**Observation of tandem running behavior in mating pairs of Asian dampwood termite, *Hodotermopsis sjostedti***

**Nobuaki Mizumoto1,2\*, William Chambliss1, Carroll P Elijah1, Tomohiro, Nakazono3, Taisuke Kanao4**

1. Department of Entomology & Plant Pathology, Auburn University, Auburn, AL, 36849, USA

2. Okinawa Institute of Science and Technology, Onna-son, Okinawa, 904-0495, Japan

3. Laboratory of Insect Ecology, Graduate School of Agriculture, Kyoto University, Kyoto, Japan 606-8502

4. Faculty of Science Yamagata University Yamagata 990-8560 Japan

\*: Correspondence: [nzm0095@auburn.edu](mailto:nzm0095@auburn.edu)

**Abstract**

As a social insect, termite colonies can grow to a group of millions of individuals, yet all colonies start from a single mating pair. Recent studies indicate that the pair formation process shows a large diversity among species, especially in basal lineages. Thus, comparative information is integral to estimating the ancestral state of this essential stage of the termite life cycle. The Asian dampwood termite, *Hodotermopsis sjostedti*, has been well-studied as a model basal termite of caste differentiation processes. Yet, their pair formation remains undocumented. In this study, we found that mating pairs of *H. sjostedti* show clear tandem running behavior. Both females and males played a leading role, with females showing more leader roles, and they switched their leading roles even within the same pair. We also found that dish size affected tandem movement coordination; pairs showed faster and more stable tandem running in a larger dish. We also provide a tracking dataset of 17 body parts, including antennae movement and leg moments during tandem runs, which can be utilized in future comparative studies. This study supports the idea that tandem running existed in the early ancestors of termites and sheds light on the origin of termite mate pairing.

**Introduction**

Social insects play a dominant role in ecosystems, either as predators, pollinators, or decomposers, contributing to global biomass (Bar-On et al., 2018; Eggleton, 2020; Tuma et al., 2020). The ecological success of social insects is often owed to the large size of their colony, ranging from hundreds to millions of individuals. Thus, extensive research efforts have focused on colony functions, regulated by their caste systems, where parents monopolize reproduction, and offspring will either develop into working castes that are responsible for colony tasks or alates that disperse to start a new colony (Noirot, 1991; Oster and Wilson, 1978). However, highlighting mature colonies of social insects often obscures the fact that most colonies need to start from one or a few reproductive individuals dispersed from their original colonies, except for a few species (Cronin et al., 2013). The first critical task of these dispersers is finding a mating partner; such pairing behavior is as important as sophisticated social behaviors to complete their colony life cycles.

Termites are one of the major lineages of eusocial insects and have evolved from subsocial wood-feeding cockroach ancestors (Bell et al., 2007). Termite colonies usually start with a monogamous mating pair, which will be a king and a queen in the mature colony (Chouvenc, 2022; Nutting, 1969). Termite mate pairing is often described as follows; in a short period of the year, numerous alates fly off to disperse. Once they land on the ground, they shed their wings to walk to search for a mating partner. Upon encounter, the pair performed tandem running, with the males following the females while searching for a nest site. However, this description is biased toward the observation of several neoisopteran termites, and pairing processes are actually documented to be diverse, especially in other lineages (Mizumoto et al., 2022). Some do not show tandem running, but females and males separately come to the nest sites (Sugio et al., 2020; Wilkinson, 1962). Some show tandem running, but the leader role is more flexible (Grasse, 1942; Lüscher, 1951; Mizumoto et al., 2022). Furthermore, *Cryptocercus* woodroach, a sister group of termites, should adopt a distinct pairing process from termites, as they are socially monogamous but genetically not (Yaguchi et al., 2021). Therefore, it is important to study the diversity of tandem running behavior, especially in basal lineages, which are often cryptic.

Asian dampwood termite, *Hodotermopsis sjostedti*,is an extensively studied species for their caste development system (e.g., (Kobayashi et al., 2023; Koshikawa et al., 2005; Miura et al., 2004, 2000; Nii et al., 2019; Oguchi et al., 2016; Oguchi and Miura, 2023; Shimoji et al., 2019)). However, their basic biology is not well understood. For example, termite nesting strategies can be classified based on how they utilize their food and nest resources (Abe, 1987; Korb, 2008; Mizumoto and Bourguignon, 2020), and *H. sjostedtri* was originally classified as a one-piece nester whose entire colony is completed within a single piece of wood (Abe, 1987). However, a later field study clearly demonstrated that this species is actually multiple-piece nesters that nest across multiple wood pieces by interconnecting them with underground tunnels (Kitade et al., 2012). In terms of mate pairing, although there are several observations on swarming flight in nature (Ohmura and Makihara, 2005), studies on developmental mechanisms (Kobayashi et al., 2023; Miura et al., 2000; Oguchi et al., 2016; Oguchi and Miura, 2023), and identification of sex-specific chemicals (Lacey et al., 2011), yet no information about tandem running behavior.

Here, we study the tandem running behavior of *H. sjostedti*. We observe their tandem running in the same methodological framework as previous studies in other genera (Mizumoto et al., 2021; Mizumoto and Dobata, 2019). Also, we qualify their behavior using deep learning posture tracking to compare the female leader and the male leader. Finally, given the large body size of this species, we compare the observation between two different-sized dishes.

**Methods**

*Behavioral observation*

The colony of *Hodotermopsis sjostedti* was collected at Yakushima Island, Kagoshima prefecture in when?, 2023. The colony included nymphs. The colony was maintained in the laboratory. In July, 2024, we confirmed that these nymphs are differentiated into alates. We moved the plastic containers with nests to 27°C, and alates flew to come out of the nests. Alates were then collected, separated by sex, introduced to be dealated by manually pinching wings with forceps, and color-marked with one dot of paint (PX-20; Mitsubishi) on the abdomen to distinguish sex identities. These termites were isolated individually for more than 30 minutes before the experiments.

We introduced a female-male pair into the experimental arena. The experimental arenas consist of a petri dish (φ = 90 and 140 mm, respectively) covered with a layer of moistened plaster that was polished before each trial. We recorded termite movements in the arena for 30 minutes using a video camera (HC-X1500-K, Panasonic) with a resolution of 3840x2160 pixels at 59.96 frames per second (FPS). In total, we obtained videos of 10 pairs for the 90 mm dish and the 150 mm dish. Because only one colony was available, all pairs were from the nest mates. All the videos were cropped to 2000x2000 pix to only include the arena in the frame before the video analysis.

*Data processing*

All videos were analyzed using SLEAP v 1.4.0 (Pereira et al., 2022) to estimate the movement of the body parts of each individual. The model was based on that developed for *Reticulitermes speratus* and *Coptotermes formosanus* in a previous study (Mizumoto and Reiter, 2025), with a 17-node skeleton: antenna tips (LR), antenna middle (LR), antenna base (LR), head (middle of mouth parts), head-pronotum boundary, pronotum-mesonotum boundary, metanotum-abdomen boundary, abdomen-tip, fore legs (LR), mid legs (LR), and the hind legs (LR). First, we tracked the videos at 90 mm dish. We labeled X individuals from Y videos for training. We trained a U-Net-based model with a multi-animal top-down approach, with a receptive field size of X pixels for the centroid and Y pixels for the centered instance, on Nvidia GeForce RTX 4090, where augmentation was done by rotating images from -180 to 180 degrees. The mean Average Precision (mAP) and mean Average Recall (mAR) of this model were 0.687 and 0.766, respectively. While tracking after the inference, we used the instance similarity method with the greedy matching method. Then, based on the model developed for the 90 mm dish, we performed the tracking for the 150 mm dish. We used the same procedure as above, where we labeled X individuals from Y videos for training

All pose estimation data were converted to HDF5 files, which were further converted into FEATHER files, using Python. We employed a linear interpolation method to address missing values in the dataset after downsampling the data into 30 FPS. After scaling all data from pixels to mm (2000 pixels = arena size), we used a median filter with a kernel size of 5 to reduce noise. We extracted the position of the head, body center (metanotum-abdomen boundary), and abdomen-tip for further analysis.

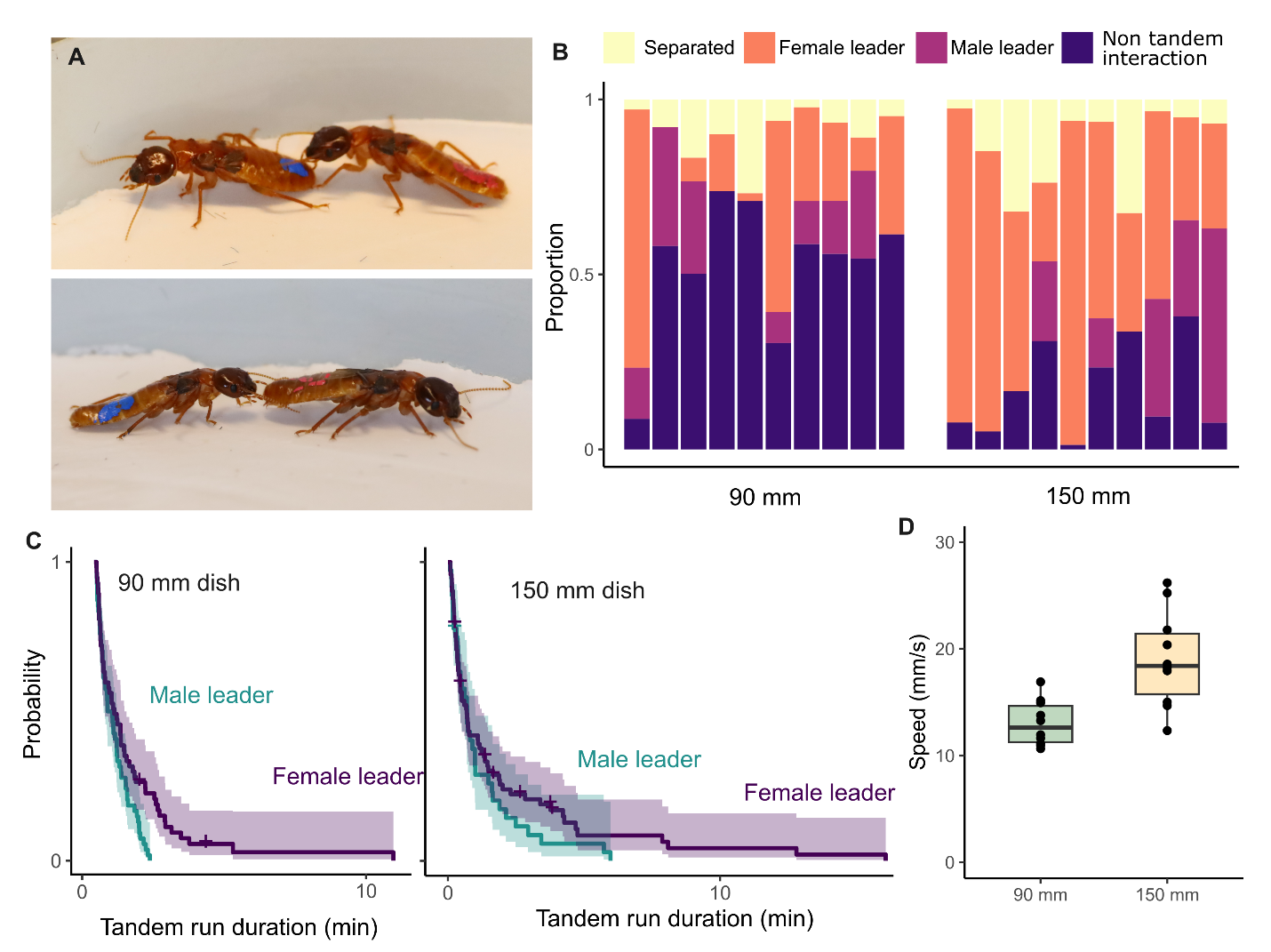
*Data analysis*

All data analysis was performed in R (version). We automatically determined whether pairs were in tandem and who was the leader for each frame, based on the postures and spatial position of partners. First, we regarded as two individuals being in interaction when the distance between the body centers of partners was less than two body lengths, based on the frequency distribution of this distance. In this process, we ignored the short interaction events or non-interaction events less than 2 seconds to smooth the data. Second, during interactions, we classified termite heading orientation as female-leader and male-leader. We obtained the heading directions of females and males as vectors from the abdomen tips to the head front. Then, a pair was in the female leader when the male was behind relative to the female heading direction, and the female was front relative to the male heading direction, and vice versa. If a pair spent more than half of the time in a female-leader position during an interaction event, we regarded the interaction event as a female-leader tandem run. This classified all frames into female-leader tandem, male-leader tandem, other interactions (including tandem runs where they switch leader-follower roles), and non-interactions.

We compared the duration of each tandem running event between leader sexes and two different dish sizes, using mixed-effects Cox models, with leader sex, dish size, and their interaction being treated as a fixed effect and each pair id as a random effect. We used the coxme() function in the coxme package in R (Therneau, 2015). The likelihood ratio test was used to test for statistical significance of the explanatory variable (type II test), with the Anova() function in the car package. We also compared the number of leader switching events between two different dish sizes, using a generalized linear model with Poisson error and a log link function. Finally, we compare the moving speed of leaders between the two dish sizes using a t-test.

**Results**

The termite, *Hodotermopsis sjostedti*, showed a clear tandem running behavior with both females and males performing leader roles (Fig. 1A, Video 1). We also observed both female-female and male-male same sex tandem running during sample preparation, as in the other termite species (Matsuura et al., 2002; Mizumoto et al., 2024b, 2022). We detected tandem running behavior from all the pairs we observed (Fig. 1B), but the patterns were different between leader sexes and dish sizes. In general, we observed more frequent female-led tandem runs than male-led tandem runs (Fig. 1B), where female-led tandems were more stable than male-led tandems (mixed-effects Cox model, χ21 = 8.69, *P* = 0.003; Fig. 1C). The pattern was consistent between two different dish sizes (dish size: χ21 = 2.17, *P* = 0.14, interaction: χ21 = 0.66, P = 0.416; Fig. 1C). Leader role was swapped even within a pair during 30 minute observations (Table 1), with no difference between dish sizes (GLM, χ21 = 0.067, *P* = 0.796). During tandem running, the leader movement speeds were influenced by the dish size, where termites moved faster in a larger dish (t-test, *t*12.85 = 3.82, *P* = 0.002; Fig. 1D).



**Figure 1.** Description of tandem running behavior in *Hodotermopsis sjostedti*. (A) Male-led and female-led tandem runs. Termites with red markings are females and those with blue markings are males. (B) Proportion of time in each state of the pair during observation. Each bar represents one pair. (C) Comparison of tandem running between female-led and male-led tandem running, and two different sizes of experimental arena. Kaplan–Meier survival curves were generated for each species, and the symbol “+” indicates the censoring due to the end of observations. (D) Comparison of leader moving speed during tandem running between different sizes of dish.

**Discussion**

Our observations clearly showed that dealates of *H. sjostedti* show tandem running behavior, with both females and males playing both leader and follower roles (Fig. 1, Video 1). In many species of termites, females play a leader role in tandem running (Mizumoto et al., 2022). Still, documentation of tandem running with both female and male leaders has been limited in several Kalotermitidae species (summarized in (Mizumoto et al., 2022)), including *Kalotermes flavicollis* (Grasse, 1942; Lüscher, 1951), *Cryptotermes havilandi* (Lüscher, 1951) (but suspected as *dudleyi*. See (Mizumoto et al., 2022)), *Paraneotermes simplicicornis* (Carr, 1972), and *Glyptotermes* *fuscus* and *satsumensis* (Mizumoto et al., 2022). In addition, the fossil record indicates that the extinct kalotermitid termite, *Electrotermes affinis*, shows male-led tandem running behavior (Mizumoto et al., 2024a). However, even though the previous ancestral state reconstruction estimated that the ancestor of termites exhibited tandem running, with both females and males being leaders (Mizumoto et al., 2022), there was no record of that behavior in other lineages than Kalotermitidie. Thus, our observation on *H. sjostedti* is critical as this species is Hodotermopsidae in a distinct clade of Teletisoptera (Hodotermopsidae, Stolotermitidae, Hodotermitidae, and Archotermopsidae) (Wang et al., 2022), highlighting the diversity of pairing process of this group (Mizumoto et al., 2022).

Although the biology of *Hodotermopsis* is often compared with that of *Zootermopsis* as a related species (e.g., (Miura et al., 2004)), our observations suggest that these two groups use distinct mate-pairing processes. The pairing process of *Zootermopsis* species has been documented in several papers (Castle, 1934; Howse, 1970; Shellman-Reeve, 2001, 1999, 1994; Stuart, 1969), their use of tandem running behavior is less clear (summarized in Fig. S12 in (Mizumoto et al., 2022)). A previous study treated the tandem running status of *Zootermopsis* as a female-led tandem (Mizumoto et al., 2022), yet original descriptions clearly mention that the tandem pairing is weaker than other termite species with static tandem running behavior (Castle, 1934; Howse, 1970). By using the same experimental setup as the current study, we could not observe the clear tandem running in *Zootermopsis nevadensis*, collected in Hyogo Prefecture, Japan (although small sample size; *n* = 3 pairs, on Jan 4th, 2022). These observations indicate that the pairing process of *H. sjostedti* is distinct from *Zootermopsis* species. It is reasonable that these species exhibit different nesting habitats, with *Hodotermopsis* being a multiple-piece nester and *Zootermopsis* being a one-piece nester. One future direction is to study the relationship between nesting habitat and the pairing process in a phylogenetic comparative framework.

One limitation of the current study is that our observation is limited to one colony. In other species, it is known that tandem running behavior can be affected by individual conditions, such as body size (Husseneder and Simms, 2008; Matsuura et al., 2002) and time after swarming (Mizumoto et al., 2024c). Thus, reflecting individual status, there should be a quantitative variation of tandem running propensity across different colonies. However, it is unrealistic to suppose the colony variation in the pairing mode, with some colonies exhibiting tandem running while others using different pairing methods. For example, in *Marginitermes hubbardi*, a laboratory observation demonstrates that this species does not usually show tandem running behavior except for one pair (Carr, 1972). One of the authors observed a tandem running behavior of *M. hubbardi* on the tree trunk in the field condition (one personal observation by N. Mizumoto on July 31, 2019, in Tempe, Arizona), implying that there might be a specific condition for this species to exhibit tandem running behavior. Thus, it might be difficult to prove the lack of tandem running only from the laboratory observations. However, even with limitations, our study provides a positive observation of the clear tandem running behavior of *H. sjostedti*, which should be valid in field environments.

Notably, we found that the termite tandem running behavior may be affected by the size of observational arenas (Fig. 1), with termites moving fast and showing more tandems in the larger arena. Instead, in a smaller arena, pairs of *H. sjostedti* spent more time on non-tandem running interactions, such as grooming. The termite, *H. sjostedti*, is one of the largest termites (12-13 mm body length of dealates in our study) (Mizumoto and Bourguignon, 2021). Since tandem running behavior is an exploratory behavior for a nest site for colony foundation, the 90 mm arena may have been too small to be recognized as an open space for this species. This is in contrast to other smaller species with clear tandem running in 90 mm or even smaller dish sizes (Mizumoto and Reiter, 2025). Because arena size can affect the free walking behavior in insects (Scharf et al., 2024), it could be important to provide a large enough arena for the observing species to detect their tandem running behavior.

In conclusion, our study contributes to the understanding of the diversity and evolution of mate-pairing behavior in termites. Even though mate pairing plays a crucial role in the life cycle of termites, little attention has been paid to it compared to other social behaviors. One challenge is that mate pairing is a seasonal event, which can be observed in a limited period of the year for each species. Yet, given the cryptic diversity of the tandem running behavior in non-neoisoptera termites, species-specific descriptive efforts are essential.

**Author contributions**

N.M.: conceptualization, data curation, formal analysis, funding acquisition, investigation, methodology, project administration, validation, visualization, supervision, writing-original draft.

W.C.: formal analysis, methodology, writing-editing

E.C.: formal analysis, methodology, supervision, writing-editing

T.N.: resources, writing-editing

T.K.: resources, writing-editing

**Acknowledgments**

We thank Kensei Kikuchi, XYZ for helping during the sampling of termites, and Dr. Thomas Bourguignon for providing experimental spaces. This study is supported by a JSPS (Japan Society for the Promotion of Science) Research Fellowship for Young Scientists CPD (Cross-border Post Doctorate) (20J00660) to N.M., a Grant-in-Aid for Early-Career Scientists (21K15168) to N.M., IPSF fellowship from OIST to N.M., and USDA National Institute of Food and Agriculture, Hatch projects number 7007938.

**References**

Abe T. 1987. Evolution of life types in termites In: Kawano S, Connell J, Hidaka T, editors. Evolution and Coadaptation in Biotic Communities. Tokyo: University of Tokyo Press. pp. 125–148.

Bar-On YM, Phillips R, Milo R. 2018. The biomass distribution on Earth. *Proceedings of the National Academy of Sciences* **115**:6506–6511. doi:10.1073/pnas.1711842115

Bell WJ, Roth LM, Nalepa CA. 2007. Cockroaches Ecology, Behavior and Natural History, The Jhons Hopkins University Press. JHU Press.

Carr RV. 1972. The tergal grand and coutship behavior in the termites *Pterotermes occidentis*, *Marginitermes hubbardi* and *Paraneotermes simplicicornis* (Isoptera: Kalotermitidae). The university of Arizona.

Castle GB. 1934. The dampwood termites of western United States, genus *Zootermopsis* (formerly Termopsis). In: Kofoid CA, editor. Termites and Termite Control. Berkeley: University of California Press. pp. 273–310.

Chouvenc T. 2022. Eusociality and the transition from biparental to alloparental care in termites. *Functional Ecology* **36**:3049–3059. doi:10.1111/1365-2435.14183

Cronin AL, Molet M, Doums C, Monnin T, Peeters C. 2013. Recurrent evolution of dependent colony foundation across eusocial insects. *Annual Review of entomology* **58**:37–55. doi:10.1146/annurev-ento-120811-153643

Eggleton P. 2020. The State of the World’s Insects. *Annual Review of Environment and Resources* **45**:61–82. doi:10.1146/annurev-environ-012420-050035

Grasse PP. 1942. L’essaimage des termites: essai d’analyse causale d’un complexe instinctif. *Laboratoire d’Evolution des Etres Organises*.

Howse PE. 1970. Termites: a study in social behaviour.

Husseneder C, Simms DM. 2008. Size and heterozygosity influence partner selection in the Formosan subterranean termite. *Behavioral Ecology* **19**:764–773. doi:10.1093/beheco/arn041

Kitade O, Hayashi Y, Takatsuto K. 2012. Variation and diversity of symbiotic protist composition in the damp-wood termite *Hodotermopsis sjoestedti*. *Japanese Journal of Protozoology* **45**:29–36. doi:10.18980/jjprotozool.45.1-2\_29

Kobayashi K, Oguchi K, Miura T. 2023. Physiological and developmental mechanism of regressive molt in a damp-wood termite Hodotermopsis sjostedti. *Front Ecol Evol* **11**. doi:10.3389/fevo.2023.1200081

Korb J. 2008. The ecology of social evolution in termites In: Korb J, Heinze J, editors. Ecology of Social Evolution. Springer Berlin Heidelberg. pp. 151–174. doi:10.1007/978-3-540-75957-7\_7

Koshikawa S, Cornette R, Hojo M, Maekawa K, Matsumoto T, Miura T. 2005. Screening of genes expressed in developing mandibles during soldier differentiation in the termite Hodotermopsis sjostedti. *FEBS Letters* **579**:1365–1370. doi:10.1016/j.febslet.2005.01.031

Lacey MJ, Sémon E, Krasulová J, Sillam-Dussès D, Robert A, Cornette R, Hoskovec M, Žáček P, Valterová I, Bordereau C. 2011. Chemical communication in termites: *syn*-4,6-dimethylundecan-1-ol as trail-following pheromone, *syn*-4,6-dimethylundecanal and (5*E*)-2,6,10-trimethylundeca-5,9-dienal as the respective male and female sex pheromones in *Hodotermopsis sjoestedti* (Isoptera, Archotermopsidae). *Journal of Insect Physiology* **57**:1585–1591. doi:10.1016/j.jinsphys.2011.07.018

Lüscher von M. 1951. Beobachtungen über die Koloniegründung bei verschiedenen afrikanischen Termitenarten. *Schweizerisches Tropeninstitut Basel* **8**:36–43.

Matsuura K, Kuno E, Nishida T. 2002. Homosexual tandem running as selfish herd in *Reticulitermes speratus*: novel antipredatory behavior in termites. *Journal of Theoretical Biology* **214**:63–70. doi:10.1006/jtbi.2001.2447

Miura T, Hirono Y, Machida M, Kitade O, Matsumoto T. 2000. Caste developmental system of the Japanese damp-wood termite *Hodotermopsis japonica* (Isoptera: Termopsidae). *Ecological Research* **15**:83–92. doi:10.1046/j.1440-1703.2000.00320.x

Miura T, Koshikawa S, Machida M, Matsumoto T. 2004. Comparative studies on alate wing formation in two related species of rotten-wood termites: Hodotermopsis sjostedti and Zootermopsis nevadensis (Isoptera, Termopsidae). *Insect Soc* **51**:247–252. doi:10.1007/s00040-003-0736-2

Mizumoto N, Bourguignon T. 2021. The evolution of body size in termites. *Proceedings of the Royal Society B: Biological Sciences* **288**:20211458. doi:10.1098/rspb.2021.1458

Mizumoto N, Bourguignon T. 2020. Modern termites inherited the potential of collective construction from their common ancestor. *Ecology and Evolution* **10**:6775–6784. doi:10.1002/ece3.6381

Mizumoto N, Bourguignon T, Bailey NW. 2022. Ancestral sex-role plasticity facilitates the evolution of same-sex sexual behavior. *Proceedings of the National Academy of Sciences of the United States of America* **119**:e2212401119. doi:10.1073/pnas.2212401119

Mizumoto N, Dobata S. 2019. Adaptive switch to sexually dimorphic movements by partner-seeking termites. *Science Advances* **5**:eaau6108. doi:10.1126/sciadv.aau6108

Mizumoto N, Hellemans S, Engel MS, Bourguignon T, Buček A. 2024a. Extinct and extant termites reveal the fidelity of behavior fossilization in amber. *Proc Natl Acad Sci USA* **121**:e2308922121. doi:10.1073/pnas.2308922121

Mizumoto N, Lee S-B, Chouvenc T. 2024b. The strength of sexual signals predicts same-sex pairing in two *Coptotermes* termites. *Behavioral Ecology* arae067. doi:10.1093/beheco/arae067

Mizumoto N, Lee SB, Valentini G, Chouvenc T, Pratt SC. 2021. Coordination of movement via complementary interactions of leaders and followers in termite mating pairs. *Proceedings of the Royal Society B: Biological Sciences* **288**:20210998. doi:10.1098/rspb.2021.0998

Mizumoto N, Nagaya N, Fujisawa R. 2024c. Wasted Efforts Impair Random Search Efficiency and Reduce Choosiness in Mate-Pairing Termites. *The American Naturalist* 000–000. doi:10.1086/732877

Mizumoto N, Reiter S. 2025. Maintaining tandem movement cohesion through antennal movements in termites. doi:10.1101/2025.02.13.638054

Nii R, Oguchi K, Shinji J, Koshikawa S, Miura T. 2019. Reduction of a nymphal instar in a dampwood termite: heterochronic shift in the caste differentiation pathways. *EvoDevo* **10**:10. doi:10.1186/s13227-019-0123-8

Noirot C. 1991. Caste differentiation in Isoptera: basic features, role of pheromones. *Ethology Ecology & Evolution* **3**:2–7. doi:10.1080/03949370.1991.10721899

Nutting WL. 1969. Flight and colony foundation. In: Krishna K, Weesner FM, editors. Biology of Termites. New York: Academic Press. pp. 233–282. doi:10.1016/B978-0-12-395529-6.50012-X

Oguchi K, Miura T. 2023. Upregulation of Hox genes leading to caste-specific morphogenesis in a termite. *EvoDevo* **14**:12. doi:10.1186/s13227-023-00216-w

Oguchi K, Shimoji H, Hayashi Y, Miura T. 2016. Reproductive organ development along the caste differentiation pathways in the dampwood termite Hodotermopsis sjostedti. *Insectes Sociaux* **63**:519–529. doi:10.1007/s00040-016-0495-x

Ohmura W, Makihara H. 2005. Swarming of *Hodotermopsis japonica* Holmgren in Amami Oshima Island. *Japanese Journal of Environmental Entomology and Zoology* **16**:49–51.

Oster GF, Wilson EO. 1978. Caste and Ecology in the Social Insects. Princeton: Princeton Univ. Press.

Pereira TD, Tabris N, Matsliah A, Turner DM, Li J, Ravindranath S, Papadoyannis ES, Normand E, Deutsch DS, Wang ZY, McKenzie-Smith GC, Mitelut CC, Castro MD, D’Uva J, Kislin M, Sanes DH, Kocher SD, Wang SSH, Falkner AL, Shaevitz JW, Murthy M. 2022. SLEAP: A deep learning system for multi-animal pose tracking. *Nature Methods* **19**:486–495. doi:10.1038/s41592-022-01426-1

Scharf I, Hanna K, Gottlieb D. 2024. Experimental arena settings might lead to misinterpretation of movement properties. *Insect Science* **31**:271–284. doi:10.1111/1744-7917.13213

Shellman-Reeve JS. 2001. Genetic relatedness and partner preference in a monogamous, wood-dwelling termite. *Animal Behaviour* **61**:869–876. doi:10.1006/anbe.2000.1674

Shellman-Reeve JS. 1999. Courting strategies and conflicts in a monogamous, biparental termite. *Proceedings of the Royal Society of London B* **266**:137–144. doi:10.1098/rspb.1999.0613

Shellman-Reeve JS. 1994. Limited nutrients in a dampwood termite: nest preference, competition and cooperative nest defence. *Journal of Animal Ecology* **63**:921–932.

Shimoji H, Mizumoto N, Oguchi K, Dobata S. 2019. Caste-biased locomotor activities in isolated termites. *Physiological Entomology* **45**:50–59. doi:10.1111/phen.12315

Stuart AM. 1969. 7 Social Behavior and Communication In: Krishna K, Weesner FM, editors. Biology of Termites. New York: Academic Press. pp. 193–232. doi:10.1016/b978-0-12-395529-6.50011-8

Sugio K, Miyaguni Y, Yoshimura T. 2020. Synchronization of alate emergence among colonies and dispersal strategy in the Ryukyu dry-wood termite *Neotermes sugioi* (Isoptera: Kalotermitidae). *Insectes Sociaux* 1–8. doi:10.1007/s00040-020-00766-5

Therneau TM. 2015. coxme: mixed effects Cox models.

Tuma J, Eggleton P, Fayle TM. 2020. Ant-termite interactions: an important but under-explored ecological linkage. *Biological Reviews* **95**:555–572. doi:10.1111/brv.12577

Wang M, Hellemans S, Šobotník J, Arora J, Buček A, Sillam‐Dussès D, Clitheroe C, Lu T, Lo N, Engel MS, Roisin Y, Evans TA, Bourguignon T. 2022. Phylogeny, biogeography and classification of Teletisoptera (Blattaria: Isoptera). *Systematic Entomology* **47**:581–590. doi:10.1111/syen.12548

Wilkinson W. 1962. Dispersal of alates and establishment of new colonies in *Cryptotermes havilandi* (Sjöstedt) (Isoptera, Kalotermitidae). *Bulletin of Entomological Research* **53**:265–286. doi:10.1017/S0007485300048124

Yaguchi H, Kobayashi I, Maekawa K, Nalepa CA. 2021. Extra-pair paternity in the wood-feeding cockroach Cryptocercus punctulatus Scudder: Social but not genetic monogamy. *Molecular Ecology* **30**:6743–6758. doi:10.1111/mec.16185

**Table 1**. The number of leader role switches for each pair.

|  |  |  |  |
| --- | --- | --- | --- |
| video | dish size | leader switches |  |
| Hod\_sjo\_FM\_90\_A\_02 | 90 mm | 0 |  |
| Hod\_sjo\_FM\_90\_A\_03 | 90 mm | 2 |  |
| Hod\_sjo\_FM\_90\_A\_05 | 90 mm | 1 |  |
| Hod\_sjo\_FM\_90\_A\_06 | 90 mm | 2 |  |
| Hod\_sjo\_FM\_90\_A\_07 | 90 mm | 1 |  |
| Hod\_sjo\_FM\_90\_A\_08 | 90 mm | 0 |  |
| Hod\_sjo\_FM\_90\_A\_09 | 90 mm | 0 |  |
| Hod\_sjo\_FM\_90\_A\_10 | 90 mm | 1 |  |
| Hod\_sjo\_FM\_90\_A\_14 | 90 mm | 0 |  |
| Hod\_sjo\_FM\_90\_A\_15 | 90 mm | 1 |  |
| Hod\_sjo\_FM\_150\_A\_02 | 150 mm | 1 |  |
| Hod\_sjo\_FM\_150\_A\_03 | 150 mm | 2 |  |
| Hod\_sjo\_FM\_150\_A\_05 | 150 mm | 1 |  |
| Hod\_sjo\_FM\_150\_A\_06 | 150 mm | 0 |  |
| Hod\_sjo\_FM\_150\_A\_07 | 150 mm | 2 |  |
| Hod\_sjo\_FM\_150\_A\_08 | 150 mm | 0 |  |
| Hod\_sjo\_FM\_150\_A\_09 | 150 mm | 1 |  |
| Hod\_sjo\_FM\_150\_A\_10 | 150 mm | 0 |  |
| Hod\_sjo\_FM\_150\_A\_14 | 150 mm | 0 |  |
| Hod\_sjo\_FM\_150\_A\_15 | 150 mm | 0 |  |

**Legend for Video 1**. The example video clips of male-led (left) and female-led (right) tandem runs.