SHORT COMMUNICATION

Christoph Kleineidam · Roman Ernst · Flavio Roces

Wind-induced ventilation of the giant nests of the leaf-cutting ant *Atta vollenweideri*

Abstract To understand the significance of elaborate nest architecture for the control of nest climate, we investigated the mechanisms governing nest ventilation in a large field nest of *Atta vollenweideri*. Surface wind, drawing air from the central tunnels of the nest mound, was observed to be the main driving force for nest ventilation during summer. This mechanism of wind-induced ventilation has so far not been described for social insect colonies. Thermal convection, another possible force driving ventilation, contributed very little. According to their predominant airflow direction, two functionally distinct tunnel groups were identified: outflow tunnels in the upper, central region, and inflow tunnels in the lower, peripheral region of the nest mound. The function of the tunnels was independent of wind direction. Outflow of air through the central tunnels was followed by a delayed inflow through the peripheral tunnels. Leaf-cutting ants design the tunnel openings on the top of the nest with turrets which may reinforce wind-induced nest ventilation.

Introduction

Ant societies have developed a number of behavioural adaptations to cope with seasonal and daily variations of climate parameters. At the beginning of colony life, queens have to select a suitable place to found the nest (Brian 1952). After founding, the workers build and modify the nest in which, to a certain degree, an auto-

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mated control of microclimate is achieved (Horstmann and Schmid 1986; Lüscher 1961).

Leaf-cutting ants (genus *Atta*) build some of the largest and most complex nests (Hölldobler and Wilson 1990). A single colony excavates 15 m³ of soil during colony growth to create a subterranean nest that houses up to five million individuals. The nests contain subterranean chambers situated at depths of up to 6 m that are connected to the nest surface and to each other by numerous tunnels (Jonkman 1980b). Inside the chambers, the ants cultivate a symbiotic fungus on collected leaf material. The fungus serves as the main food source for the developing brood and, to a lesser extent, for the adults (Martin 1987; Quinlan and Cherrett 1979; Weber 1966).

In such huge colonies, both fungus and ants consume large amounts of oxygen. Supply of fresh air as well as removal of CO_2 cannot be sufficiently achieved by diffusion because the chambers are located deep below the nest surface in soil with low porosity and high water content (Withers 1978). Thus, beside the needs for stable temperature and humidity conditions, a non-diffusive gas exchange with the environment is necessary.

In principle, there are two main driving forces for passive nest ventilation: temperature-induced (thermal convection) and wind-induced air movement.

For the giant nests of leaf-cutting ants, thermal convection has been proposed as the ventilation mechanism (Hölldobler and Wilson 1990; Weber 1972). Air movement by thermal convection recquires a temperature gradient between nest and environment which can be achieved either by absorption of sunlight or by production of metabolic heat. However, due to the low heat tolerance of the fungus, colonies of leaf-cutting ants are limited in heating the nest interior. The fungus suffers severe damage at temperatures above 30°C (Powell and Stradling 1986; Quinlan and Cherrett 1978), and temperatures above 30°C have never been measured in nest areas where the fungus is located (Eidmann 1935; Weber 1972). Thus, these findings challenge the hypothesis of thermal convection in nests of leaf-cutting ants.

In an earlier study we have already shown that wind, the second possible force driving nest ventilation, influences nest microclimate (Kleineidam and Roces 2000). Wind may either force air into the nest openings at the upwind side, or draw air from openings of tunnels perpendicular to wind direction, both resulting in the exchange of gases between the environment and the nest. Workers of the leaf-cutting ant *Atta vollenweideri* modify the external architecture of their nest by building complex turrets and closing most of the nest openings in autumn (Daguerre 1945; Jonkman 1980a), probably as a response to changing climatic conditions. To understand the complex co-ordinated nest building activities and to determine the significance of changes in nest architecture, a detailed knowledge of the mechanisms governing nest ventilation is necessary. In the present study we address the question of how air is exchanged in large field nests of *A. vollenweideri* by focusing on nest ventilation during summer. We describe the flow conditions in the tunnels in relation to nest architecture and as a function of wind velocity, and propose a nest ventilation mechanism that can be exploited by the ants.

Materials and methods

Field experiments were done in the National Park Río Pilcomayo, Formosa Province, Argentina (58°W; 25°S) during summer. The annual average temperature in this region is 23°C and the mean precipitation is 1,200 mm (mean relative humidity 79%). Precipitation surpasses evaporation in all months of the year except in August (Pujalte et al. 1995).

The habitat of *A. vollenweideri* is a flat palm savannah with heavy clay soil. Nest density in the research area ranged between 1–2 mature nests per hectare (Jaqueline Röschard, personal communication). A mature nest with a characteristically dome-shaped mound of about 16 m^3 and a circular base (height: 1.0 m, radius: 3.1 m) was investigated as a model system. The 169 initially visible tunnels were homogeneously distributed on the mound surface and the number changed insignificantly during the investigation period of 2 months (December 1997–January 1998). The cross-sectional area of the tunnels was measured at the narrowest part of the first 10 cm away from the openings. Estimating from the size of the mound, the nest was over 4 years old, indicating that the growth phase was completed (Jonkman 1978).

Airflow velocity in the tunnels was measured with specially designed thermal anemometers (see Electronic Supplementary Material). The sensors had a bi-directional characteristic and were placed in the tunnels at a depth of 10 cm.

We recorded airflow velocity in groups of five or six tunnels simultaneously on three different days, always in the afternoon when air current by convection is expected to be largest. Recording duration ranged from 113 to 156 min and the surface wind directions were different on all days of the measurements (N/E; S/W; E/SE). Airflow velocity and direction were measured in a total of 17 tunnels homogeneously distributed over the nest surface. From the flow velocity recordings in the tunnels the ratios of inflow (F_{IN}) and outflow (F_{OUT}) were calculated as $F_{IN}=(T_{IN}/T)\times100\%$ and $F_{OUT}=100\%-F_{IN}$, where T is the total measuring time and T_{IN} is the sum of times of inflow.

The dynamic relationships between air velocity fluctuations in the tunnels provide information about the mechanism by which wind drives nest ventilation (drawing air out and/or forcing air in). We analysed the dynamic relationships between flow transients (changes in air velocity) in different tunnels by cross-correlation. The first derivative dv/dt of the flow velocity was calculated to reduce the interfering influence of the baseline level of airflow in the tunnels. The dv/dt time series of all tunnels were then cross-correlated with each other, showing time lags from 0 to 24 s (corresponding 0 to 12 samples).

For this analysis we used a single recording, during which the wind velocity decreased continuously. Wind direction was N/E and the total recording time was 156 min. Three independent periods of 20 min duration were selected, each representing a category of surface wind velocity. Mean wind velocity in the three categories was 6.6 m s^{-1} (high wind), 2.2 m s^{-1} (low wind) and 0.70 m s^{-1} (breeze).

The dependency of airflow velocity in the tunnels on surface wind velocity was evaluated using Pearson correlations. For the calculation of correlation coefficients, the data of air velocity in the tunnels were transformed with $f(x)=x^{1/3}$ to obtain normally distributed values (Sachs 1988).

Results

Visual inspection of the nest showed that only very few of the tunnel openings, all located at the base of the mound, are used as entrances by foraging workers. We found cleared, well established foraging trails in 18 out of 169 openings at the investigated nest. At all other openings, only single workers loaded with leaves were observed during the foraging periods, suggesting that most of the tunnels serve other purposes. The openings differed in shape, and rim structures often formed a collar around the openings of the tunnels (see Electronic Supplementary Material). Other openings had no conspicuous structures. Following rain, the ants often built impressive turrets with many holes above the openings in the central area of the nest mound (see Electronic Supplementary Material).

Classification of nest tunnels and positions of tunnel openings

Individual tunnels served predominantly either as inflow tunnels (inflow ratio F_{IN} >50%) or as outflow tunnels (F_{IN}<50%), shown by the two-peaked distribution in Fig. 1 (right). The mean inflow ratio was F_{IN}=80.9±4.0% (n=8) for inflow tunnels and F_{IN}=18.7±3.3% (n=9) for outflow tunnels. These two categories were significantly different from each other (Mann-Whitney U test: U=0, P<0.001).

Since the tunnels could be clearly classified based on flow direction, we investigated the distribution pattern of inflow and outflow openings as a function of distance from the mound centre (top of the nest). Figure 1 (left) shows the plot of the radial distance of the tunnel openings from the centre (d_c) versus F_{IN}. A sharp separation between a central outflow region and a peripheral inflow region was found. We calculated the radius d_c of the circle separating the two regions by a non-linear regression using a sigmoidal model as d_c=217±2.3 cm (r=0.95, P<0.001).

The flow direction in a tunnel may depend on wind direction, since wind may force air into the openings at the upwind side. To test this possibility, we classified the tunnels into two groups. One group contained all tunnel
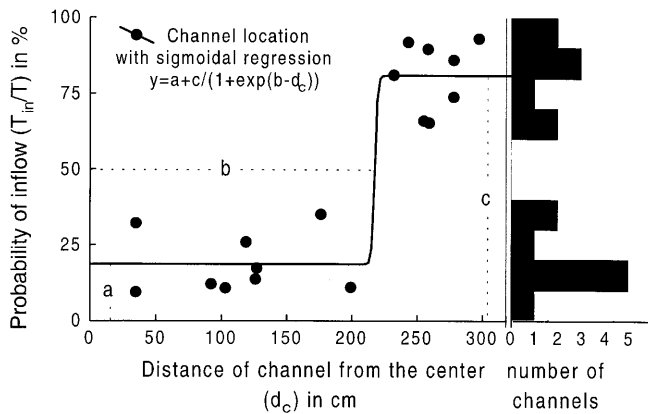
Fig. 1 Inflow probability as a function of distance from the centre of the nest (*left*). A sigmoidal regression describes more than 90% of the variance. The inflection point marks the border between inflow tunnels at the periphery and outflow tunnels in the centre. Two distinct groups representing inflow and outflow tunnels can be discriminated statistically with respect to their inflow probability (*right*)
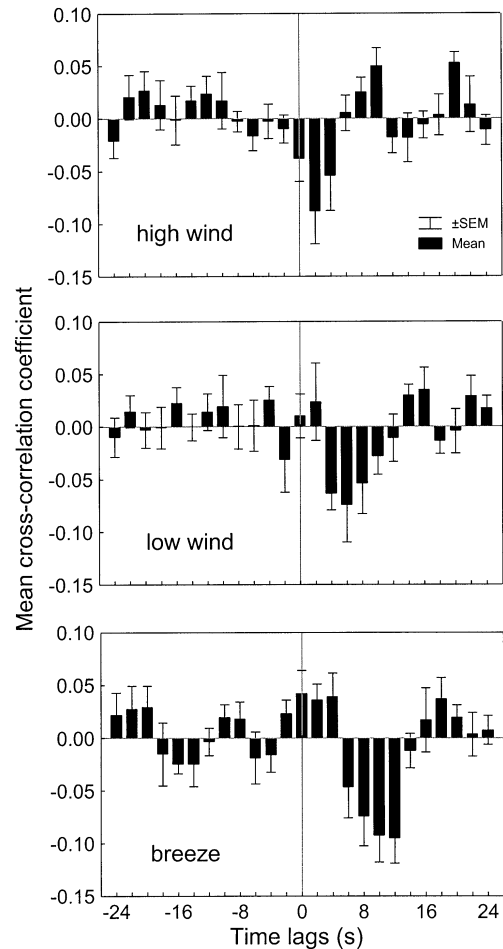

Fig. 2 Phase relation of airflow in inflow tunnels to outflow tunnels for the three different wind categories. For cross-correlation analysis, the first derivatives of the air velocities were used. Each data set of the two outflow tunnels was cross-correlated with each data set of the three inflow tunnels

openings oriented upwind (*n*=8) and the other group contained the openings oriented downwind (*n*=9). However, F_{IN} values of the two groups were not significantly different from each other (mean F_{IN} upwind: 54.53%, downwind: 42.12%, *U*=30, *P*=0.61, Mann-Whitney *U* test), indicating that the function of the tunnels does not depend on wind direction.

Relationship between wind velocity and airflow in the tunnels

In order to assess the dynamic relationship between inflow and outflow, the airflow transients (see Methods) of each of three previously identified inflow tunnels were cross-correlated with each of two outflow tunnels. We found a clear relationship between flow transients in outflow tunnels versus inflow tunnels: First, outflow transients preceded inflow transients. Second, the average delay between outflow and inflow transients depended on the mean air velocity. The average delay was 2 s at high wind velocities and 12 s in breezy conditions, shown in Fig. 2 by the mean cross-correlation coefficients for the three wind categories.

For the analysis of the influence of external wind on airflow in the tunnels, the time series of the inflow recordings were aligned based on average delay, as presented above. With this correction, the correlation coefficients of air velocities between inflow and outflow ranged from *r*=0.50 to *r*=0.58 in all wind categories and were statistically indistinguishable, whereas without correction for the delay they were considerably lower (max. *r*=0.45) and differed between wind categories. Outflow transients were not delayed to external wind transients.

As expected, the wind velocity (v_s) was correlated with the airflow velocities (v_c) in the tunnels. Figure 3 shows the scatter plot of v_c versus v_s and the linear regression for high wind conditions. The correlation between v_s and v_c in the outflow tunnels (*r*=0.60, *P*<0.001) was stronger than the correlation between v_s and v_c in the inflow tunnels (*r*=0.38, *P*<0.001) and the difference between the two correlation coefficients was statistically significant (*t*-test, *P*<0.01). The higher correlation coefficient *r* obtained from the outflow tunnels indicates that outflow depends more strongly than inflow on surface wind.

Estimation of the magnitude of wind-induced nest ventilation

Based on the airflow ratios in different tunnels, we estimated the effectiveness of wind-induced nest ventilation. We calculated the exchanged air volume using the mean flow velocities and the tunnel diameters. Even at low
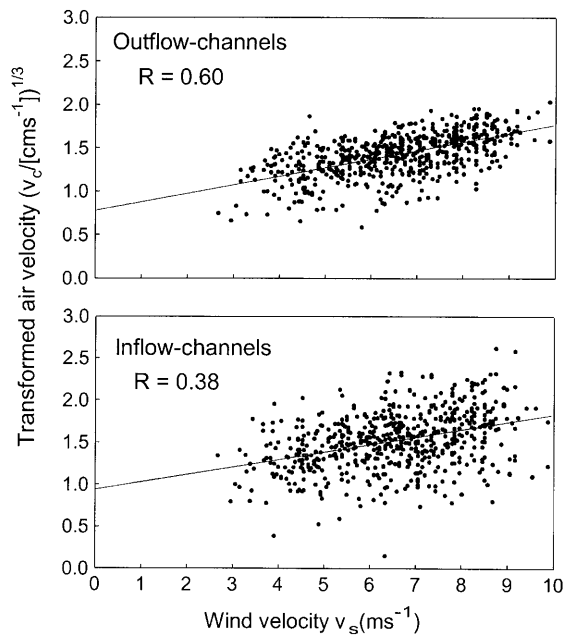
Fig. 3 Correlation between surface wind velocity and air velocity (transformed values) in two outflow tunnels (*upper*, pooled) and three inflow tunnels (*lower*, pooled). The slopes of both regressions are not significantly different. Note the higher correlation of outflow tunnels with surface wind

surface wind velocities, the estimated outflow through a single, most central tunnel was higher than 1.5 $m^3 h^{-1}$.

Using the equation previously obtained for high wind conditions (see Fig. 3), we extrapolated the non-wind-induced airflow velocity in the tunnels. Without wind, an air velocity of only 0.48 cm s^{-1} can be expected in outflow tunnels, whereas air velocity was observed to be 1.25, 2.58 and 4.62 cm s^{-1} at natural wind velocities of 3, 6 and 9 m s^{-1}, respectively. The results show that, without wind, low air volumes flow through the nest, and that wind increased airflow in the tunnels between three- and tenfold.

Discussion

Wilson and Sheehy (cited in Stahel and Geijskes 1939) were the first to study nest ventilation in the leaf-cutting ants *Atta sexdens* and *Atta cephalotes*. Using small puffs of smoke presented at different openings, they observed that some nest openings 'suck in' air. Stahel and Geijskes (1939) tested the hypothesis that thermal convection is the driving force for nest ventilation, but did not find the expected dependency of nest ventilation on daily changes in environmental temperature. Conversely, Jacoby (1939) observed air movements in the central channels of *A. sexdens* nests during the night and at low temperatures, suggesting thermal convection as the driving force in this forest species. Thermal convection still is the ventilation mechanism proposed in the literature for the giant nests of leaf-cutting ants (Hölldobler and Wilson 1990; Weber 1972).

In this study we have provided evidence for a ventilation mechanism so far not described in social insects. We have shown that ventilation of *A. vollenweideri* nests during summer relies mainly on wind drawing air from the nest. Our data were obtained from a single nest. Since soil, habitat and external architecture of the nests were highly homogeneous in the studied area, we are confident that our results on wind-induced ventilation are representative of *A. vollenweideri* in their main habitat. However, other leaf-cutting ant species and also *A. vollenweideri* living in a different habitat may not be able to capitalize on wind-induced ventilation. Wind-induced nest ventilation has also been suggested for the nests of some termite species but the underlying mechanism remains unknown (Weir 1973).

Inflow and outflow did not occur arbitrarily in the tunnels of the nest of *A. vollenweideri*. The tunnels were functionally determined for inflow or outflow to a high degree (81%). The clear separation of inflow openings at the outer (lower) mound region and of outflow openings at the central (upper) region suggests a highly ordered nest architecture below the surface that ensures oxygen supply to the chambers containing fungus and brood.

Some openings at the periphery faced upwind, while the openings of the central tunnels on top of the mound were parallel to the direction of the wind. However, wind was not forced into the inflow openings and inflow of air at the periphery was observed to be independent of wind direction. Our data show that the first reaction to surface wind was outflow of air from the nest. Thus, we conclude that ventilation is driven by surface wind drawing air through the openings of tunnels at the centre of the mound.

Two different physical principles can account for this mechanism. One is a pressure difference resulting from lower pressure at the top than at the periphery of the mound. Lower pressure at the top stems from a higher local wind velocity due to the shape of the mound. The governing equation describing this phenomenon is Bernoulli's law. This principle has been proposed for the ventilation of the burrows of prairie dogs (Vogel et al. 1973). The other principle is air movement based on viscous entrainment. For termites (*Macrotermes subhyalinus*) it has been speculated, based on the mound architecture, that viscous entrainment drives nest ventilation (Darlington et al. 1997). Viscous entrainment (viscous dragging) is caused by shear stress between a fast moving fluid (surface wind) and a stagnant fluid (air in the tunnels). Our data do not allow us to distinguish between these two physical principles, which may even act simultaneously.

Workers are able to alter the shape of channel openings by building turrets which are found only centrally on the nest mound (Daguerre 1945; Jonkman 1980a; personal observations). These structures could enhance nest ventilation, both by viscous entrainment and by Bernoulli's effects. Consequently, the building of turrets on the central openings may be a colony response to unfavourable microclimatic conditions and may result in enhanced

nest ventilation, an effect that has yet to be shown experimentally (see Electronic Supplementary Material).

The unusual ability of leaf-cutting ant workers to measure absolute CO_2 concentrations (Kleineidam and Tautz 1996; Kleineidam et al. 2000) makes CO_2 one likely trigger of regulatory responses (Kleineidam and Roces 2000), and a high sensitivity to air movements, as shown for termites (Howse 1966), could serve to locate outflow channels. We hope the results of our study will stimulate further investigation on these aspects of social organization.

Our study shows that wind-induced nest ventilation, drawing air from central openings, is highly effective during summer. However, in autumn, colonies of *A. vollenweideri* close most (about 90%) of the nest entrances (Jonkman 1980a), so that wind-induced nest ventilation is presumably strongly reduced. Thermal convection may play an important role during cold periods as discussed for ant species living in temperate zones (Kirchner 1998). Whether or not the leaf-cutting ants rely on thermal convection for nest ventilation during winter, and exploit the wind-induced mechanisms only during summer, will be the subject of a further study.

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Wind-induced ventilation of the giant nests of the leaf-cutting ant *Atta vollenweideri*

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Turrets on the nest mound of *Atta vollenweideri*

The huge nest mounds of the leaf-cutting ant *Atta vollenweideri* have a large number of openings which connect via tunnels to the subterranean nest chambers (Fig.1). Workers modify the external architecture of the nest by constructing conspicuous turrets with large lateral holes on the central openings of the nest mound. These openings are not used during foraging activity, but seem to be involved in the control of microclimatic conditions within the nest. The turrets, the height of which may reach more than 20 cm, thus exceeding 20-fold the body length of a worker, are usually reinforced with twigs between the clay crumbs and have several large holes with thickened rims (Fig. 2). Numerous workers are involved in building a turret within one or two days. Afterwards the turrets are not maintained by the colony, and subsequent rains usually wash them away.

Fig. 1 A mature nest of the leaf-cutting ant *Atta vollenweideri* in the palm savannah of Gran Chaco (Argentina). The mound has a diameter of 6 m and a volume of about 16 m^3. 169 openings give access to the nest interior which houses several million colony members and their symbiotic fungus
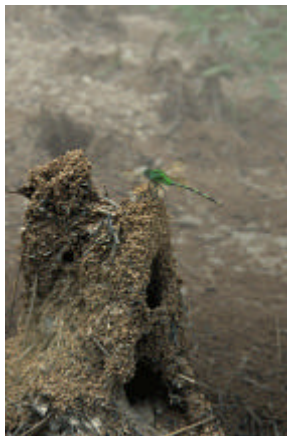Fig 1.gif
(807x567 Pixel, 323 KB)

Fig. 2 Turret built by workers of the leaf-cutting ant *Atta vollenweideri* (height: ~20 cm), showing several lateral holes and reinforcement with twigs. This kind of structure is built only on central nest openings and presumably enhances nest ventilation
Fig. 2.pdf
(PDF 128 KB)

We have demonstrated that wind drags air from the central openings and thus is the driving force for nest ventilation. Therefore, these openings are expected to play a dominant role in nest ventilation. Our results suggest that the purpose of turret building is to elevate the tunnel openings, thus exposing them to higher wind velocities. Although the increase in height of an opening above ground by a turret is small compared to the total elevation of the mound, its impact on nest ventilation may still be high because of the steep gradient of wind velocity close to the surface (Geiger 1965).

Small turrets have been found upon nest entrances in few other leaf-cutting ant species. In these cases, they do not necessarily promote nest ventilation. Nests of *Acromyrmex landolti* have a single small turret which has been shown to protect the colony against flooding (Navarro and Jaffé 1985). Even the small colonies of *Trachmyrmex turrifex*, consisting of only two or three dozen individuals build a single cylindrical turret with a height of 1 to 4 cm (Wheeler 1907), the function of which is unknown.

In contrary, mature colonies of *Atta vollenweideri* construct turrets only on the central openings. Openings near the ground level lack such structures, a phenomenon contradicting the idea that turrets are constructed to provide protection against flooding. Young colonies of this species, which are particularly endangered during flooding, protect their inhabitants not by building turrets, but by tightly closing the nest entrances at heavy rain conditions (Kleineidam and Roces 2000).

Since the occurrence of conspicuous turrets has only been reported for colonies of the grassland-inhabiting species *Atta vollenweideri* and not for the forest species *A. sexdens* or *A. cephalotes*, it is tempting to speculate that grassland-inhabiting species may capitalize on wind-induced ventilation because they inhabit open habitats, while forest species may rely on thermal convection or on other unknown mechanisms for the ventilation of their nests.

Anemometers

The bidirectional characteristic of the anemometers was achieved by the sensor design shown in Fig. 3. Two thermistors of the same type (Heraeus 1Pt100) are mounted on opposing sides of a printed chip board (PCB). The thermistors are heated by the current drawn from the power source. Airflow perpendicular to the PCB surface causes the thermistor facing the air stream to be cooled down relative to the thermistor on the opposite side of the PCB. The resulting difference in voltage drop is amplified and adapted to the input signal range of a data logger by the signal conditioning circuit shown in Fig. 4. The thermistors TH1, TH2 together with the resistors R1, R2, R3, R4 form a Wheatstone bridge. The bridge voltage is sensed by a differential amplifier which is formed by the three operational amplifiers (OP) A1, A2 and A3. Output signal offset can be adjusted by P1. OP A4 provides a low pass filter and gain control (P2). The sign of the output signal corresponds to the direction of the flow across the sensor. The sensor shows highest sensitivity when it is mounted perpendicular to the airflow direction, as indicated by the arrows in Fig. 3.
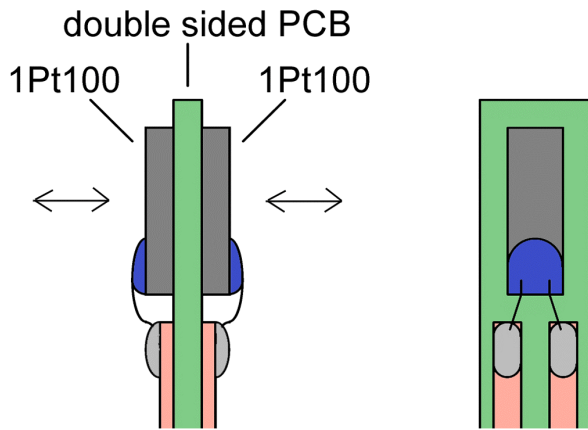
Fig. 3 Airflow sensor consisting of two thermistors (Pt100) mounted on a 5 mm wide, printed chip board (PCB). Lateral view *left* and frontal view *right*
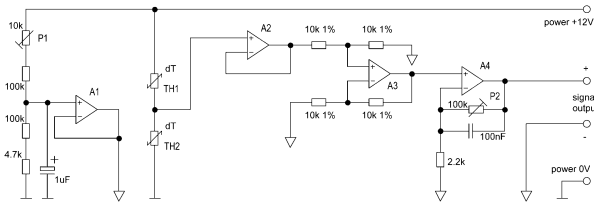

Fig. 4 Sensor signal conditioning circuit. A1-A4: LM324 (or eq. single supply voltage type, always use quad. type OpAmp). TH1, TH2: 2* Heraeus 1 Pt100. Design by R. Ernst.
Fig. 4.pdf
(PDF 10 KB)

The relation between airflow velocity and bridge voltage is demonstrated by the calibration curve of one of the sensors (Fig. 5A). The usable measuring range of about ±15 cms^{-1} is limited by saturation effects. A logistic function describes the relation between airflow speed and bridge voltage very well. Fitting a function of the form u/[mV]=a+c/(1+exp(b*s/[cm/s])) to the calibration curves always yielded correlation coefficients of r > 0.999. For our measurements, the individual fit functions of the sensors were used to compute airflow speed values from sensor signal voltages. The response characteristic of the sensors to flow transients is shown in Fig. 5B. Fitting exponential functions to the response curves yielded time constants of typically 2.4 s, showing that the sensors have a relatively high temporal resolution and are able to capture fast airflow fluctuations.
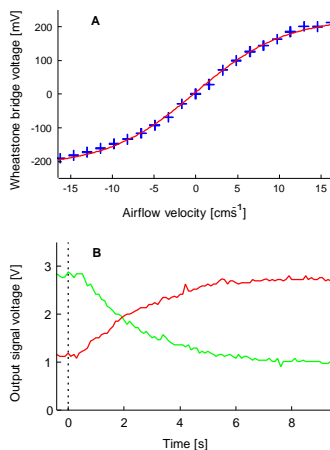

Fig 5 A Sensor calibration curve. Logistic fit: y=-213.2+438.7/(1+exp(-0.1885*x)), R=0.9993. **B** On/off response curves. The *red curve* shows the response to an airflow velocitiy shift from 0 cms^{-1} to 5 cms^{-1} and the *green curve* represents the response to a shift from 5 cms^{-1} to 0 cms^{-1}
Fig 5.pdf
(PDF 15 KB)

The sensors were mounted in the centre of small tubes of 16 mm diameter and 55 mm length. The tubes had coarse wire screens on both openings to prevent ants from entering. The anemometer tubes were placed in the tunnels at a depth of 10 cm and were fixed with a wire. All anemometers were oriented in such a way that a negative sign of the sensor output voltage indicated outflow and a positive sign inflow of air into the nest mound. In this position the zero value of flow was determined by temporarily covering the opening of the tunnel. The diameters of the tunnels selected for measurements were at least 3 cm. Surface wind was measured at 1.8 m above ground beside the nest with a conventional unidirectional airflow sensor (Siemens Matsushita Typ C1011 A80).

All sensor signals were recorded at a sampling rate of 30 min^{-1} with a data logger based on a programmable micro controller module (Wilke Technology, BasicTiger AXN-1/1 V1.06n, resolution of analogue inputs: 10 bit). The individual gain of the analogue inputs was adjusted such that the measuring range was $\pm$ 10.24 cms^{-1} at a resolution of 0.02 cms^{-1}. The influence of surface wind on air velocity in the tunnels is illustrated in Fig. 6. With increasing wind velocity (lower trace), air velocity in both inflow and outflow tunnels increased (upper traces). Surface wind was gusty on all days of the experiments, and airflow in the tunnels showed strong fluctuations. These conditions allowed us to investigate the dynamic of nest ventilation as shown in Fig. 2 of our short communication article.
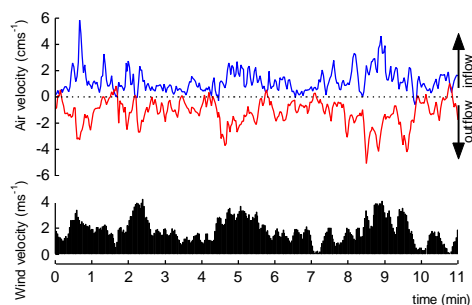

Fig. 6 Example for simultaneous recordings of surface wind velocity 1.8 m above ground (*lower trace, black*) and air velocity in two different tunnels (*middle, red and upper, blue trace*) during a period of 16 min
Fig 6.pdf
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