J Insect Behav (2023) 36:195–209
https://doi.org/10.1007/s10905-023-09834-7

RESEARCH

# Sensitivity and Orientation to Sustained Airflow by *Coptotermes formosanus* Soldier Termites (Isoptera, Rhinotermitidae)

**Bramantyo Wikantyoso · Wakako Ohmura · Tomoya Imai · Yoshihisa Fujii · Setiawan Khoirul Himmi · Sulaeman Yusuf**

Received: 23 November 2022 / Revised: 9 May 2023 / Accepted: 24 May 2023 / Published online: 10 June 2023


**Abstract** Airflow is a crucial variable for insect orientation and navigation, particularly in flying insects whose antennae have several setae with flexible sockets. Termites occasionally dispatch their soldier caste to the frontline of the nest or shelter tube opening as the colony is alerted by the disturbances or preparing the alates' nuptial flight. Hence, soldier termites' contact with airflow outside the nest is inevitable. We analyzed subterranean termite (*Coptotermes formosanus*) soldiers' sensitivity and orientation toward sustained airflow by manipulating the organs that bear setae with flexible sockets (e.g., antennal trimming, thorax pronotum covering). Four functional groups of soldier termites were tested against 10 min sustained airflow in three test chamber types. Soldier termites showed highly variable sensitivity and orientation toward airflow. The soldiers with antennae tended to orient and spend more time in the "region of interest" near the chamber opening. Adding airflow into the chamber increased movement. Significantly lower sensitivity toward the airflow source occurred when the antennae were trimmed and the pronotum was covered. When the antennae were trimmed, setae on the pronotum and other body parts might enhance the sensitivity to airflow, but their spatial ability was reduced as the soldiers demonstrated an alerting behavior by frequently bumping into the wall and opening their mandibles. The alerting behavior was significantly lower when air flowed into the chamber. These results demonstrated that setae with flexible sockets on the antennae and pronotum assisted soldier termites' orientation to the airflow and enhanced their spatial ability.

**Keywords** Defensive caste · individual behavior · trajectory · air motion · formosan subterranean termite

B. Wikantyoso (✉) · W. Ohmura · T. Imai
Research Institute for Sustainable Humanosphere (RISH), Kyoto University, Gokasho, Uji, Kyoto, Japan
e-mail: bram002@brin.go.id

W. Ohmura
e-mail: murasan@rish.kyoto-u.ac.jp

T. Imai
e-mail: imai.tomoya.4c@kyoto-u.ac.jp

B. Wikantyoso · S. K. Himmi · S. Yusuf
Research Center for Applied Zoology, National Research and Innovation Agency (BRIN), Bogor, Indonesia
e-mail: khoi003@brin.go.id

S. Yusuf
e-mail: sula002@brin.go.id

Y. Fujii
Graduate School of Agriculture, Kyoto University, Kyoto, Japan
e-mail: fujii.yoshihisa.6s@kyoto-u.ac.jp

## Introduction

Air current or airflow is important for flight initiation among flying insects as it affects both their flying orientation (Pasek 1988; Riley et al. 1999; Fuller et al. 2014), and migration timing (Åkesson 2016; Hu et al. 2016). Terrestrial insects can also use airflow to help their navigation in open spaces (Wolf and Wehner 2000, 2005; Müller and Wehner 2007). In the Formosan termite *Coptotermes formosanus*, a minimum wind velocity is necessary for the initiation of the nuptial flight of the alates; however, flight will not take place when the wind velocity is higher than 3.7 km/h (Leong et al. 1983; Watson and Gay 1991; Sugio and Miyaguni 2019). In the eastern subterranean termite *Reticulitermes flavipes*, the occurrence of wind/airflow was suggested to be an important cue to initiate restarting flight after an instantaneous measurement of flight speed (Shelton et al. 2006).

Termite nests have a natural ventilation system (King et al. 2015). Since subterranean termites have a limited period to go outside the nest during the swarming season, they spend most of their time in the nest and the shelter tube (Matsuura et al. 2007; Chouvenc et al. 2017). Termite communication in the nest may also depend on the airflow. For example, airflow might circulate a queen's volatile pheromone around the gallery to inhibit worker differentiation into supplementary queens and to stimulate egg-carrying and piling behavior (Matsuura et al. 2010). In the case of subterranean termites, apart from alates during a nuptial flight, only the soldier caste goes outside to defend the nest. At least three circumstances might encourage soldiers of subterranean termites to leave the nest: (1) protecting the workers while they build and repair the nest; (2) releasing alates during the nuptial flight; and (3) protecting the nest or gallery against external breaches, such as a human-made opening or airflow (Tschinkel and Close 1973; Watson and Gay 1991; King et al. 2015). Subterranean termite soldiers thus face stimuli outside the nest, such as heat, light, and air current or airflow. The effects of short air puffs, heat, and light on soldier termites have been investigated (Hertel et al. 2011; Ohmura et al. 2011; Delattre et al. 2019; Woon et al. 2019), but the effects of a sustained airflow on the sensitivity and orientation of subterranean termite soldiers have not been established.

In flying insects, mechanosensors that are located on the wing have crucial functions. The mechanosensors can acquire information concerning fast rotation during flight (Sherman and Dickinson 2003), evaluate the wing load (Hengstenberg 1988), and receive information about movement orientation (Pass 2018). The wing-margin setae of the silk moth *Bombyx mori* respond to air-borne vibration, and they filter the wing-beat frequency and direction (Ai et al. 2010; Ai 2013). Some terrestrial insects have mechanosensors on their cerci that sense the airflow of moving entities such as predators (Camhi et al. 1978; Kumagai et al. 1998). In the damp-wood termite *Hodotermopsis sjostedti*, mechanosensory setae on the antennae, mouthparts, and thorax of alates and soldiers are modified to have longer pegs compared to the pseudergates (worker caste) (Ishikawa et al. 2007).

*Coptotermes formosanus* soldiers have long-peg setae with flexible sockets positioned on the marginal and medial side of the body such as the pronotum (Wikantyoso et al. 2022) and antennae (Tarumingkeng et al. 1976; Yanagawa et al. 2009; Fu et al. 2020). The existence of a setal peg in a flexible socket was suggested to sense airflows (Dumpert and Gnatzy 1977; Tautz 1977; Shimozawa and Kanou 1984). Thus, flexible setae may mediate soldier termites' sensing of airflow and affect their orientation. To test this morphology-based hypothesis, we analyzed the behavior and orientation of *C. formosanus* soldiers with their antennae trimmed and pronotum setae masked by cyanoacrylate gel. The orientation of the termites in response to airflow was recorded with an image-based tracking analysis system (Yamanaka and Takeuchi 2018). We also compared the function of the setae between the control and three treated groups.

## Materials and Methods

We prepared four functional groups: soldier termites without antennae (TRIM), soldier termites with pronotum setae covered by gel (COV), soldier termites without antennae and with covered setae (TRIM-COV), and soldier termites without manipulation as the control group (CONT).

### Termite Preparation

Laboratory-reared colonies of *Coptotermes formosanus* were reared in a dark room at 27–28 °C and 85% relative humidity at Kyoto University, Japan. Soldier termites were taken from the colony and kept in a Petri dish (90 × 15 mm) with wet cellulose paper as a base. The antennae of soldier termites of the TRIM group were trimmed with fine scissors between the fourth and fifth flagellomere (Fig. 1a, b), after a cold-anesthesia procedure under a stereo microscope (Yanagawa et al. 2010). Each termite was placed individually in a smaller Petri dish (35 × 10 mm) maintained at 28 °C prior to the airflow test. For their recovery after antennal trimming, soldier termites were incubated for ~ 12–24 h (Camhi and Johnson 1999).

For the COV group, cyanoacrylate gel was quickly applied (Böröczky et al. 2013) to cover the termite's setae on the pronotum marginal and medial parts (Fig. 1c–e) to limit mechanosensory setal movement (Westin et al. 1977; Camhi et al. 1978) (Fig. 1f). The room temperature was set to 28 °C during the incubation and the successive testing. Each termite was placed individually in the test chamber with dry cellulose paper as a base to undergo a 10 min acclimatization period prior to a test. Soldier termites that did not move or assess the chamber by walking around during the acclimatization were not used.

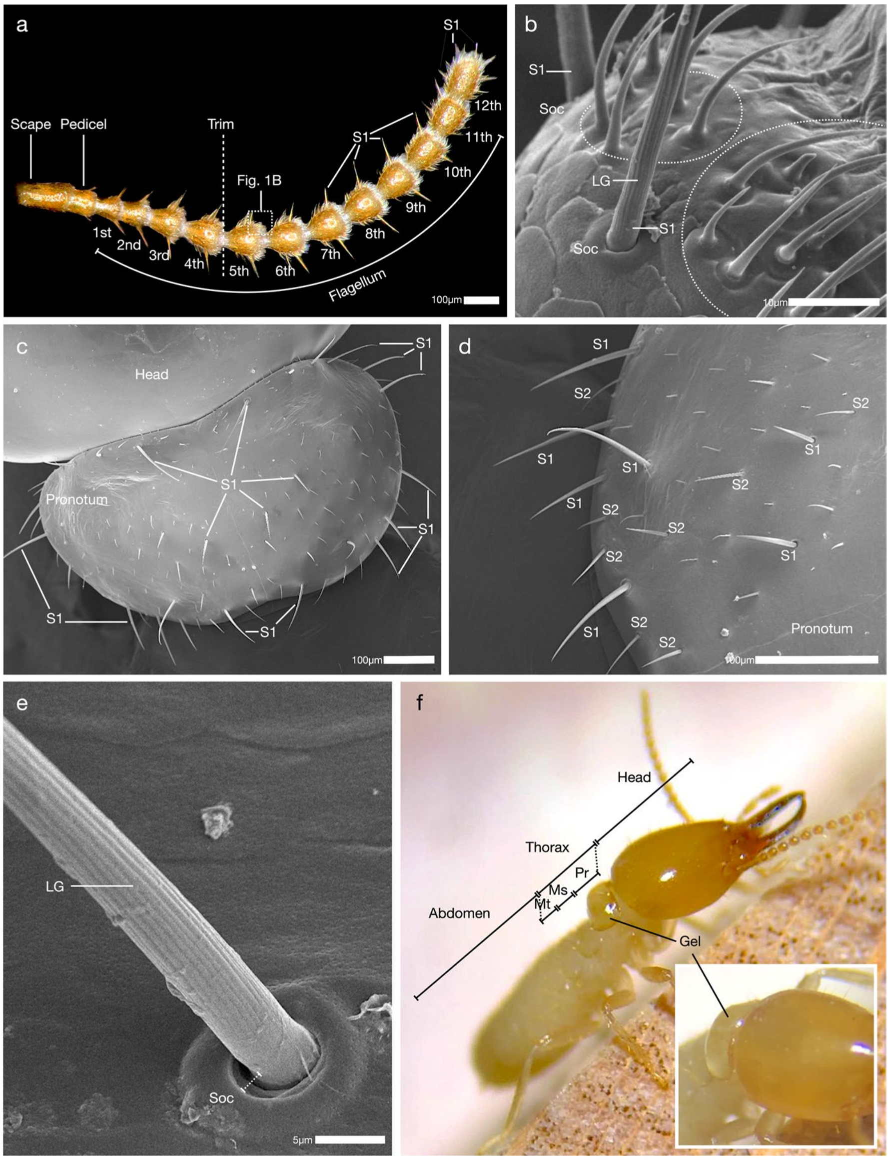


**Fig. 1** The setae on the antennae and pronotum of *C. formosanus* soldier. **a** The entire 12 segments of the soldier termite's antennae. **b** The mechanosensory setae on the antennae had a flexible socket and longitudinal groove characteristics, whereas the other shorter setae (in the dotted circle) did not have a flexible socket. **c** Setae on the pronotum located on the marginal and medial sides. **d** The flexible setae in two different lengths, long- and short-peg setae. **e** On the pronotum, long-peg setae and short-peg setae had flexible sockets and longitudinal groove characteristics. **f** The whole body of a soldier termite, Cyanoacrylate gel was applied to the pronotum part of the thorax that was identifiable by its reflective surface. S1: long-peg flexible setae, S2: short-peg flexible setae, LG: longitudinal grooves, Soc: flexible socket, Pr: pronotum, Ms: mesonotum, Mt: metanotum

### Microscopy Observations

The setal characteristics were observed by light and scanning electron microscopy (SEM). Light microscopy observation was conducted using a digital microscope (VHX-5000, Keyence Corp., Osaka, Japan). For the SEM analysis, termite specimens were washed with 70% acetone for 1 min in an ultrasonic cleaner (Branson 5510 J-DTH: Yamato Scientific, Tokyo). The samples were then transferred to aqueous osmic acid (OsO4, 2%) solutions and treated at 4 °C overnight for staining. Dehydration was performed with serial aqueous acetone solutions (70%, 85%, 95%, 100%, absolute). After the specimens were air-dried, they were fixed on a copper stub with electron conductive glue (Dotite: Fujikura Kasei, Tokyo). Before the SEM observation, the specimens were coated with platinum by a JEC-3000FC auto-fine coater (JEOL, Tokyo) with a setting of 20 mA for 120 s. The platinum-coated samples were observed with a JSM-7800 F (JEOL, Tokyo) at an accelerating voltage of 5 kV.

### Test Chamber Preparation

Three types of chambers were used: a closed chamber (CC), an open chamber (OC), and an open chamber with airflow (AF, Fig. 2). The closed chamber was prepared by using a sterilized polystyrene Petri dish (35 × 10 mm) that was unmodified and used upside down on a paper sheet (Fig. 2a). For the open chambers, a modified Petri dish with a lid was prepared by making 25 mm$^2$ openings on one side of both Petri dish lid and the Petri dish base so that both openings would match when the lid and the base were paired. Rubber tubes (4 mm inner dia., 6 mm outer dia., 5 cm long) were attached to the opening on the Petri dish base. The tube-end and the Petri dish opening on the lid were connected by rotating the lid part (Fig. 2b, c). The chamber with airflow (AF) had the same structure as the open chamber but with the addition of sustained airflow from regulated clean-dry air (1 L/m) to the chamber via the rubber tube. The clean-dry airflow came from a 7000 L compressed air tank (Kist, Kyoto, Japan). The OC and AF chambers were designed and built to be as homologous as possible. Given the opening (25 mm$^2$) and tube size (6 mm outer dia.), we determined that the entry tube should cover most of the opening. The Petri dish had four "rests" below the lid, which provided a gap (< 0.5 mm) between the lid and base part for the air to flow out of the chamber gradually during the test (Fig. 2c). A region of interest (ROI) was created to represent the approach zone which was established in parallel by creating a 1 × 1 cm imaginary area in front of the chamber opening (Fig. 2d). For both the OC and AF chambers, a piece of 1 mm filter mesh was placed between tube and opening to avoid the soldier termites escape from the chamber.

### Airflow Test

The sensitivity and orientation of the CONT, TRIM, COV, TRIM + COV groups of soldier termites were

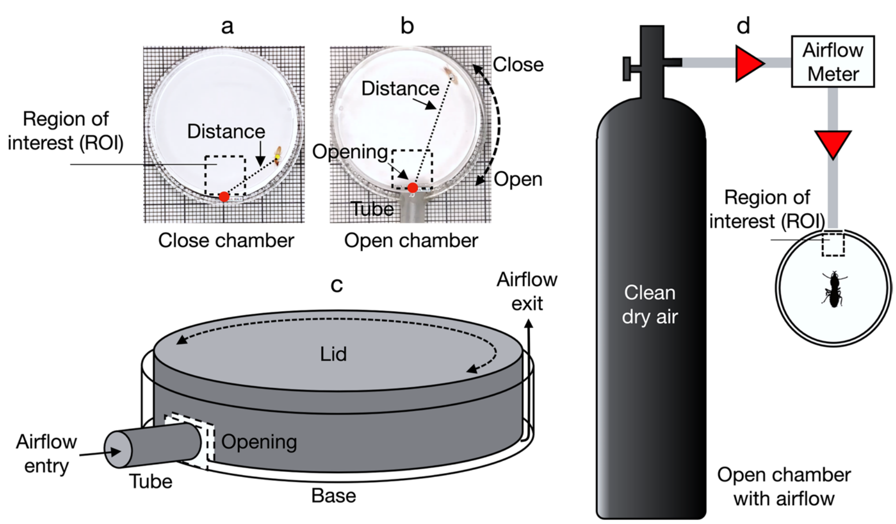


**Fig. 2** The experimental designs. **a** Closed chamber (CC). **b** Open chamber (OC). **c** The modified chamber for the test includes the opening on the cap and base of the Petri dish connected by a tube as the air-flow tunnel. **d** The design of the OC with airflow (AF) from compressed clean-dry air. Dashed square (**a**, **b**, **d**) represents the region of interest (ROI)

evaluated in all three types of chambers (CC, OC, AF). Eight repetitions were prepared for each group. In the beginning, 10 soldier termites (8 replicates and 2 replacements) were prepared for each control and three treatment groups (CONT, COV, TRIM, and COV-TRIM group). Termites from each group of treatment were randomly picked out and separately observed in the CC chamber. Some termites might stay still and not move during 10 min observation in the CC chamber. In this case, replacements were prepared. Eight termites that showed normal response and movement (exploring and circling the chamber) in the CC chamber were used in the consecutive observation in OC and AF chambers. In total, 32 termites were used in four different treatment groups (eight replicates each) and each treatment group went through three different chamber types (96 disposable chambers in total).

During the test, the orientation of the soldier termites to the ROI was recorded for 10 min by a 1080 HD video camera at 30 frames per second (fps). The video camera was placed on the top of the chamber and illuminated by a white LED lamp. The percentage of soldier termites in the $1 \times 1$ cm ROI was recorded and calculated. The distance between the soldier termites and the chamber opening was also determined. The movements of soldier termites in the chamber were recorded to establish their trajectory.

### Behavior Assessment

During the 10 min airflow test, we assessed the behavior of the termites with trimmed antennae (TRIM) and gel applied (COV) to determine whether these treatments would significantly affect their behavior prior to the test in the closed chamber. We also conducted behavior observations in OC and AF chambers to examine the effects of the different chamber conditions. Four types of soldier termite behaviors or body postures were observed: (1) head banging (drumming), i.e., soldier termite bangs its head against the substrate; (2) body jittering, i.e., soldier termite quickly shakes its body forward and backward several times; (3) mandible opening (biting pose), in which soldier termite opens its mandible wide during walking, standing still, or bumping into a wall; and (4) biting, in which soldier termite leans its body forward and launches a bite by strongly closing its mandible.

### Image Analysis

To visualize the soldier termites' orientation, the 10 min image records from the video camera during the airflow tests were converted into 18,000 frames and then preprocessed and analyzed using an image-based open-source quantitative analysis tracking system, UMATracker (Yamanaka and Takeuchi 2018). Three types of analysis were conducted: an orientation/trajectory analysis, a region analysis, and a distance analysis. Each soldier termite's orientation was obtained by extracting the coordinates of the termite's position in the chamber, which were extracted from the termite centroid and the estimated direction at 30 fps. The termite trajectory was established by overlaying all extracted coordinates of each soldier termite's orientation during the 10 min recording ($\pm$9000 frames).

In the region analysis, soldier termite coordinates inside the $1 \times 1$ cm region in each frame were used to determine the percentage inside the ROI. The distance analysis was conducted to collect the distance information between termites and the designated position during 10 min observation. In this study, the designated position is the chamber opening or the source of airflow (red dot, Fig. 2a, b). The distance and time spent by soldier termites when they approached the chamber opening or airflow source were recorded. The distance between the termite soldier and the opening was determined by using the pixels of each frame. The distance analysis used a threshold value, determined as the farthest distance within the region of interest (ROI) drawn straight from the chamber opening. Our conversion from the records showed that 1 cm was equal to 149.34 pixels long on average. The furthest threshold coordinate from the center of the opening gate in the distance analysis was thus 1.12 cm, equal to 164.28 pixels.

### Statistical Analysis

The data were analyzed by a one-way analysis of variance (ANOVA) with the IBM SPSS Statistics 28 program (IBM, Armonk, NY, USA). The statistical significances between and within different treatment group pairs were evaluated with a multiple comparison test (Tukey's HSD, $p = 0.05$). The differences between and within the treatment groups were tested, and significance between all groups and within each treatment group is indicated in the figures by italic letters ([a,b,c]) and asterisks (*), respectively.

## Results

### The Morphological Characterization of the Setae in the Termite Antennae

The overall structures of the termite antennae and pronotum are depicted in Fig. 1. Light microscopy was used to observe the setal distribution on the antennae along the base (scape and pedicel) and antennae flagellum (12 flagellomeres). The pronotum setae had a long peg, and the setae at the pronotum marginal part protruded laterally (Fig. 1a). The SEM observations identified flexible sockets around the base of the setae, which were not observed on the other shorter setae. The sockets roundly protruded and surrounded the base of the setal pegs (Fig. 1b).

On the pronotum, setae with flexible sockets were scattered all over the surface, with longer setae located at the pronotum marginal area. Long and short setae with flexible sockets were observed (Fig. 1c, d). The base of the setal pegs and sockets had an interval that displayed the flexibility of the peg. The setal cuticular wall had longitudinal grooves extending from the base to the tip, similar to that on the antennae (Fig. 1e). The appearance of the setae with flexible sockets on the antennae and pronotum was confirmed by an SEM analysis. We tested the hypothesis regarding soldier termites' sensitivity to airflow by comparing the behavior of the individuals whose sensing organs were physically disturbed.

### Region and Distance Analysis Results

Overall, the percentages of soldier termites in the region of interest in the closed chamber and open chamber were highly variable across all treatment groups ($\alpha = 0.05$). When air flowed into the chamber, the percentage in the ROI was significantly higher in the CONT ($p = 0.015$) and COV groups ($p = 0.018$) groups compared to TRIM and COV-TRIM groups (Fig. 3a).

When the chamber type was changed, soldier termites might check the entering airflow or try to get through the chamber opening by frequently moving the antennae and touching the covering filter mesh. When soldier termites got close to the opening or airflow source, they entered the ROI and the distance to the chamber opening or airflow source was shorter; when they walked away from the opening or airflow source, this distance was longer. When the distance was beyond the threshold, soldier termites were no longer inside the ROI, and we considered they were ignoring the opening or the airflow source existence.

Each line represents each group treatment (CONT, COV, TRIM, COV-TRIM) in different chamber types (CC, OC, AF), and 12 lines illustrate the combination of treatment and chamber types. The control group and covered pronotum group soldier termites in the AF chamber spent the longest time in the ROI or close to the airflow source, 3.46 min ($p = 0.001$) and 3.09 min ($p = 0.030$), respectively. Both treatment groups were significantly different from the soldier termites of the control group in the closed chamber, which mostly spent the time exploring the chamber and had no tendency to stay and check the chamber opening (24.6 s in ROI, Fig. 3b).

The analysis results also demonstrated that soldier termites had different orientations in three chamber types. Opening the chamber significantly affected the soldier termites' orientation ($p = 0.049$), and the additional airflow significantly escalated the movement of soldier termites with antennae toward the ROI compared to the closed chamber ($p = 0.042\text{E-}03$). Trimming the antennae caused the percentage in the ROI to decline. However, soldier termites still significantly set their course more toward the ROI compared to the orientation in both the closed and open chambers ($p = 0.010$ and $p = 0.023$, respectively, Fig. 3c). The soldier termites with a normal pronotum significantly spent longer times in the ROI when the air was flowing compared to the closed chamber ($p = 0.256\text{E-}03$). Covering the pronotum lowered the percentage in the ROI and eliminated the significance (Fig. 3a,d).

### Soldier Termites' Trajectories

The trajectories of soldier termites in the 10 min recordings are qualitatively illustrated in Fig. 4. Twelve representative trajectories are presented from the four treatment groups in the three types of testing chambers. In each trajectory figure, as many as 18,000 coordinates from the extraction result were overlayed and put in one frame. Overall, the trajectories showed a circular motion in all treatment groups and all types of testing chambers. The trajectories in

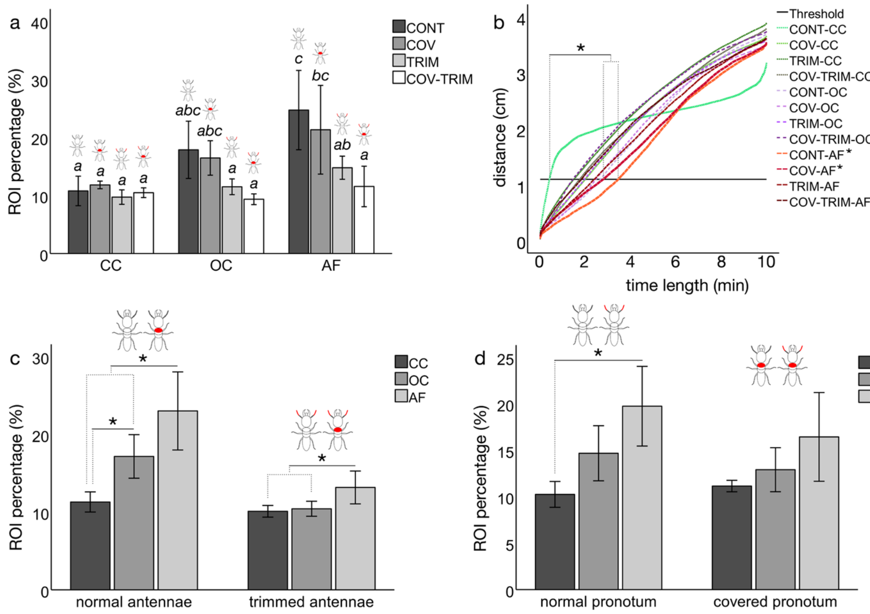


**Fig. 3** The results of the region analysis showing the percentages of soldier termites ($n=8$) recorded inside the region of interest (ROI). **a** The ROI percentages in the four treatment groups. **b** The analysis of the distances of the soldier termites from the chamber opening, recorded under the threshold. **c** The ROI percentage differences between chamber types under the antennae-trimming treatment. **d** The ROI percentage differences between chamber types under pronotum-covering treatment. CONT: no treatment, COV: gel-covered pronotum, TRIM: trimmed antennae, COV-TRIM: gel-covered pronotum and trimmed antennae, CC: closed chamber, OC: open chamber, AF: chamber with an airflow. The significance between (letters $^{a,b,c}$) and within (*) groups (α: 0.05)

the closed chamber were around the perimeter and center of the chamber, indicating a random orientation across the treatment groups. In the open chamber, the trajectories at the center were fewer, and thus several random straight orientation paths (bold arrowhead in Fig. 4) through the center of the chamber were visible, demonstrating that the orientation of the soldier termites with antennae changed from a circular orientation following the chamber perimeter. When the air was flowing, straight orientation paths that were in a line with the chamber opening were more obvious and initiated from a similar site (blank arrowhead in Fig. 4). However, the straight orientation path was observed less frequently in the TRIM and COV-TRIM groups.

## Behavior Analysis

We observed each soldier termite's reaction to each treatment and chamber type. When the soldier termites bumped the wall or hesitated, they suddenly opened their mandibles and sometimes stopped walking around (Fig. 5). The behavior was not significantly different between the CONT and COV groups. In contrast, the soldier termites in the TRIM groups would frequently open their mandibles. The behavioral differences were significant between control and treatment groups in the closed chamber (TRIM, $p=0.022$E-03; COV-TRIM, $p=0.030$E-03; Fig. 6a). Losing the antennae caused the soldier termites to suddenly open their mandible when they abruptly bumped into the chamber wall.

Soldier termites also responded differently in the three different chamber types. Among the soldier termites with intact antennae, mandible-opening behavior was observed significantly more frequently in the open chamber compared to the closed chamber ($p=0.172$E-03). However, this behavior was not significantly different compared to the soldier termites in the chamber with airflow ($p=0.102$; Fig. 6b). Interestingly, when air flowed into the chamber, the mandible-opening behavior was remarkably lower compared to the behavior in the CC and OC types. The mandible opening behavior was significantly higher in the soldier termites with

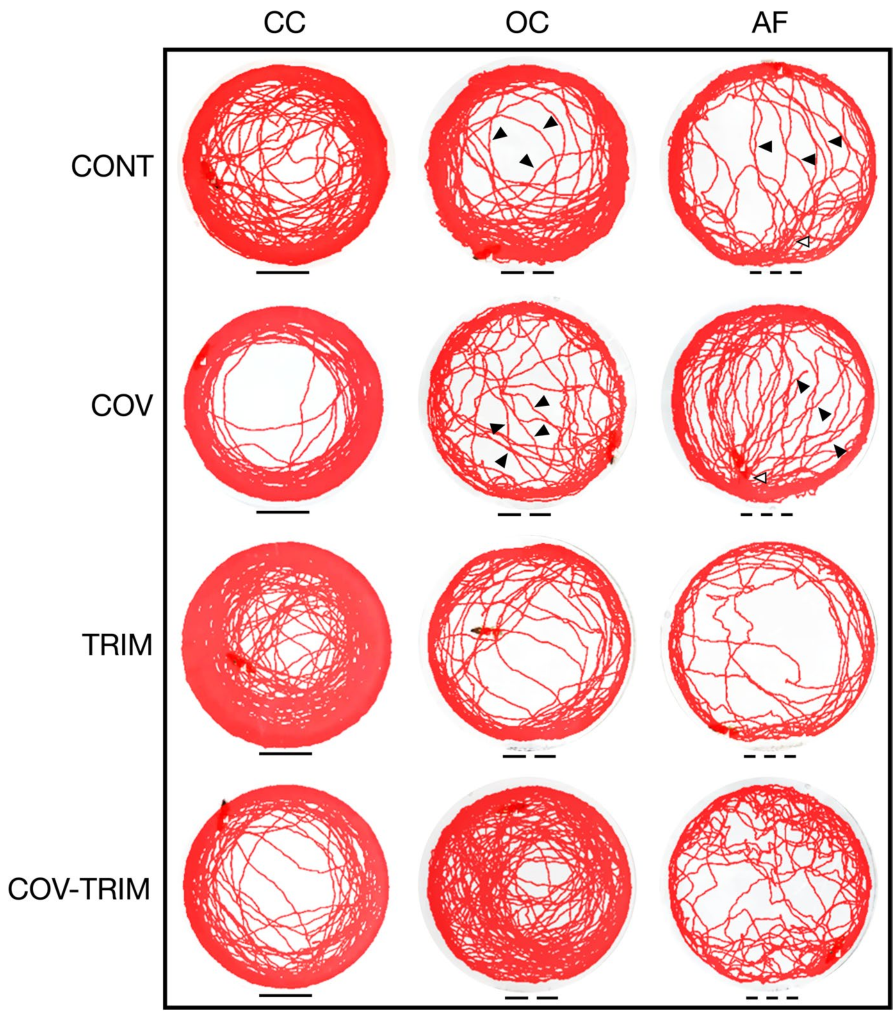


**Fig. 4** The trajectories of the soldier termites in the CC (*one long dash*), OC (*two dashes*), and AF (three dashes) chambers. CONT: no treatment, COV: gel-covered pronotum, TRIM: trimmed antennae, COV-TRIM: gel-covered pronotum and trimmed antennae, CC: closed chamber, OC: open chamber, AF: chamber with an airflow

trimmed antennae (CC, $p=0.019\text{E-}03$; OC, $p=0.002$; Fig. 6b) and those with a normal pronotum (CC, $p=0.033$; OC, $p=0.039$; Fig. 6c). The significant ability of the airflow to keep the mandible-opening behavior low was lost when the pronotum was covered (CC, $p=0.411$; OC, $p=0.123$; Fig. 6c).

## Discussion

Our microscopy observations revealed that setae with long pegs existed on the antennae and pronotum of *C. formosanus* soldiers, and we hypothesized that the setae with flexible sockets are specialized to sense airflow, given that a long peg seta with a flexible socket is sensitive to faint perturbations such as air puffs and airborne vibration-induced air current (Dumpert and Gnatzy 1977; Tautz 1977; Shimozawa and Kanou 1984). To test this hypothesis, we compared the behavior of the soldier termites whose sensing organs were physically disturbed: (1) those with pronotum setae covered by gel, (2) those with antennae whose distal part after the 4th flagellum was trimmed off, and (3) those with both gel and trimming treatments.

### Soldier Termite Sensitivity to Airflow

Airflow can be sensed by terrestrial insects to help their navigation and by flying insects to help their orientation. The desert ants *Cataglyphis fortis* use the wind to determine their foraging and homing trail (Wolf and Wehner 2000, 2005; Müller and Wehner 2007). *Drosophila* sense the airspeed as they neutralize unstable oscillation during their flight (Fuller et al.

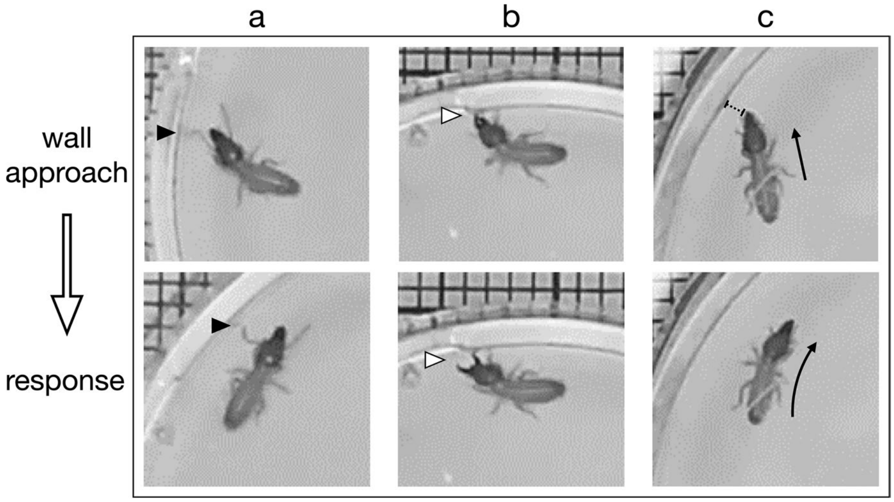


**Fig. 5** Mandible-opening behavior was observed when a soldier termite abruptly bumped into a wall. **a** A soldier termite with normal antennae used its antennae to frequently swab the wall (*bold arrowhead*) as it approaches the chamber perimeter. **b** A soldier termite with trimmed antennae exhibited an alerting behavior (*blank arrowhead*) as it abruptly bumped into the wall and opened its mandible. **c** A soldier termite with trimmed antennae in the chamber with airflow stopped before the wall and continued to move in another direction (*arrow*) without opening its mandible

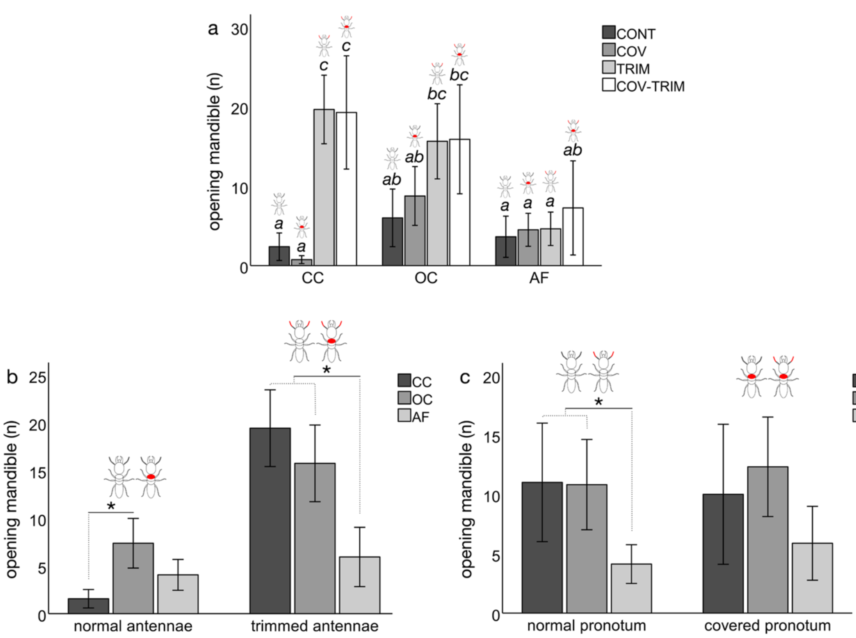


**Fig. 6** The number of mandible-opening behaviors ($n=8$). **a** Comparison of mandible-opening behavior in the treatment groups. **b** Comparison of mandible-opening behavior in the CC, OC, and AF chamber types under the antennae-trimming treatments. **c** Comparison of mandible-opening behavior in the CC, OC, and AF chamber types under pronotum-covering treatments. CONT: no treatment, COV: gel-covered pronotum, TRIM: trimmed antennae, COV-TRIM: gel-covered pronotum and trimmed antennae, CC: closed chamber, OC: open chamber, AF: chamber with an airflow. The significance between (letters $^{a,b,c}$) and within (*) groups (α: 0.05)

2014). The results of our present analyses indicated that *C. formosanus* soldier termites were able to sense airflow and locate the chamber opening. Although the responses were highly variable across the treatment groups, the soldier termites tended to spend a longer time in the region of interest by the opening. The existence of airflow amplified the soldiers' course to the airflow source.

In several areas, the nuptial flight of *C. formosanus* alates has been suggested to occur with wind velocity $\leq 1$ m/s (Leong et al. 1983) up to 7 m/s (Sugio and Miyaguni 2019). However, soldier termites might have a decisive role in the initiation of the event, as alates will not emerge after soldier termites stick out their antennae and the measured wind velocity is not appropriate (Leong et al. 1983). Apart from the trail pheromone from the worker termites that might attract the soldier termites (Matsumura et al. 1968; Traniello 1982), we speculated that the air velocity, airflow, or air pressure changes around cracks or openings might be important variables for the nuptial flight. Our present findings demonstrated that in the absence of nest-mates and predators, soldier termites sensed the airflow and their orientation was also affected.

An approximately 3 cm/s airflow naturally streams down in the nests of the termite *Odontotermes obesus* as the nest's air-conditioning system (King et al. 2015). In this study, we used 1 L/min of airflow which is equal to 1.33 m/s (tube inner dia.: 4 mm). We thus suspected that the air velocity around the gallery or nest crack is higher than the air velocity in the nest gallery. The orientation of subterranean termite depends in part on the guiding tunnel gallery, and further research is necessary to understand the response against airflow of other castes or soldier termites of different species, particularly on open-air foraging termites, such as the genera *Hospitalitermes*, *Longipeditermes*, *Lacessititermes*, *Macrotermes*, etc. (Kalshoven 1958; Jander and Daumer 1974; Sugio 1995; Miura and Matsumoto 1998).

## Airflow Enhances the Soldier Termites' Spatial Ability

When the shelter tube or nest is broken and a predator comes in, termite soldiers can be defensively alerted by the vibration or odors that might be brought by the intruders into the galleries (Evans et al. 2009; Ishikawa and Miura 2012; Oberst et al. 2017). In the absence of chemical stimulants, soldier termites of *Hodotermopsis sjostedti* and *Coptotermes* spp. may also be defensively alerted by the opened nest and unexpected air puffs, respectively (Hertel et al. 2011; Ishikawa and Miura 2012; Delattre et al. 2019). However, sustained airflow and unexpected air puffs may affect soldier termite orientation differently (Camhi and Tom 1978). In termites, defensive responses may be exhibited as head banging or drumming, body jittering or jerking, attack posture, and biting (Lubin and Montgomery 1981; Röhrig et al. 1999; Ohmura et al. 2009; Hertel et al. 2011; Ishikawa and Miura 2012; Delattre et al. 2019).

In the present study, the *C. formosanus* soldiers did not exhibit any defensive responses toward a sustained airflow, with the exception of the mandible-opening behavior. This behavior was rarely followed by an attacking posture or direct biting. The sustained airflow also did not trigger body jittering or head drumming as defensive signals. Therefore, we suspected that the mandible-opening behavior is an alerting behavior in response to the reduction of spatial ability, since the soldier termites had limited ability to receive signals from the flagellum part of the trimmed antennae. The mandible-opening behavior might be induced by unprompted circumstances beyond the soldier termites' sensing range. In the trimmed antennae group, an alerting behavior began with abrupt bumping into the wall, hesitation, or sudden stop during movement as soldier termites hardly evaluate the distance to the wall. This behavior was remarkably higher when the soldier termites lost more than half of the antennae flagellum.

In the cockroach *Periplaneta americana*, which is closely related to the Isoptera, the spatial ability to follow the testing chamber wall by using antennae flagellum acted as a tactile sensor, even when the visual organs were covered (Camhi and Johnson 1999). Cockroach antennae may convert tactile sensory signals to evaluate the distance to the wall (Cowan et al. 2006). This also may explain that in the absence of airflow, antennal tactile sensors might help soldier termites find the chamber opening, as we observed that the soldier termites were oriented in a circular manner following the wall. Our results also demonstrated that the airflow addition into the chamber enhanced the spatial ability, as the soldier termites in all three treatment groups showed less alerting behavior that was due to bumping into the chamber wall (Fig. 6). The addition of airflow also encouraged the soldier termites with antennae to make more use of the center chamber space by making straight paths from the chamber opening and relying less on the chamber wall (Fig. 4). In the absence of antennae, the modification of the spatial ability might be related to the existence of other setae with flexible sockets on the rest of the antennae scape and pedicel or other body parts, which have the anatomical characteristics to sense the airflow dynamic at the chamber wall.

### Antennae and Body Setae as Soldier Termite Airflow Sensory System

Antennae are important for insect navigation as they are filled with various sensory receptors or sensilla (Tarumingkeng et al. 1976; Altner et al. 1981; Yanagawa et al. 2009; Fu et al. 2020), which are usually called setae or bristle as discriminative characteristics in insect taxonomy (Simpson et al. 1999; Takematsu 1999; Constantino 2000; Bourguignon and Roisin 2011; Jeong and Ahn 2022). In the more detailed anatomy of crickets, setae lodged in flexible sockets on the cercus are called "filiform mechanosensory receptors" that are sensitive to air currents, while setae with no flexible sockets are called "bristles" that are sensitive to touch (Jacobs 1995). Long-peg setae on soldier termite antennae have also been anatomically demonstrated to have flexible sockets and outer dendrite segments of mechanosensory cells (Tarumingkeng et al. 1976; Yanagawa et al. 2009; Fu et al. 2020).

Our present analyses demonstrated that setae with a long peg and flexible socket are distributed on the antennal surface in *C. formosanus* soldiers. Losing the fifth to twelfth flagellomeres altered the soldier termites' orientation and sensitivity toward the airflow source. Based on the observations of *C. formosanus* by Yanagawa et al. (2009), we estimated that trimming the fifth to twelfth flagellomeres caused the soldier termites to lose approximately 94.8% of their setae with flexible sockets. Antennae have been demonstrated to be important for terrestrial and flying insects' ability to detect airflow (Wolf and Wehner 2005; Müller and Wehner 2007; Fuller et al. 2014), as the loss of antennae altered these insects' orientation to a food source (Wolf and Wehner 2000). The soldiers of open-air foraging termites have antennae with longer flagellomere segments compared to their workers and the soldiers of subterranean termites (Yanagawa et al. 2009; Syaukani 2010; Fu et al. 2020). Longer flagellomeres segments may provide more area to bear setae with flexible sockets. The present experiment was conducted in a solo test with clean dry air to exclude distraction from variables such as the pheromones, the cuticular carbon odor of the termite nestmates, the temperature, and humidity changes of the air (Tschinkel and Close 1973; Sponsler and Appel 1991; Bland et al. 2001; Yanagawa et al. 2010; Mitaka and Akino 2021). Moreover, a small colony size or small nest or gallery opening at the early stage of colony foundation by subterranean reproductive termites may force soldier termites to forage in limited numbers or alone (Matsuura 2002; Korb and Thorne 2017; Yanagihara et al. 2018), and these soldier termites may display behavior as an individual.

The present study also demonstrated that in the absence of antennae, airflow still significantly stimulated soldier termites toward the region of interest, with their pathway being through the perimeter rather than the chamber center area. In the absence of antennae, *P. americana* cockroaches tend to walk closer to walls (Camhi and Johnson 1999). It was also suggested that covering the setae on the pronotum of soldier termites tends to lower their orientation to the source of airflow. Wikantyoso et al. (2022) showed that setae of various lengths on the *C. formosanus* soldiers' pronotum had at least a tubular body as the characteristic of mechanoreceptor, with around one-third of the total number of setae having long pegs and apparent flexible sockets. In our present investigation, intervals between sockets and the base of setal pegs on the pronotum were also clearly observed. However, covering the pronotum setae might not have had enough impact to reduce the airflow sensitivity, because setae as mechanosensors were scattered not only on the pronotum, but all over the soldier termites' body including the antennae (Ishikawa et al. 2007), such as on their scape and pedicel part of the remaining trimmed antennae (Yanagawa et al. 2009), and the head part near the fontanelle and mouthparts (Ishikawa et al. 2007; Wikantyoso et al. 2022).

In cockroaches, covering the whole cerci eliminates the response to airflow (Westin et al. 1977; Camhi et al. 1978). It is also possible that the arrangement of all setae with flexible sockets on soldier termites' entire head, thorax, and abdominal part might work as a unit, considering the termite's relatively small body size. In subterranean termite *C. curvignathus* soldiers, the pronotum and head capsule have more setae with flexible sockets compared to the other *Coptotermes* spp. (Wikantyoso et al. 2021, 2022). Setae patches together with the organ to which those belong work together to sense airflow, and not as a separate component (Gewecke 1974). Flexible sockets benefit the setal peg movement or deflection in a certain direction and may serve as an input for the nerve terminal (Thurm 1965; Dumpert and Gnatzy 1977; Tautz 1977; French and Sanders 1979; Shimozawa and Kanou 1984; Keil 1997; Iwasaki et al. 1999; Wikantyoso et al. 2022). Setae with flexible sockets were observed in the present study, and they assisted the soldier termites' responses to sustained airflow. Future termite research including electrophysiology analyses is necessary to confirm the singular setal sensitivity on termites' antennae and body parts to airflow and airborne vibrations-induced air current.

## Conclusion

*Coptotermes formosanus* soldiers showed highly variable sensitivity and orientation towards airflow. The sensitivity of the soldier termites toward an airflow source was significantly lower when the antennae were trimmed and when the pronotum was covered. Antennae are important organs for soldier termite airflow-related orientation and spatial ability. Without antennae, soldier termites demonstrated an alerting behavior by bumping the wall and opening their mandibles. Setae with flexible sockets on the antennae and pronotum assisted the soldier termites' orientation to the airflow and established their spatial ability by significantly reducing the alerting behavior.

**Acknowledgements** We would like to express our gratitude to Prof. Hiroyuki Yano for facilitating the SEM observations, which were performed with the help of the Cellulosic Advanced Nanomaterials Development Organization (CAN-DO) in RISH, Kyoto University, Japan. We are deeply indebted to Dr. Aya Yanagawa for her assistance with the pivotal discussion. We are extremely grateful to Dr. Ayako Wada-Katsumata for the methodological suggestions, and we are also thankful to Dr. Matthew T. Kamiyama for giving valuable input about the manuscript. We acknowledge the Innovative Humano-habitability Laboratory members of RISH, Kyoto University, and the Urban Entomology Laboratory members of the Research Center for Applied Zoology, National Research and Innovation Agency (BRIN), Indonesia.

**Author Contributions** All authors contributed equally as main contributors to the study conception, design, and work. Bramantyo Wikantyoso, Wakako Ohmura, and Tomoya Imai performed material preparation and data collection. Bramantyo Wikantyoso, Wakako Ohmura, Tomoya Imai, and Setiawan Khoirul Himmi conducted data analysis. Bramantyo Wikantyoso, Wakako Ohmura, Tomoya Imai, and Yoshihisa Fujii prepared Figs. 1, 2, 3, 4, 5 and 6. Wakako Ohmura, Tomoya Imai, Yoshihisa Fujii, and Sulaeman Yusuf contributed to the supervision and leadership. Bramantyo Wikantyoso wrote the first draft of the manuscript, and all authors reviewed the manuscript.

**Data Availability** The data that support the findings of this study are available from the corresponding author upon reasonable request. Data are located in the Laboratory of Innovative Humano-habitability at RISH, Kyoto University.

**Declarations**

**Competing Interests** The authors have no competing interests to declare that are relevant to the content of this article.

## References

Ai H (2013) Sensors and sensory processing for airborne vibrations in silk moths and honeybees. Sensors 13:9344–9363. https://doi.org/10.3390/s130709344

Ai H, Yoshida A, Yokohari F (2010) Vibration receptive sensilla on the wing margins of the silkworm moth *Bombyx mori*. J Insect Physiol 56:236–246. https://doi.org/10.1016/j.jinsphys.2009.10.007

Åkesson S (2016) Flying with the winds: differential migration strategies in relation to winds in moth and songbirds. J Anim Ecol 85:1–4. https://doi.org/10.1111/1365-2656.12450

Altner H, Routil C, Loftus R (1981) The structure of bimodal chemo-, thermo-, and hygroreceptive sensilla on the antenna of *Locusta migratoria*. Cell Tissue Res 215:289–308. https://doi.org/10.1007/BF00239116

Bland JM, Osbrink WLA, Cornelius ML, Lax AR, Vigo CB (2001) Solid-phase microextraction for the detection of termite cuticular hydrocarbons. J Chromatogr A 932:119–127. https://doi.org/10.1016/S0021-9673(01)01239-0

Böröczky K, Wada-Katsumata A, Batchelor D, Zhukovskaya M, Schal C (2013) Insects groom their antennae to enhance olfactory acuity. Proc Natl Acad Sci USA 110:3615–3620. https://doi.org/10.1073/pnas.1212466110

Bourguignon T, Roisin Y (2011) Revision of the termite family Rhinotermitidae (Isoptera) in New Guinea. Zookeys 148:55–103. https://doi.org/10.3897/zookeys.148.1826

Camhi JM, Johnson EN (1999) High-frequency steering maneuvers mediated by tactile cues: antennal wall-following in the cockroach. J Exp Biol 202:631–643. https://doi.org/10.1242/jeb.202.5.631
Camhi JM, Tom W (1978) The escape behavior of the cockroach *Periplaneta americana*: I. turning response to wind puffs. J Comp Physiol 128:193–201. https://doi.org/10.1007/BF00656852
Camhi JM, Tom W, Volman S (1978) The escape behavior of the cockroach *Periplaneta americana*: II. Detection of natural predators by air displacement. J Comp Physiol 128:203–212. https://doi.org/10.1007/BF00656853
Chouvenc T, Scheffrahn RH, Mullins AJ, Su N-Y (2017) Flight phenology of two *Coptotermes* species (Isoptera: Rhinotermitidae) in Southeastern Florida. J Econ Entomol 110:1693–1704. https://doi.org/10.1093/jee/tox136
Constantino R (2000) Key to the soldiers of South American *Heterotermes* with a new species from Brazil (Isoptera: Rhinotermitidae). Insect Syst Evol 31:463–472. https://doi.org/10.1163/187631200X00499
Cowan NJ, Lee J, Full RJ (2006) Task-level control of rapid wall following in the american cockroach. J Exp Biol 209:1617–1629. https://doi.org/10.1242/jeb.02166
Delattre O, Šobotník J, Jandák V, Synek J, Cvačka J, Jiříček O, Bourguignon T, Sillam-Dussès D (2019) Chemical and vibratory signals used in alarm communication in the termite *Reticulitermes flavipes* (Rhinotermitidae). Insectes Soc 66:265–272. https://doi.org/10.1007/s00040-018-00682-9
Dumpert K, Gnatzy W (1977) Cricket combined mechanoreceptors and kicking response. J Comp Physiol 122:9–25. https://doi.org/10.1007/BF00611245
Evans TA, Inta R, Lai JCS, Prueger S, Foo NW, Fu EW, Lenz M (2009) Termites eavesdrop to avoid competitors. Proc R Soc Edinb Biol 276:4035–4041. https://doi.org/10.1098/rspb.2009.1147
French AS, Sanders EJ (1979) The mechanism of sensory transduction in the sensilla of the trochanteral hair plate of the cockroach, *Periplaneta americana*. Cell Tissue Res 198:159–174. https://doi.org/10.1007/BF00234843
Fu B-X, Rong N-H, Hong J, Zhu Z-R, Mo J-C, Zhang D (2020) Comparative study with scanning electron microscopy on the antennal sensilla of two main castes of *Coptotermes formosanus* Shiraki (Blattaria:Rhinotermitidae). Micron 129:102777. https://doi.org/10.1016/j.micron.2019.102777
Fuller SB, Straw AD, Peek MY, Murray RM, Dickinson MH (2014) Flying *Drosophila* stabilize their vision-based velocity controller by sensing wind with their antennae. Proc Natl Acad Sci USA 111:E1182–E1191. https://doi.org/10.1073/pnas.1323529111
Gewecke M (1974) The antennae of insects as air-current sense organs and their relationship to the control of flight. In: L Barton Browne (ed) Experimental analysis of insect behaviour. Springer Berlin Heidelberg, Berlin, Heidelberg, pp 100–113
Hengstenberg R (1988) Mechanosensory control of compensatory head roll during flight in the blowfly *Calliphora erythrocephala* Meig. J Comp Physiol A 163:151–165. https://doi.org/10.1007/BF00612425
Hertel H, Hanspach A, Plarre R (2011) Differences in alarm responses in drywood and subterranean termites (Isoptera: Kalotermitidae and Rhinotermitidae) to physical stimuli. J Insect Behav 24:106–115. https://doi.org/10.1007/s10905-010-9240-x
Hu G, Lim KS, Reynolds DR, Reynolds AM, Chapman JW (2016) Wind-related orientation patterns in diurnal, crepuscular and nocturnal high-altitude insect migrants. Front Behav Neurosci 10. https://doi.org/10.3389/fnbeh.2016.00032
Ishikawa Y, Koshikawa S, Miura T (2007) Differences in mechanosensory hairs among castes of the damp-wood termite *hodotermopsis sjostedti* (Isoptera: Termopsidae). Sociobiology 50:895–907
Ishikawa Y, Miura T (2012) Hidden aggression in termite workers: plastic defensive behaviour dependent upon social context. Anim Behav 83:737–745. https://doi.org/10.1016/j.anbehav.2011.12.022
Iwasaki M, Itoh T, Tominaga Y (1999) Mechano- and phonoreceptors. In: Eguchi E, Tominaga Y (eds) Atlas of arthropod sensory receptors: dynamic morphology in relation to runction 1. Springer Japan, Tokyo, p 177–190
Jacobs GA (1995) Detection and analysis of air currents by crickets. Bioscience 45:776–785. https://doi.org/10.2307/1312630
Jander R, Daumer K (1974) Guide-line and gravity orientation of blind termites foraging in the open (Termitidae: *Macrotermes*, *Hospitalitermes*). Insectes Soc 21:45–69. https://doi.org/10.1007/BF02222979
Jeong W-J, Ahn K-J (2022) Taxonomy of korean *Ischnosoma* Stephens (Coleoptera: Staphylinidae). J Asia Pac Biodivers 15:285–292. https://doi.org/10.1016/j.japb.2021.10.007
Kalshoven LGE (1958) Observations on the black termites, *Hospitalitermes* spp., of Java and Sumatra. Insectes Soc 5:9–30. https://doi.org/10.1007/BF02222427
Keil TA (1997) Functional morphology of insect mechanoreceptors. Microsc Res Tech 39:506–531. https://doi.org/10.1002/(sici)1097-0029(19971215)39:6%3c506::aid-jemt5%3e3.0.co;2-b
King H, Ocko S, Mahadevan L (2015) Termite mounds harness diurnal temperature oscillations for ventilation. Proc Natl Acad Sci USA 112:11589–11593. https://doi.org/10.1073/pnas.1423242112
Korb J, Thorne B (2017) Sociality in termites. In: Rubenstein DR, Abbot P (eds) Comparative social evolution. Cambridge University Press, Cambridge, pp 124–153
Kumagai T, Shimozawa T, Baba Y (1998) Mobilities of the cercal wind-receptor hairs of the cricket, *Gryllus bimaculatus*. J Comp Physiol A 183:7–21. https://doi.org/10.1007/s003590050230
Leong KLH, Tamashiro M, Yates JR, Su N-Y (1983) Microenvironmental factors regulating the flight of *Coptotermes formosanus* Shiraki in Hawaii (Isoptera; Rhinotermitidae). Proc Hawaii Entomol Soc 24:287–291
Lubin YD, Montgomery GG (1981) Defenses of *Nasutitermes* termites (Isoptera, Termitidae) against *Tamandua* anteaters (Edentata, Myrmecophagidae). Biotropica 13:66–76. https://doi.org/10.2307/2387872
Matsumura F, Coppel HC, Tai A (1968) Isolation and identification of termite trail-following pheromone. Nature 219:963–964. https://doi.org/10.1038/219963a0

Matsuura K (2002) Colony-level stabilization of soldier head width for head-plug defense in the termite *Reticulitermes speratus* (Isoptera: Rhinotermitidae). Behav Ecol Sociobiol 51:172–179

Matsuura K, Himuro C, Yokoi T, Yamamoto Y, Vargo EL, Keller L (2010) Identification of a pheromone regulating caste differentiation in termites. Proc Natl Acad Sci USA 107:12963–12968. https://doi.org/10.1073/pnas.1004675107

Matsuura K, Kobayashi N, Yashiro T (2007) Seasonal patterns of egg production in field colonies of the termite *Reticulitermes speratus* (Isoptera: Rhinotermitidae). Popul Ecol 49:179–183. https://doi.org/10.1007/s10144-006-0030-4

Mitaka Y, Akino T (2021) A review of termite pheromones: multifaceted, context-dependent, and rational chemical communications. Front Ecol Evol 8. https://doi.org/10.3389/fevo.2020.595614

Miura T, Matsumoto T (1998) Open-air litter foraging in the nasute termite *Longipeditermes longipes* (Isoptera: Termitidae). J Insect Behav 11:179–189. https://doi.org/10.1023/A:1021039722402

Müller M, Wehner R (2007) Wind and sky as compass cues in desert ant navigation. Naturwissenschaften 94:589–594. https://doi.org/10.1007/s00114-007-0232-4

Oberst S, Bann G, Lai JCS, Evans TA (2017) Cryptic termites avoid predatory ants by eavesdropping on vibrational cues from their footsteps. Ecol Lett 20:212–221. https://doi.org/10.1111/ele.12727

Ohmura W, Kataoka Y, Kiguchi M (2011) Influence of wavelength on phototaxis of the termite, *Reticulitermes speratus* (Kolbe). Jpn J Appl Entomol Zool 22:185–190

Ohmura W, Takanashi T, Suzuki Y (2009) Behavioral analysis of tremulation and tapping of termites (Isoptera). Sociobiology 54:269–274

Pasek JE (1988) Influence of wind and windbreaks on local dispersal of insects. Agric Ecosyst Environ 22–23:539–554. https://doi.org/10.1016/0167-8809(88)90044-8

Pass G (2018) Beyond aerodynamics: the critical roles of the circulatory and tracheal systems in maintaining insect wing functionality. Arthropod Struct Dev 47:391–407. https://doi.org/10.1016/j.asd.2018.05.004

Riley JR, Reynolds DR, Smith AD, Edwards AS, Osborne JL, Williams IH, McCartney HA (1999) Compensation for wind drift by bumble-bees. Nature 400:126–126. https://doi.org/10.1038/22029

Röhrig A, Kirchner WH, Leuthold RH (1999) Vibrational alarm communication in the african fungus-growing termite genus *macrotermes* (Isoptera, Termitidae). Insectes Soc 46:71–77. https://doi.org/10.1007/s000400050115

Shelton TG, Hu XP, Appel AG, Wagner TL (2006) Flight speed of tethered *Reticulitermes flavipes* (Kollar) (Isoptera: Rhinotermitidae) alates. J Insect Behav 19:115–128. https://doi.org/10.1007/s10905-005-9012-1

Sherman A, Dickinson MH (2003) A comparison of visual and haltere-mediated equilibrium reflexes in the fruit fly *Drosophila melanogaster*. J Exp Biol 206:295–302. https://doi.org/10.1242/jeb.00075

Shimozawa T, Kanou M (1984) Varieties of filiform hairs: range fractionation by sensory afferents and cereal interneurons of a cricket. J Comp Physiol A 155:485–493. https://doi.org/10.1007/BF00611913

Simpson P, Woehl R, Usui K (1999) The development and evolution of bristle patterns in Diptera. Development 126:1349–1364. https://doi.org/10.1242/dev.126.7.1349

Sponsler RC, Appel AG (1991) Temperature tolerances of the Formosan and Eastern subterranean termites (Isoptera: Rhinotermitidae). J Therm Biol 16:41–44. https://doi.org/10.1016/0306-4565(91)90050-C

Sugio K (1995) Trunk trail foraging of the fungus-growing termite *Macrotermes carbonarius* (Hagen) in Southeastern Thailand. Tropics 4:211–222. https://doi.org/10.3759/tropics.4.211

Sugio K, Miyaguni Y (2019) Characteristics of dispersal flight of the Formosan subterranean termite, *Coptotermes formosanus* Shiraki (Isoptera: Rhinotermitidae) in Okinawa. Jpn J Appl Entomol Zool 30:63–69. https://doi.org/10.11257/jjeez.30.63

Syaukani (2010) A guide to the nasus termites (Nasutitermitinae, Termitidae) of Kerinci Seblat Nasional Park, Sumatra. Nagao Natural Environment Foundation, Japan

Takematsu Y (1999) The genus *Reticulitermes* (Isoptera: Rhinotermitidae) in Japan, with description of a new species. Entomol Sci 2:231–243

Tarumingkeng RC, Coppel HC, Matsumura F (1976) Morphology and ultrastructure of the antennal chemoreceptors and mechanoreceptors of worker *Coptotermes formosanus* Shiraki. Cell Tissue Res 173:173–178. https://doi.org/10.1007/bf00221373

Tautz J (1977) Reception of medium vibration by thoracal hairs of caterpillars of *Barathra brassicae* L. (Lepidoptera, Noctuidae). J Comp Physiol 118:13–31. https://doi.org/10.1007/BF00612334

Thurm U (1965) An insect mechanoreceptor. I. Fine structure and adequate stimulus. Cold Spring Harb Symp Quant Biol 30:75–82. https://doi.org/10.1101/sqb.1965.030.01.011

Traniello JFA (1982) Recruitment and orientation components in a termite trail pheromone. Naturwissenschaften 69:343–345. https://doi.org/10.1007/BF00480461

Tschinkel WR, Close PG (1973) The trail pheromone of the termite, *Trinervitermes trinervoides*. J Insect Physiol 19:707–721. https://doi.org/10.1016/0022-1910(73)90079-6

Watson JAL, Gay FJ (1991) Isoptera (Termites), vol. 1. In: Naumann ID (ed) Insects of Australia: A textbook for students and research workers 2. Melbourne University Press, Melbourne, p 330–347

Westin J, Langberg JJ, Camhi JM (1977) Responses of giant interneurons of the cockroach *Periplaneta americana* to wind puffs of different directions and velocities. J Comp Physiol 121:307–324. https://doi.org/10.1007/BF00613011

Wikantyoso B, Imai T, Himmi SK, Yusuf S, Hata T, Yoshimura T (2022) Ultrastructure and distribution of sensory receptors on the nonolfactory organs of the soldier caste in subterranean termite (*Coptotermes* spp). Arthropod Struct Dev 70:101201. https://doi.org/10.1016/j.asd.2022.101201

Wikantyoso B, Tseng S-P, Himmi SK, Yusuf S, Yoshimura T (2021) Morphometric analysis of *Coptotermes* spp. soldier caste (Blattodea: Rhinotermitidae) in Indonesia and evidence of *Coptotermes gestroi* extreme head-capsule shapes. Insects 12:477. https://doi.org/10.3390/insects12050477

Wolf H, Wehner Rd (2000) Pinpointing food sources: olfactory and anemotactic orientation in desert ants, *Cataglyphis fortis*. J Exp Biol 203:857–868. https://doi.org/10.1242/jeb.203.5.857

Wolf H, Wehner Rd (2005) Desert ants compensate for navigation uncertainty. J Exp Biol 208:4223–4230. https://doi.org/10.1242/jeb.01905

Woon JS, Boyle MJW, Ewers RM, Chung A, Eggleton P (2019) Termite environmental tolerances are more linked to desiccation than temperature in modified tropical forests. Insectes Soc 66:57–64. https://doi.org/10.1007/s00040-018-0664-1

Yamanaka O, Takeuchi R (2018) UMATracker: an intuitive image-based tracking platform. J Exp Biol 221. https://doi.org/10.1242/jeb.182469

Yanagawa A, Shimizu S, Noma K, Nishikawa M, Kazumasa O, Yokohari F (2009) Classification and distribution of antennal sensilla of the termite *Coptotermes formosanus* (Isoptera: Rhinotermitidae). Sociobiology 54:327–349

Yanagawa A, Yoshimura T, Yanagawa T, Yokohari F (2010) Detection of a humidity difference by antennae in the termite *Coptotermes formosanus* (Isoptera: Rhinotermitidae). Sociobiology 56:255–269

Yanagihara S, Suehiro W, Mitaka Y, Matsuura K (2018) Age-based soldier polyethism: old termite soldiers take more risks than young soldiers. Biol Lett 14:20180025. https://doi.org/10.1098/rsbl.2018.0025