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RESEARCH ARTICLE

Ventilation of multi-entranced rodent burrows by boundary layer eddies

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ABSTRACT

Rodent burrows are often assumed to be environments wherein the air has a high concentration of CO_2. Although high burrow $[CO_2]$ has been recorded, many studies report burrow $[CO_2]$ that differs only slightly from atmospheric concentrations. Here, we advocate that one of the reasons for these differences is the penetration into burrows of air gusts (eddies), which originate in the turbulent boundary layer and prevent build-up of CO_2. We have characterized the means by which burrows of Sundevall's jird, which are representative of the burrows of many rodent species with more than one entrance, are ventilated. Our results demonstrate that, even at low wind speeds, the random penetration of eddies into a burrow through its openings is sufficient to keep the burrow $[CO_2]$ low enough to be physiologically inconsequential, even in its deep and remote parts.

KEY WORDS: Sundevall's jird, CO_2 concentration, Burrow ventilation, Turbulent boundary layer, Eddy

INTRODUCTION

An implicit assumption that underlies many physiological studies related to burrowing rodents is that, relative to atmospheric values for these gases, the fractional concentration of CO_2 (F_{CO_2}) near the animals within the burrow is high and, concomitantly, the fractional concentration of oxygen (F_{O_2}) is low (e.g. Burda et al., 2007; and references therein; Maclean, 1981; Studier and Baca, 1968; Studier and Procter, 1971; Wilson and Kilgore, 1978; Withers, 1978). This assumption is founded on two premises. The first is that the metabolic demands of active small mammals are high (review by Lovegrove, 2003). The second is that the flux of O_2 and CO_2 between the burrow and the atmosphere is limited mainly by diffusion through still air along the burrow lumen and through the surrounding soil (Wilson and Kilgore, 1978; Maclean, 1981).

Studies of the actual respiratory gas concentrations within mammalian burrows are few. A review of these studies shows that the presumption of high F_{CO_2} and low F_{O_2} in the burrow is not always supported [see table 3 in Roper et al. (Roper et al., 2001)]. For example, F_{CO_2} and F_{O_2} in occupied burrows, both artificial burrows occupied by Merriam's kangaroo rat *Dipodomys merriami*

(e.g. Soholt, 1974) and natural burrows occupied by the African mole rats *Georhychus capensis* and *Cryptomys damarensis* (e.g. Roper et al., 2001), differ little from atmospheric values. In other instances, the assumption is upheld; namely, high maximum F_{CO_2} and/or low F_{O_2} have been reported, for example, in burrows of Middle East blind mole rats *Spalax ehrenbergi* (Arieli, 1979) and for golden hamsters *Mesocricetus auratus* (Kuhnen, 1986). Context is important to these results. Blind mole rats build their burrows in heavy, sometimes wet, soils and block the burrow entrances. The golden hamsters, for their part, were torpid and occupied burrows dug under artificial conditions in sand boxes with gas-impervious sides. To our knowledge, there are no studies that have monitored respiratory gas concentrations directly near the burrow's occupants.

Nevertheless, physiological studies of burrowing rodents have often been conducted in an assumed context of the burrow's high F_{CO_2} (Ar, 1987; Ar et al., 1977; Bar-Ilan et al., 1985; Baudinette, 1974; Boggs et al., 1984). As indicated above, this assumption is not always supportable, which colors how we think about adaptation to subterranean life. On the one hand, in mammals, persistent breathing of air containing high F_{CO_2} causes chronic respiratory acidosis (e.g. Douglas et al., 1979; Schaefer, 1982). Therefore, burrow dwellers should be physiologically adapted to tolerate high F_{CO_2} in the air they breathe (e.g. Ar, 1987; Arieli and Ar, 1979; Arieli et al., 1977; Marder and Bar-Ilan, 1975). On the other hand, no special physiological adaptations should be expected if air in burrow environments does not differ appreciably in content from atmospheric air. It is therefore of interest to understand how gas exchange between the burrow environment and atmosphere actually works.

Various processes may contribute to the ventilation of burrows. These include diffusion of gases in air along the burrow and through the walls of the burrow lined by the porous soil matrix (Wilson and Kilgore, 1978); piston-like movements induced by the animal moving along burrow tunnels (e.g. Ar and Piontkewitz, 1992; Ar et al., 2004); passive convection caused by temperature and humidity gradients between the burrow and the environment (e.g. Kleineidam et al., 2001; Turner, 2001); and forced convection driven by wind at the surface (Olszewski and Skoczen, 1965; Roper and Moore, 2003; Vogel et al., 1973; White et al., 1978).

To our knowledge, the relative contribution of each of the above mechanisms to powering burrow gas exchange has not been quantified. We therefore undertook to study gas exchange mechanisms for artificial burrows of Sundevall's jird (*Meriones crassus* Sundevall 1842). We chose this species of gerbillid rodent because it is very widespread, ranging from Morocco to Pakistan and inhabits a variety of arid environments (Krasnov et al., 1996), and because the physical characteristics of its burrows, i.e. depth, length of tunnels, number of openings, are similar to those of many other rodent burrows in temperate and in hot desert regions (Goyal and Ghosh, 1993; Walsberg, 2000; Shenbrot et al., 2002).

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Here, we report on the contribution of an undocumented mechanism of wind-driven gas exchange. This mechanism is the result of the interaction between wind in the turbulent atmospheric boundary layer that is in contact with the soil surface and the burrow's entrances. The proposed mechanism differs from wind-induced burrow ventilation as reported by Vogel et al. (Vogel et al., 1973), which is commonly thought to be unidirectional flow through the burrow induced by Venturi effects, as exemplified by the induced-flow mechanism that operates in the multi-entranced burrow systems of the black-tailed prairie dog, *Cynomys ludovicianus*. The induced-flow mechanism requires multiple burrow entrances at different heights to span a boundary layer velocity profile. However, many burrows do not meet the architectural requirements for induced flow. In addition, Vogel and colleagues' mechanism does not account for the instantaneous fluctuation of wind velocity in turbulent regimes, which are ubiquitous in nature.

The mechanism that we propose involves the penetration of turbulent eddies into the burrow environment, which promotes gas exchange by mixing burrow and atmospheric air. Turbulent flow within the boundary layer comprises eddies whose average size decreases as the ground surface is approached (Stull, 1988). These eddies can detach from the main stream and move vertically towards the ground surface (Paw U et al., 1995). This is the main mechanism responsible for the transport of sensible heat and other scalars in the internal boundary layer. We posit that some of these down-welling eddies could penetrate into a burrow and refresh burrow air by mixing atmospheric air with it. The result would be a decrease in $[CO_2]$ in the burrow and an increase of $[O_2]$. The objective of the present study was to test whether our hypothesis regarding the role of intermittent air gusts in the ventilation of burrows is supportable.

RESULTS

Wind-induced convection by the irregular penetration of eddies

In order to validate the technique for the detection of eddy penetration, we built an artificial burrow to the design described in Fig. 1A, but made of PVC tubing (Fig. 1C). We positioned 12 type-T thermocouples along its center and two thermocouples outside, above the tunnel's entrances. We buried the burrow next to the others (see Materials and methods), with the same compass orientation of the entrances. When the entrances of the PVC burrow were plugged, the temperature measured by the thermocouples inside remained constant, but while they were open the temperature fluctuated considerably (Fig. 2).

We examined the potential effects of eddy penetration on the ventilation regime of the artificial burrow depicted in Fig. 1A. We found that eddies penetrated the burrow from either one of the two entrances (Fig. 3), but never simultaneously. The duration of each eddy and the intervals between eddies varied. Some eddies penetrated partially into the burrow while others moved through it and exited via the second opening. The reason for this phenomenon was probably the different speeds of the eddies, which were not measured. The number of penetrations recorded was calculated as the total number of peak temperatures recorded irrespective of the opening through which the eddy entered the burrow. The frequency of events increased with wind speed up to $4.5 \ \mathrm{m \ s^{-1}}$ (Fig. 4A–C); above that speed, penetration decreased over the range of speeds measured. More eddies reached the northwestern side of the burrow than the southeastern side. This was probably due to the fact that in the geographic region where measurements were made, northwest is the dominant wind
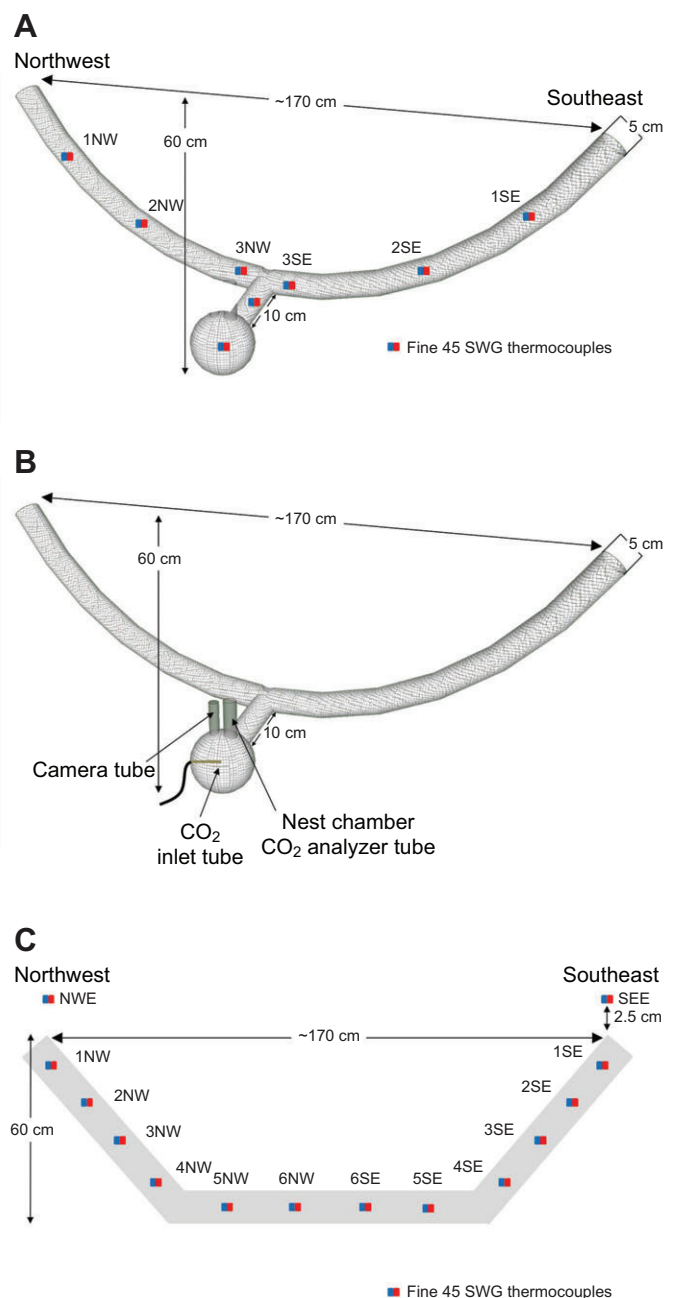

Fig. 1. Schematic diagrams of artificial Sundevall's jird burrows designed according to the configuration of a natural burrow. (A) Shape and dimensions of a burrow built of fine-wire mesh, with the compass directions of the entrances and thermocouple placement. Such a burrow could also be covered in plastic wrap to prevent gas exchange with the soil in which it was buried. (B) Same as A, but showing positions of CO_2 inlet tube, infrared gas analyzer and camera in the brood chamber. (C) Burrow built of PVC, used only to validate eddy penetration. The tube diameter was 4.4 cm; the model's other dimensions were similar to those of the mesh models. NWE and SEE – positions of thermocouples above NW and SE entrances. The figures are not drawn to scale. See Materials and methods for additional details. SWG, standard wire gauge.

direction throughout the year, and, despite the alternating nature of penetrations, more eddies entered from that direction. Considerably fewer eddies reached the corridor leading from the main tunnel to the nest chamber and no eddies were detected inside the nest chamber (Fig. 4D).
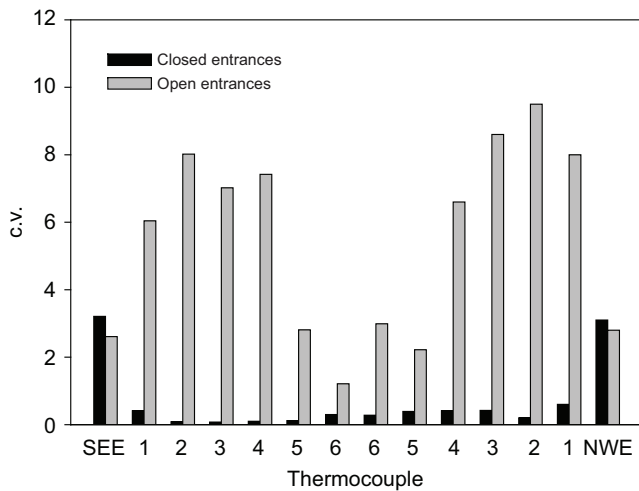
Fig. 2. The coefficient of variation for temperature measurements by an array of thermocouples positioned along an artificial Sundevall's jird burrow. The burrow was made of PVC tubes (diameter d=4.4 cm; see Fig. 1C) and buried in the soil. Thermocouple positions inside the PVC tunnel are numbered as in Fig. 1C. The SE entrance (SEE) and NW entrance (NWE) thermocouples were positioned outside and 2.5 cm above the southeastern and the northwestern entrances, respectively. Measurements were made when tunnel entrances were closed and when they were open. The coefficient of variation (c.v.=s.d./mean) is a dimensionless ratio.

Parallel mechanisms for burrow ventilation

Half-hourly averages of wind speed and nest chamber [CO_2], measured in permeable and impermeable burrows (Fig. 1C) under three conditions are presented in Fig. 5. The data were analyzed using a non-parametric measure when they were not normally distributed and/or homoscedastic. When convection was the only possible mechanism for ventilation of the nest chamber (in the impermeable burrow with entrances open, Fig. 5A), F_{CO_2} decreased

exponentially with wind speed (Spearman rank order correlation coefficient −0.802, $P<0.001$), so that, at low wind speed (>2 m s^{-1}), small changes resulted in large decreases in chamber [CO_2]. Wind speeds >3 m s^{-1} did not affect [CO_2] in the chamber. The maximum [CO_2] measured in the impermeable burrow was 25,660 ppm, ~65 times the atmospheric [CO_2] of ~390 ppm (NOAA, 2012). This value was measured when wind speed was ~1 m s^{-1} blowing from ~50° NE. When diffusion in still air through the burrow and into the soil was the only possible mechanism for ventilation of the nest chamber (in the permeable burrow with entrances plugged, Fig. 5B), as predicted, chamber F_{CO_2} was independent of wind speed. Nest chamber [CO_2] ranged between 8600 and 10,400 ppm. When both mechanisms were active (in the permeable burrow with open entrances, Fig. 5C), [CO_2] decreased linearly with wind speed from 8600 ppm at 1 m s^{-1} to 2800 ppm at 3.9 m s^{-1} (Spearman rank order correlation coefficient −0.718, $P<0.001$). When CO_2 was not injected into the nest chamber, thereby simulating an unoccupied burrow, atmospheric [CO_2] (NOAA, 2012) was 2.91 s.d. less than the mean [CO_2] in the nest chamber (606.07 ppm) (Fig. 6).

The two data sets, one for where convection through the openings was the only mechanism for ventilation and that for where both convection and diffusion took place at the same time, were collected on different days, during which the above-ground environmental characteristics were similar (wind speed, Spearman rank order correlation ρ=0.816, $P<0.001$, Fig. 7; and wind direction, angular correlation coefficient=−0.708, $P=0.014$, Fig. 8). It is therefore possible to compare the two data sets.

DISCUSSION

Our results clearly indicate that eddy penetration can be a significant mechanism of gas exchange in two-entranced artificial burrows resembling the natural burrow system of the Sundevall's jird (*M. crassus*). Eddies penetrated to different depths along the main tunnel of the burrow. Some eddies were sufficiently energetic to sweep all the way through the burrow. While the number of eddies that
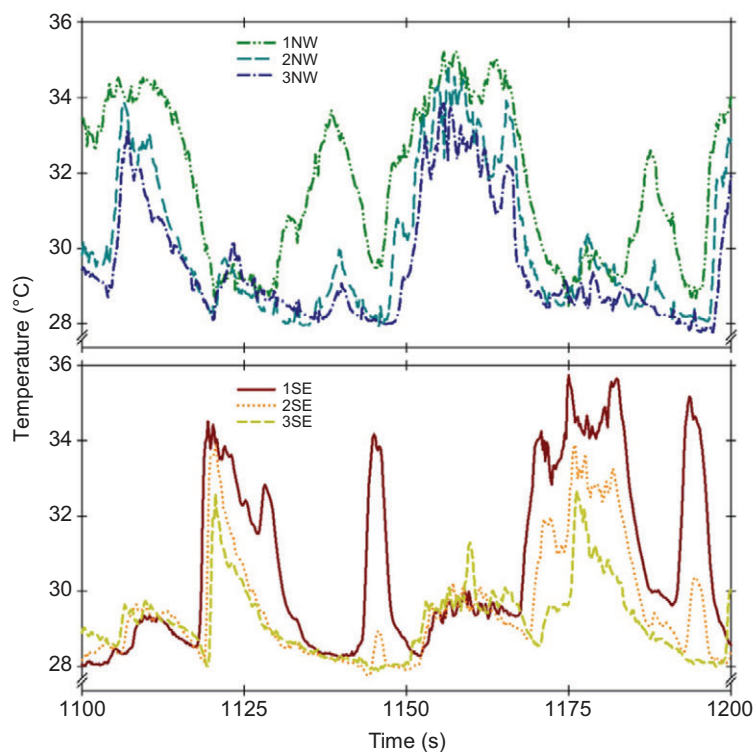

Fig. 3. Temperatures at six locations along the main tunnel of an impermeable artificial Sundevall's jird burrow, as a function of time. The figure illustrates the irregular nature of ventilation by eddies; eddies move atmospheric air that is warmer than burrow air into the burrow, causing a sequential, momentary rise in temperature along the main tunnel. The penetration of eddies alternates between the two entrances. For the same time sequence, the top panel shows the penetration of an eddy from the northwestern entrance, starting at location 1NW, and advancing deeper along the tunnel to locations 2NW and 3NW; the bottom panel shows the penetration of an eddy from the southeastern entrance starting at location 1SE and advancing deeper along the tunnel to locations 2SE and 3SE.
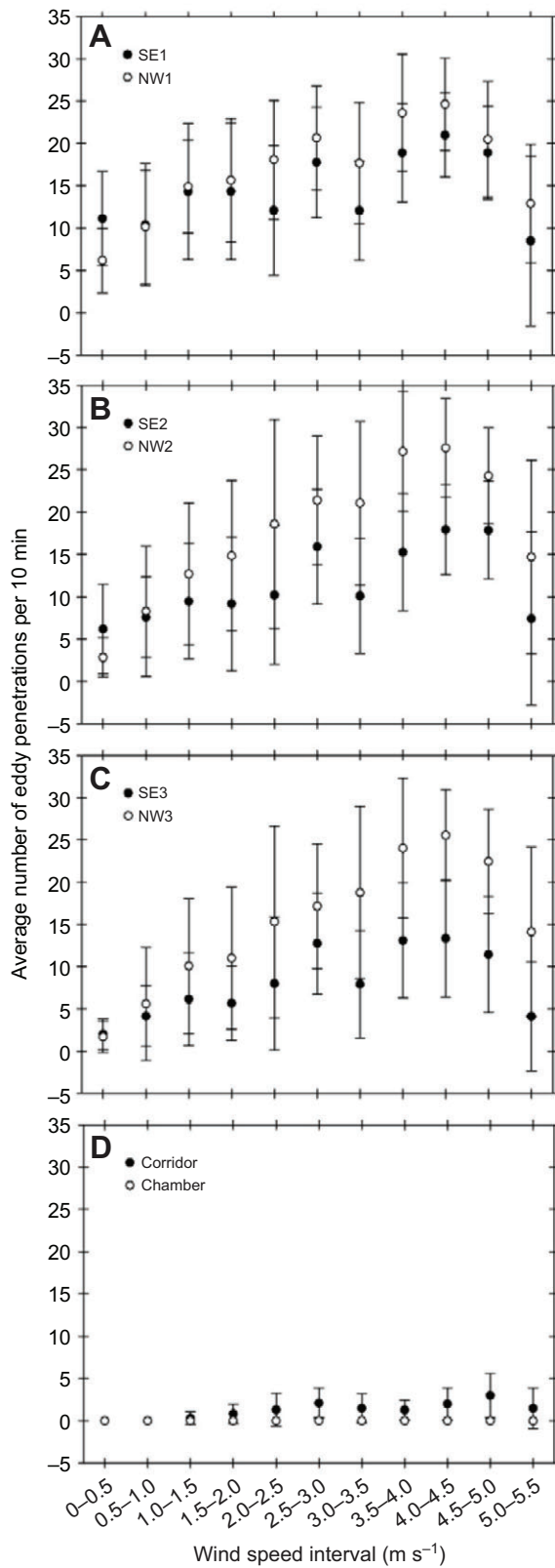
Fig. 4. The average number of ventilation events per 10 min at locations along the main tunnel, corridor and nest chamber of an artificial Sundevall's jird burrow as a function of wind speed interval between 09:00 h and 17:00 h. The average number of ventilation events at (A) 33 cm, (B) 66 cm and (C) 99 cm from the southeastern and northwestern entrances, and (D) in the middle of the corridor and in the nest chamber. Values are means ± s.d.
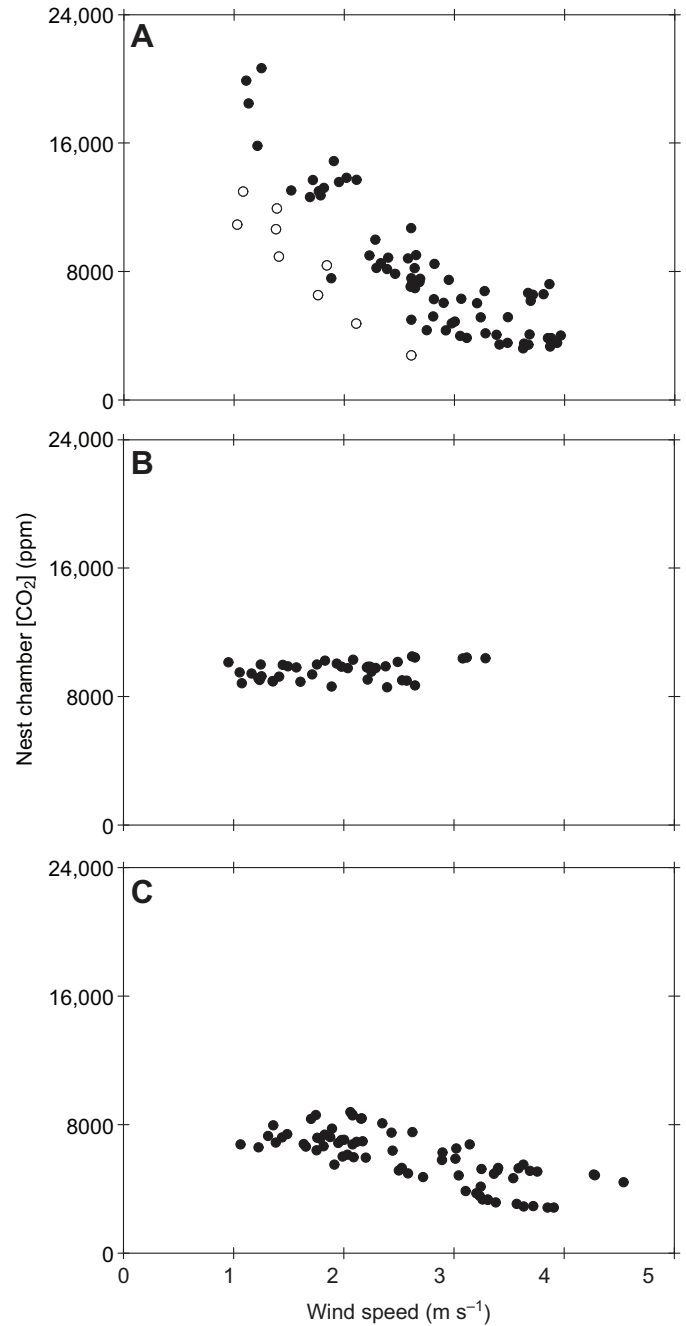

Fig. 5. Half-hour averages of [CO_2] inside the nest chamber of artificial Sundevall's jird burrows as a function of wind speed during continuous injection of CO_2 into the nest chamber. A decrease in [CO_2] is a measure of the ventilation of the nest chamber as a result of the following mechanisms: (A) convection through the openings of the burrow, (B) gas diffusion in still air through the burrow and the soil, and (C) convection and diffusion taking place at the same time. The open circles in A are data points for 1 day of measurements (28 May 2012) and are consistently lower than the other data points measured in the same set up, but the pattern is the same. When convection was the only mechanism for ventilation (A), external wind speed had a substantial effect on [CO_2] in the nest chamber; CO_2 concentration was 5–6 times higher in the nest chamber at low wind speed (<2 m s^{-1}) than it was at high wind speed (>3 m s^{-1}). When gas diffusion was the only mechanism for ventilation (B), external wind speed did not affect chamber [CO_2]. When both mechanisms for ventilation were simultaneously enabled (C), [CO_2] at low wind speed was considerably lower than when ventilation occurred by convection alone. At wind speeds >3 m s^{-1}, the [CO_2] in both cases was similarly low.
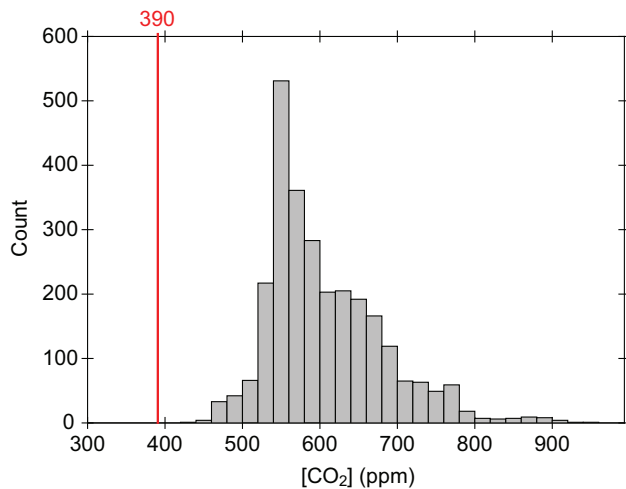
Fig. 6. Control measurements of [CO_2] inside the nest chamber of an artificial Sundevall's jird burrow. CO_2 was sampled every 1 min on five non-consecutive days between 08:00 h and 16:00 h. The red line is atmospheric [CO_2] (NOAA, 2012), 2.909 s.d. lower than the mean [CO_2] in the nest chamber (606.07 ppm).

penetrated the main tunnel of the burrow increased with wind speed for winds of up to 4.0–4.5 m s^{-1} (Fig. 4A–C), at higher wind speeds the number of eddy penetrations decreased.

Few eddies were detected inside the corridor leading from the main tunnel into the nest chamber, and none at all inside the nest chamber (Fig. 4D); thus, the nest chamber seems not to be directly ventilated by eddy penetration. However, our findings indicate that the accumulation of CO_2 in chambers that are deep, dead-ended and distant from the entrances is prevented because each eddy that brings fresh atmospheric air into the burrow results in steep gradients in CO_2 concentration between the nest chamber and main
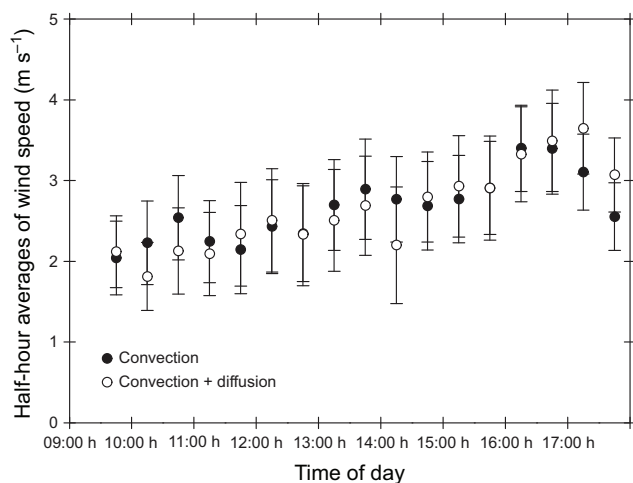

Fig. 7. Ambient wind speed and direction, measured and averaged every half-hour, on the 14 days in which CO_2 was continuously injected into the nest chambers of artificial Sundevall's jird burrows to simulate the presence of a dam and four pups. Decreasing [CO_2] (washout) was used as a measure of nest chamber ventilation. Means of 7 days of measurement in which ventilation resulted from convection through the openings of the burrow or from a combination of wind-driven convection and diffusion through still air through the burrow and into the soil are shown. Values are means ± s.d. There is a strong correlation between the wind speed on the different days of measurement (Spearman rank order correlation, ρ=0.816, *P*<0.00).

tunnel that enhance the diffusion of CO_2 from the nest chamber into the main tunnel.

Vogel et al. (Vogel et al., 1973) described a mechanism of ventilation in black-tailed prairie dog burrows based on unidirectional flow caused by pressure differences between two burrow entrances protruding to different heights into the surface boundary layer. Ever since, the concept of unidirectional flow through burrows has been widely accepted, and the fact that flow in the boundary layer is turbulent and transient was usually not considered relevant to the flow within the burrow. These complex flows can complicate considerably the exchanges between the burrow air and the atmosphere. In badger setts, Roper and Moore (Roper and Moore, 2003) observed that wind-induced air movements penetrated differentially to at least several meters and these were strongly and positively correlated with ambient wind speed. They suggested that if air moves into the entrances of badger setts, it must do so by direct penetration of wind and not by induced flow of air into the burrow as in prairie dog burrows (Vogel et al., 1973). However, they did not explain what mechanism underlies this phenomenon.

We are aware of only one report in the literature of episodic wind-induced turnover of air: in the single-opening, horizontal burrows of the European bee-eater (White et al., 1978). Despite this paper being cited at least 50 times since its publication, the only paper that cited it in the context of burrow ventilation is that of Ar and Piontkewitz (Ar and Piontkewitz,1992), but they did not examine the importance and relevance of the eddy penetration mechanism relative to their own results. While White et al. (White et al., 1978) showed how turbulent flow effects ventilation of single-ended burrows, we found that ventilation by the intermittent penetration of eddies applies to burrows with more than one entrance.

The two distinct paths for CO_2 to exit burrows are through the burrow's openings and via the soil surrounding the burrow. To test our hypothesis that burrow ventilation occurs by several mechanisms working in parallel, the predominant one depending on ambient conditions, particularly wind speed, we used changes in nest chamber [CO_2] as CO_2 is fed into the burrow at a constant rate as an indication of the degree of burrow ventilation.

When convection was the only mechanism for ventilation (Fig. 5A), variation of external wind speed had a substantial effect on [CO_2] in the nest chamber; [CO_2] was 5–6 times higher in the nest chamber at low wind speed (<2 m s^{-1}) than it was at high wind speed (>3 m s^{-1}). The open circles in Fig. 5A are data for 1 day of measurement (28 May 2012); all are consistently lower than the other data points measured in the same experimental set up on other days, but still follow the same pattern of decrease. We have no satisfactory explanation for the low values of this set of points. As expected, when diffusion was the only mechanism for ventilation (Fig. 5B), external wind speed did not affect chamber [CO_2]. When both mechanisms for ventilation were simultaneously enabled (Fig. 5C), as we assume is the case in natural burrows, [CO_2] at low wind speed was considerably lower than when ventilation occurred by convection alone. At wind speeds >3 m s^{-1}, the [CO_2] in both cases was similarly low.

We conclude that, by day, burrow ventilation is affected by at least two mechanisms, their relative importance being determined primarily by wind speed in the boundary layer. At wind speeds above 2 m s^{-1}, burrows are likely to be well ventilated and, as long as the burrow's openings are not plugged, accumulation of CO_2 should not present a major problem for the resident animal, even in cases when soil porosity is low. At very low wind speeds, which occur at night and in the early morning hours, for example, thermal
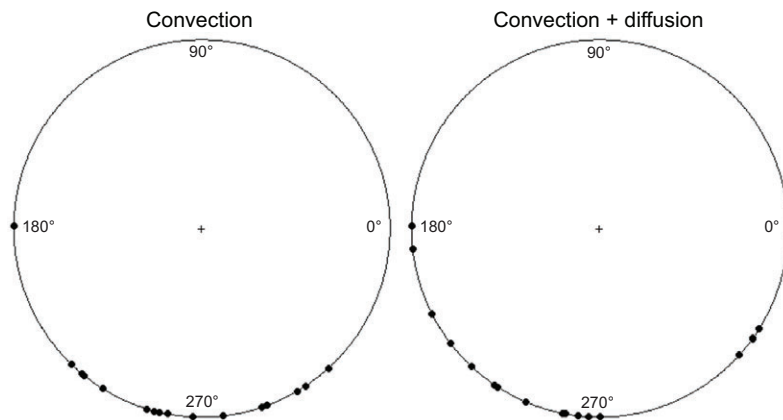
Fig. 8. Ambient wind speed and direction measured on the 14 days in which CO_2 was continuously injected into the nest chambers of artificial Sundevall's jird burrows to simulate the presence of a dam and four pups. Decreasing [CO_2] (washout) was used as measure of the ventilation of the nest chamber as a result of either wind-driven convection through the openings of the burrow or simultaneous convection and diffusion in still air through the burrow and into the soil. The wind direction on the different days of measurement is correlated (angular correlation coefficient=–0.708, P=0.014). See Materials and methods for details.

gradients could drive convection through the burrow (Ganot et al., 2012). However, Ganot and colleagues used only straight, augur-dug holes with single openings in their study, which are not characteristic of jird burrow architecture, which in itself may affect the onset and intensity of thermal convection. Our own 24 h measurements in nest chambers suggest that thermal convection does not strongly influence [CO_2] (see below).

The effect of soil porosity was considered in some studies (e.g. Arieli, 1979; Roper et al., 2001; Shams et al., 2005) and introduced into simplified models of gas exchange by Withers (Withers, 1978) and Wilson and Kilgore (Wilson and Kilgore, 1978). Wilson and Kilgore developed a mathematical model in which they considered gas diffusion to be the sole mechanism for exchange and showed that in this case soil porosity is the most important variable affecting the rate of respiratory gas transfer in (O$_2$) and out (CO_2) of the burrow, more important than the depth of the burrow or the size of the animal. The permeability of the soil to gas diffusion may change because of the presence of water that completely or partially clogs the pores that permeate the soil (Arieli, 1979; Hillel, 1998). Further, a reduction in pore diameter and pore size distribution in the upper soil layer may be caused by the impact of raindrops, which create an abiotic crust (Carmi and Berliner, 2008), and/or by its colonization by bacteria and fungi (reviewed by Belnap et al., 2006), which form a biological crust.

In separate experiments, Brickner-Braun (Brickner-Braun, 2014) let four Sundevall's jird dams give birth to, suckle and raise their pups in full-scale artificial burrows; three burrows were gas-permeable (control) and one was impermeable. After the females gave birth, Brickner-Braun measured [CO_2] and temperature at several locations along the burrow as well as wind speed at the surface, and above-ground air temperature (T_a), recording 10 min averages 24 h day^{-1} for the entire 3 week lactation period. F_{CO_2} in the permeable burrows never exceeded 0.025; a concentration not considered physiologically challenging for burrow-dwelling rodents. In the impermeable burrow, where gas exchange with the atmosphere could only occur via the entrances, F_{CO_2} in the nest chamber sometimes rose above 0.07, probably because the sensor was in the immediate vicinity of the dam and pups. Despite these periods of high F_{CO_2}, the dam and pups lived 'normally' for the entire 3 weeks of measurement, and were all in good health and weighed the same as control pups at the end of the experiment. The patterns of T_a during this experiment were similar on all measurement days. T_a peaked in the early afternoon and reached a minimum at daybreak. Inside the burrows, the temperatures became more constant as distance from the entrances increased. This is a well-documented phenomenon (e.g. Nikol'skii and Khutorskoi, 2001; Shenbrot et al., 2002). The temperature inside the nest chambers remained steady throughout the 3 weeks of measurement, with small fluctuations during any single day. Unlike unoccupied *M. crassus* burrows (Shenbrot et al., 2002), the temperature inside the nest chambers reported by Brickner-Braun (Brickner-Braun, 2014) was higher than T_a throughout the day, suggesting that the presence of the female and litter caused a substantial rise in temperature in their immediate environment because of their metabolic heat production. The steep temperature gradient between an occupied chamber and the ambient air could potentially promote and enhance ventilation by thermal convection (Kleineidam et al., 2001; Turner, 2001; Ganot et al., 2012). However, it appears that this is not an important mechanism for ventilation in occupied jird burrows, as maximum [CO_2] values were reached at night before sunrise, in spite of the large differences between T_a and burrow temperature.

Although it is often stated that burrowing mammals live under 'different' respiratory conditions (e.g. Barros et al., 2004; Baudinette, 1974; Withers, 1975), our findings suggest that the CO_2 levels that Sundevall's jirds commonly encounter in their open-ended burrows are not extreme. Therefore, under normal circumstances, there is no apparent need for this rodent species, and perhaps many others with similar burrow designs, to be physiologically adapted to tolerate high F_{CO_2}. However, if burrow entrances become plugged, inadvertently or by a flood, for example, the physiological ability to endure high [CO_2] and low [O_2] would have positive consequences on fitness.

As eddy formation takes place everywhere, tapping the energy in the turbulent boundary layer may be a ubiquitous phenomenon that is important to the ventilation of the burrows of a myriad of species – from badgers and warthogs to gerbils and jirds. Indeed, natural selection has shaped the configuration of burrows for millions of years, and they can be regarded as part of the burrowing animal's 'extended organism', while their configuration can be considered as part of its 'extended physiology' (Turner, 2000).

MATERIALS AND METHODS
Description of artificial burrows
We constructed two artificial burrows, designed according to the configuration of a natural burrow of Sundevall's jird, *M. crassus* (Shenbrot et al., 2002), a common semi-fossorial desert rodent of the Negev Desert. Burrows were constructed from 7 mm galvanized iron mesh (hardware cloth), with a spherical nest chamber, 13 cm in diameter, in the middle, connected to the main tunnel by a 10 cm long corridor (Fig. 1A,B). The diameter of the burrow entrances, main tunnel and entry corridor was 5 cm. Each burrow entrance had a 10 cm long Perspex® tube (diameter d=5 cm) inserted into it, allowing it to be plugged with a rubber stopper. The nest chambers were made from two kitchen sieves adjoined to form a sphere. The base of the sphere was placed 60 cm below the soil surface. The total volume of each burrow was 5340 cm^3. The walls of one burrow were made

permeable to gasses by wrapping the hardware cloth with medical gauze, which prevented loess getting into the burrow lumen, but permitted free movement of gases between the burrow and the soil.

In order to study the effect of gas movement by convection alone on $[CO_2]$, the walls of the second burrow were wrapped with three layers of Saran® plastic wrap and a layer of silicon rubber, making its walls impermeable to gases. We buried the burrows in a loessial soil field on the Sede Boqer campus of Ben-Gurion University of the Negev. They were inserted side by side, parallel to one another and 1 m apart, in sieved loess soil packed to a bulk density of 1.3 g cm^{-3}, as reported for natural loess soil in the Negev Desert (Shafran et al., 2005). The axis of the burrows was 300° NW to 120° SE, parallel to the prevalent wind direction (Zucker-Milwerger, 2013).

Wind-induced convection by the irregular penetration of eddies

We quantified the number of eddies that penetrated to different depths in the main tunnel, the corridor and the nest chamber of an artificial burrow (Fig. 1A), at different times of day as a function of wind speed. Eddy penetration was based on changes of air temperature inside the burrow. Each eddy is a relatively self-contained mass of air that exchanges little heat or water vapor with the surrounding air. The penetration of an eddy is therefore accompanied by a distinct pattern of temperature change.

We positioned eight, 45 standard wire gauge (SWG, 0.071 mm) type-T thermocouples along a gas-impermeable burrow. The burrow was constructed as above, but was wrapped with several layers of Saran® wrap (Fig. 1A). Six thermocouples were positioned along the main tunnel, 33 cm apart, with their tips in the tunnel center. One thermocouple was located in the middle of the corridor leading to the nest chamber, with its tip at the center of the corridor, and one thermocouple was located at the nest chamber, with its tip in the center. An eddy penetration results in a sequential, momentary rise in temperature starting at the first thermocouple, located closest to the entrance, and advancing along the tunnel deeper into the burrow (Fig. 9). The array of thermocouples allowed us to identify eddies that penetrated to different depths in the burrow. A penetration event was defined as an event in which a steep increase in the temperature of sequentially located thermocouples, relative to their temperature 10 s before the reading could be observed. The threshold values varied with location along the burrow – 0.5°C for the thermocouples located at the nest chamber and entry corridor and 1.0°C for the thermocouples located in the main tunnel (Fig. 1A). In order to avoid multiple counting of eddies due to varying durations of penetration events, we only considered gusts that were at least 10 s apart.
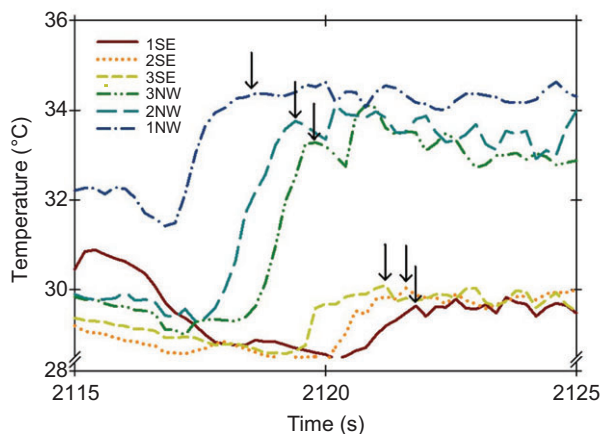

Fig. 9. Temperatures at six locations along the main tunnel of an impermeable artificial Sundevall's jird burrow as a function of time, illustrating penetration of an eddy during daytime. The eddy moves atmospheric air that is warmer than burrow air into the burrow, causing a sequential, momentary rise in temperature in each of the thermocouples along the main tunnel, starting at the first location (see Fig. 1), 1NW, closest to the northwestern entrance and advancing deeper along the tunnel to locations 2NW, 3NW, 3SE, 2SE and 1SE. The black arrows indicate the successive peak temperatures of the thermocouples and are indicative of eddy movement.

Measurements in the artificial burrow were made on four non-consecutive days during September 2012. Thermocouple temperatures were logged at 5 Hz with data loggers (Campbell Scientific models CR23X and 21X, Logan, UT, USA). We obtained 10 min wind speed averages at 3 m from the Blaustein Institutes for Desert Research meteorological station, located 250 m to the west of the study site (http://www.bgu.ac.il/BIDR/research/phys/meteorology/).

To test the suitability of the algorithm based on the approach detailed above for the detection of eddies, we built a 2 m long tunnel from PVC tubes (d=4.4 cm; Fig. 1C). The tunnel had two entrances, one at each end of a descending arm and between them a horizontal arm, the base of which was 60 cm below the soil surface. We positioned 12 fine (45 SWG=0.071 mm) type-T thermocouples along the tunnels with their tips in its center; four thermocouples were positioned along each of the tunnel's descending arms, 19.5 cm apart, and four thermocouples were positioned along the horizontal arm, 24 cm apart. Two thermocouples were positioned outside the burrow, 2.5 cm above the southeast entrance (SEE) and the northwest entrance (NWE). We measured the temperature inside and outside for a total of 40 min on 12 June 2012. During the first 20 min of measurements the entrances of the burrow were plugged and for the next 20 min they were open. A coefficient of variation (c.v.=s.d./mean, dimensionless ratio) was calculated for each of the thermocouples.

Parallel mechanisms of burrow ventilation

We did a simulation experiment in which we measured the changes in $[CO_2]$ inside the nest chambers of artificial burrows, permeable or impermeable to gas exchange with the soil, as a function of time and wind speed, while simulating the CO_2 output of an adult Sundevall's jird at rest inside the chamber. This was done by injecting CO_2 at a known rate continuously into the center of the burrow's nest chamber through a Bev-A-Line® tube (d=1.6 mm) at the end of which there was a thin 6.5 cm long stainless steel tube projecting into the center of the nest chamber (Fig. 1B). CO_2 was injected at a flow-rate of 2.5 ml min^{-1}. This flow rate corresponds to the CO_2 production of an adult Sundevall's jird dam and four pups resting at a thermoneutral temperature (our own measurements, I.B.-B. unpublished data). Concurrently, we measured $[CO_2]$ at the top of the chamber with an infrared CO_2 sensor (details below) and average above-ground wind speed and direction at a distance of 10 m from the burrows at 0.4 m above the ground with an ultrasonic anemometer (model 81000, R.M. Young Company, USA). According to the manufacturer, the anemometer has a measurement range of 0–40 m s^{-1}, a resolution of 0.01 m s^{-1} and an accuracy of ±1% rms (root mean square). CO_2 concentration inside the nest chamber was sampled every minute. Wind speed and direction were measured every second and averaged each minute.

CO_2 concentration inside the nest chamber was measured under the following conditions: (1) in the impermeable burrow with entrances open, and (2) in the permeable burrow with (a) entrances plugged with rubber stoppers; (b) open entrances; or (c) open entrances, and no injection of CO_2 into the nest chamber. We assumed that when the entrances of the impermeable burrow were open, a decrease in CO_2 concentration could result only from wind-induced convection. When the entrances of the permeable burrow were plugged, gas exchange by diffusion that could potentially include the effects of thermal gradients and be enhanced by air movement across the ground surface was the only possible mechanism available for changes in $[CO_2]$ in the nest chamber. When the entrances of the permeable burrow were open, both convection and diffusion could take place, as is usually the case in natural burrows. The fourth condition (i.e. open entrances and no injection of CO_2) served as a control; we measured baseline $[CO_2]$ in an unoccupied burrow.

Measurements were made under the first three conditions (1, 2a and b) on seven non-consecutive days (within a 30 day period), while the fourth condition (2c) was measured on five non-consecutive days. Each measurement series in a single burrow lasted 8 h and was carried out between 08:00 h and 16:00 h. Half-hourly averages were calculated for $[CO_2]$, wind speed and direction. Above-ground wind speed and direction were measured 10 m away from the burrows at 0.4 m above the ground with an ultrasonic anemometer (see details above). To the east of the study site (95–190° from N) there were several prominent structures that could have

caused changes in wind patterns. Therefore, intervals during which wind blew from their direction were omitted from analysis. The dominant wind direction throughout the year is NW.

[CO_2] inside burrows

Each nest chamber was equipped with a PVC guide tube (d=2 cm) for the insertion of a CO_2 sensor (Fig. 1B). The nest chambers were also equipped with aluminium tubes (d=1.6 cm) for the insertion of a camera (used in other experiments). All tubes could be plugged with rubber stoppers. The CO_2 sensor that we used (Vaisala CARBOCAP® model GMT221, Helsinki, Finland) measures [CO_2] *in situ*, without affecting natural air movement. The sensor's measurement range is 0–10% with accuracy at 25°C and 1 atm of ±(1.5% of range + 2% of reading) of the reading. Response time is 30 s (manufacturer's specifications). We verified these values by calibrating the sensor with gas mixtures produced by a 3-way gas-mixing pump (model M301a-F, Wösthoff GmbH, Bochum, Germany). For the slow injection of CO_2 into the nest chamber we used a modified, micro-controlled double-syringe pump (DN Infusion Pump, Holland). We replaced the usual pair of syringes with two pneumatic pistons (0.39 l, Baccara, Geva, Israel) in order to be able to inject CO_2 for as long as 2 h. The pistons were filled with pure CO_2 from a tank. Refilling, after 2 h, took less than 30 s. Flow was directed with a 3-way stopcock.

Competing interests

The authors declare no competing financial interests.

Author contributions

I.B.-B., B.P., P.B. and J.S.T. conceived and designed the experiments. I.B.-B. and D.Z.-M. carried out the experiments and analyzed the data. A.B. wrote the MATLAB program to analyze the data and analyzed data. I.B.-B., B.P. and P.B. wrote the paper and J.S.T. commented on it and approved it along with the other authors.

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