, 5(6), eaau6108. doi: 10.1126/sciadv.aau6108
- 584 Mullins, A. J., Messenger, M. T., Hochmair, H. H., Tonini, F., Su, N.-Y., & Riegel, C. (2015). Dispersal
585 flights of the Formosan subterranean termite (Isoptera: Rhinotermitidae). *Journal of Economic*
586 *Entomology*, 108(2), 707–719. doi: 10.1093/jee/fov022
- 587 Murdie, G., & Hassell, M. P. (1973). Food distribution, searching success and predator-prey models.
588 In *Mathematical Theory of the Dynamics of Biological Populations* (pp. 87–101).

- 589 Nalepa, C. A. (2011). Body size and termite evolution. *Evolutionary Biology*, 38(3), 243–257. doi:
590 10.1007/s11692-011-9121-z
- 591 Nathan, R., Getz, W. M., Revilla, E., Holyoak, M., Kadmon, R., Saltz, D., & Smouse, P. E. (2008). A
592 movement ecology paradigm for unifying organismal movement research. *Proceedings of the*
593 *National Academy of Sciences of the United States of America*, 105(49), 19052–19059. doi:
594 10.1073/pnas.0800375105
- 595 Nutting, W. L. (1969). Flight and colony foundation. In K. Krishna & F. M. Weesner (Eds.), *Biology of*
596 *termites* (Vol. 1, pp. 233–282). doi: 10.1016/B978-0-12-395529-6.50012-X
- 597 Pratt, S. C. (2005). Quorum sensing by encounter rates in the ant *Temnothorax albipennis*. *Behavioral*
598 *Ecology*, 16(2), 488–496. doi: 10.1093/beheco/ari020
- 599 R Core Team. (2019). *R*.
- 600 Reynolds, A. M., & Bartumeus, F. (2009). Optimising the success of random destructive searches:
601 Lévy walks can outperform ballistic motions. *Journal of Theoretical Biology*, 260(1), 98–103. doi:
602 10.1016/j.jtbi.2009.05.033
- 603 Scharf, I., & Ovadia, O. (2006, March 17). Factors influencing site abandonment and site selection in
604 a sit-and-wait predator: A review of pit-building antlion larvae. *Journal of Insect Behavior*, Vol.
605 19, pp. 197–218. doi: 10.1007/s10905-006-9017-4
- 606 Sillam-Dussès, D. (2011). Trail pheromones and sex pheromones in termites. In *Trail Pheromones and*
607 *Sex Pheromones in Termites*.
- 608 Sims, D. W., Humphries, N. E., Bradford, R. W., & Bruce, B. D. (2012). Lévy flight and Brownian
609 search patterns of a free-ranging predator reflect different prey field characteristics. *Journal of*
610 *Animal Ecology*, 81(2), 432–442. doi: 10.1111/j.1365-2656.2011.01914.x
- 611 Turchin, P. (1998). *Quantitative analysis of movement: measuring and modeling population*
612 *redistribution in animals and plants*. Sunderland: Sinauer.
- 613 Valentini, G., Mizumoto, N., Pratt, S. C., Pavlic, T. P., & Walker, S. I. (in press) Revealing the
614 structure of information flows discriminates similar animal social behaviors. *eLife*, doi: DOI:
615 10.7554/eLife.55395
- 616 Vargo, E. L., & Husseneder, C. (2009). Biology of subterranean termites: insights from molecular
617 studies of *Reticulitermes* and *Coptotermes*. *Annual Review of Entomology*, 54, 379–403. doi:
618 10.1146/annurev.ento.54.110807.090443
- 619 Viswanathan, G. M., Luz, M. da, Raposo, E., & Stanley, H. (2011). *The Physics of Foraging: An*
620 *Introduction to Random Searches and Biological Encounters*. Cambridge: Cambridge University
621 Press.
- 622 Wearmouth, V. J., McHugh, M. J., Humphries, N. E., Naegelen, A., Ahmed, M. Z., Southall, E. J., ...
623 Sims, D. W. (2014). Scaling laws of ambush predator “waiting” behaviour are tuned to a
624 common ecology. *Proceedings of the Royal Society of London B*, 281(1782), 20132997–20132997.
625 doi: 10.1098/rspb.2013.2997
- 626 Weimerskirch, H., Pinaud, D., Pawlowski, F., & Bost, C.-A. (2007). Does prey capture induce
627 area - restricted search? A fine-scale study using GPS in a marine predator, the wandering

- 628 albatross. *The American Naturalist*, 170(5), 734–743. doi: 10.1086/522059
- 629 Yamanaka, O., & Takeuchi, R. (2018). UMATracker: An intuitive image-based tracking platform.
630 *Journal of Experimental Biology*, 221(16), 1–24. doi: 10.1242/jeb.182469
- 631 Zimmerman, M. (2011). Speed–Accuracy Tradeoff. In J. Kreutzer, J. DeLuca, & B. Caplan (Eds.),
632 *Encyclopedia of Clinical Neuropsychology* (p. 2344). Retrieved from
633 http://link.springer.com/10.1007/978-0-387-79948-3_1247
- 634