

COMMENTARY

Transient-state mechanisms of wind-induced burrow ventilation

J. Scott Turner^{1,*} and Berry Pinshow²**ABSTRACT**

Burrows are common animal habitations, yet living in a burrow presents physiological challenges for its inhabitants because the burrow isolates them from sources and sinks for oxygen, carbon dioxide, water vapor and ammonia. Conventionally, the isolation is thought to be overcome by either diffusion gas exchange within the burrow or some means of capturing wind energy to power steady or quasi-steady bulk flows of air through it. Both are examples of what may be called ‘DC’ models, namely steady to quasi-steady flows powered by steady to quasi-steady winds. Natural winds, however, are neither steady nor quasi-steady, but are turbulent, with a considerable portion of the energy contained in so-called ‘AC’ (i.e. unsteady) components, where wind velocity varies chaotically and energy to power gas exchange is stored in some form. Existing DC models of burrow gas exchange do not account for this potentially significant source of energy for ventilation. We present evidence that at least two AC mechanisms operate to ventilate both single-opening burrows (of the Cape skink, *Trachylepis capensis*) and double-opening model burrows (of Sundevall’s jird, *Meriones crassus*). We propose that consideration of the physiological ecology and evolution of the burrowing habit has been blinkered by the long neglect of AC ventilation.

KEY WORDS: Sundevall’s jird, *Meriones crassus*, Cape skink, *Trachylepis capensis*, Turbulence, AC ventilation, Diffusion, Bulk flow, Energy storage, Pendelluft, Eddy capture

Introduction

Burrows are the living environment for many animals ranging in size from ants to aardvarks, and they vary enormously in size and complexity of structure (Kinlaw, 1999; Meadows and Meadows, 1991; Turner, 2000; Turner, 2001; Whitford and Kay, 1999). Burrows inevitably isolate their inhabitants to some degree from the atmospheric sources and sinks for exchange of respiratory gases. For animals with high metabolic demands, such as mammals and birds (or, in aggregate, termite or ant colonies), or in soils that are themselves biologically active, depletion of oxygen or accumulation of waste gases like carbon dioxide or ammonia can become problematic for a burrow’s inhabitants (MacArthur, 1984; Tomasco et al., 2010). Burrows must therefore not only act as dwellings and shelters for the animals inhabiting them but also manage the fluxes of respiratory and waste gases between the burrow and atmosphere.

Historically, physical models of gas exchange in animal burrow systems have fallen into two broad categories. In the first category, burrows are presumed to be stagnant environments in which diffusion along gradients in partial pressure is the principal driver for gas exchange (Wilson and Kilgore, 1978; Withers, 1978).

These gradients can be oriented either longitudinally along the burrow’s passageways or radially through porous soils in which the burrow might be situated. Invariably, these models lead to the conclusion that, while diffusion through burrow systems may suffice to meet the gas exchange needs of animals with low respiratory demands, it is inadequate for animals with high demands, or which have low tolerance for toxic gases that may accumulate. In the second category, gas exchange between the burrow and atmospheric air is promoted by bulk air flow through the burrow, either forced convection driven by some interaction of two or more burrow entrances with wind (Olszewski and Skioeczen, 1965; Vogel, 1978; Vogel and Bretz, 1972; Weir, 1973) or natural convection driven by gradients of air density within the burrow system itself (Ganot et al., 2012; Lüscher, 1961). Such bulk flows are often proposed as a means to overcome the diffusion limitations for gas exchange that prevail in the first category. Such reasoning implies that animals or superorganisms (such as ant or termite colonies) with high metabolic demands for gas exchange can inhabit burrows only if there is some mechanism that promotes these bulk flows of air. In the absence of such a mechanism, the implication is that the animal must have developed special adaptations to a presumably hypoxic, hypercapnic or otherwise toxic burrow environment.

In this Commentary, we argue that burrow gas exchange is a far richer phenomenon than is encompassed by these two model categories. In support of our argument, we outline some recent findings in simple burrow systems that illustrate these alternative modalities of gas exchange. We discuss how these results lead the way to a much richer grasp of how burrows can act as part of an ‘extended organism’ of the burrows’ inhabitants.

The burrow as an organ of ‘extended physiology’

The fundamental physiological problem for any living system is to match the physical flux rates of matter between the organism and its environment to the metabolic demand rates of the ultimate metabolic engines, the cells: in other words, to match delivery to demand. For respiration, the cells are the ultimate sinks or sources for the respiratory gases, oxygen and carbon dioxide, respectively. (Water vapor and ammonia can also be considered respiratory gases.) An animal’s respiratory organ systems – the lungs, heart and circulation in the case of vertebrates, the spiracles, book lungs and tracheolar systems in the case of arthropods – are interfaces for matching the physical fluxes of these gases to physiological demand. This is accomplished through various levels of physiological control and through the expenditure of internal physiological work – powering respiratory muscles, cardiac work, spiracle closure or flutter rate, etc.

A burrow system presents an additional barrier to fluxes of respiratory gases between the environment and cells, situated in series to those internal barriers, so that a burrow might be considered as much a physiological interface between the cells and the environment as the lungs, circulation, tracheoles and spiracles might be: in other words, a burrow could act as an organ of ‘extended physiology’ (Turner, 2000; Turner, 2002; Turner, 2004; Turner,

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Glossary

AC

Literally, alternating current: specifically, electrical current that changes polarity with time, and is affected by both a resistance and a capacitance. Used here as an analogy for the chaotic time-dependent variation of velocity in turbulent wind.

Antiphase

The phase difference between two periodic functions that is precisely 180 deg.

Boundary layer

The layer of fluid in the immediate vicinity of a bounding surface, where the transfer of momentum through the effect of viscosity is significant compared with the effect of inertia. Often manifests as a variation of wind speed with respect to proximity to a surface.

Convection

The concerted movement of a fluid in bulk, driven by gradients in hydrostatic pressure or density.

DC

Literally, direct current: specifically, electrical current that is steady or quasi-steady, in which current is limited solely by a resistance. Used here as an analogy for steady or quasi-steady wind.

Eddy

A swirling parcel of fluid in which momentum is stored primarily as angular momentum. Eddies arise when a fluid is subject to strong shearing forces, such as when wind flows over the ground surface, or encounters some obstacle, which may be a parcel of air that has different momentum.

Fourier series

A mathematical representation of a time series, in which a quantity, such as wind speed, can be decomposed into an infinite series of sine or cosine functions that differ in amplitude, frequency and phase.

Partial pressure

The product of total pressure and the mole fraction of a gas in a mixture of gases at a particular pressure.

Pendelluft

Literally, air pendulum. A term borrowed from respiratory physiology, which refers to patterns of microcirculation within the lung, driven by energy stored in the lung's elastic tissues. A pendelluft can arise under any circumstance where there is sufficient energy storage to overcome the inertia of air.

Poiseuille flow

Steady to quasi-steady flow through tubes that is governed by the Poiseuille equation. A hydraulic resistance term may be calculated from the Poiseuille equation that is the analogue of the electrical resistance term of Ohm's law.

Quasi-steady flow

Flow that changes sufficiently slowly that inertial or elastic effects do not affect its behavior.

Turbulence or turbulent flow

Flow that is characterized by chaotic velocity changes that arise when fluids are subject to strong shearing forces.

The nature of natural wind

Both gas exchange categories, diffusion and bulk flow, suffer from conceptual weaknesses that obscure a full understanding of the extended physiology of gas exchange in animal burrows. For example, widespread confusion is associated with an overly broad application of the term 'diffusion' to describe exchanges that operate over scales of meters, when diffusion is biologically relevant only at scales of millimeters or smaller. Bulk flow, for its part, is often presumed to operate in large burrows, despite there being little direct evidence (and in some instances, contrary evidence) that the expected bulk flows actually occur in them (Turner, 2001). Bulk flow models are also inapplicable to single-opening burrow systems, which are a common design motif in animal burrows (Bromley, 1990).

The major conceptual weakness attending these conventional categories follows from a misapprehension of the nature of natural winds. The presumption is usually made that gas exchange between burrow and air is driven by relatively steady gradients in potential energy: partial pressure gradients, steady or quasi-steady winds, or persistent and steady buoyancy gradients, any of which can drive steady or quasi-steady bulk flow of air through the burrow system or within it. Yet, natural winds are rarely steady. Rather, they are nearly always turbulent (Kowalski and Mitchell, 1976; Sutton, 1960), and this distinction carries important implications for how wind can be harnessed to do physiological work. Turbulent wind can have a steady or quasi-steady component to it, but a considerable portion of the energy in turbulent wind is tied up in unsteady and complex eddy flows, boundary layer variation, and chaotic spatial and temporal variation in velocity. The prevailing models for gas exchange in burrows do not account for this unsteady band of energy. Yet, as we shall show, the unsteady energy in turbulent winds actually plays a significant role in powering gas exchange in burrow systems.

'DC' versus 'AC'

An electrical analogy can help clarify our thinking about these questions. The prevailing models for burrow gas exchange comprise what we may call a 'DC' (direct current) analogy: steady to quasi-steady fluxes of respiratory gases powered by steady to quasi-steady gradients in potential energy (Fig. 1). In a DC conception, the magnitude of a flux depends upon the magnitude of the potential energy gradient – partial pressure gradients, induced hydrostatic pressure gradients, buoyancy gradients – and is limited by some resistance term, such as might be embodied in Poiseuille flow through a burrow structure. In considering the unsteady nature of turbulent wind, a more appropriate conception might be what we call an 'AC' (alternating current) analogy.

Whereas the DC analogy relies on steady or quasi-steady sources of energy, an AC analogy has a specific energy storage capability, embodied in a capacitance (Fig. 1). This explicitly brings the time dimension into gas exchange in a way that differs from pure DC models, which incorporate time implicitly in the form of resistance-limited DC rates (Trimmer, 1950). Consider, for example, how one might represent a time series of measurements of wind speed that varies chaotically about a mean. One can represent such a time series as a simple average of wind speed, which is equivalent to folding the time-dependent variation into a single DC term. Alternatively, one can deconstruct the time-dependent variation about the mean into a Fourier series (Bloomfield, 1976), which now describes wind speed as the sum of the average plus a series of sinusoidal variations of wind speed that differ in frequency, amplitude and phase. Thus, turbulent wind may be represented as

2005). Unlike conventional organs of physiology, in which the infrastructure of control and operation is located within the organism, a burrow's extended physiology relies upon external sources of energy to power physiological work, and upon manipulation of structure to work effectively. In the conventional conceptions of burrow gas exchange, the potential energy sources for powering the extended physiology of gas exchange are limited to gradients in gas concentration (diffusion), air density and gravitational potential (natural convection), or kinetic energy in wind (forced convection).

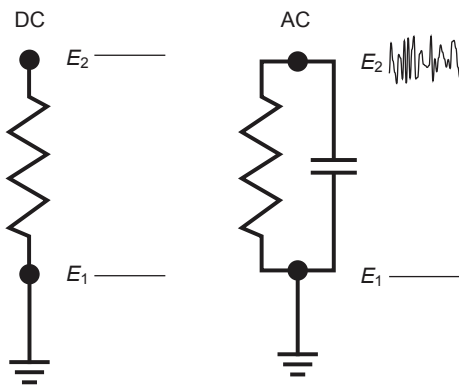


Fig. 1. 'DC' versus 'AC' electrical analogies for flow. A direct current (DC) analogy portrays a physical system where work is limited by a resistance spanning a steady potential energy gradient ($E_2 - E_1$). In the case of flow, the electrical analogy represents flow as current, potential energy as a pressure difference and resistance as losses due to viscosity. An alternating current 'AC' analogy portrays a physical system where energy is stored in a capacitor. Work is determined by the resistance spanning a time-dependent potential energy gradient, and by tapping energy stored in the capacitor. For flow, capacitance can take many forms, including hydrostatic pressure, momentum and gravitational potential.

comprising a DC component of wind speed energy (the average) and an AC component (time-dependent turbulent variation). Among other things, this allows one to characterize energy in turbulent wind as a spectrum that parses out variation ranging from a null frequency (i.e. the DC component) through the various frequencies represented by the individual terms in the series. Generally, wind speeds represented in this way show turbulent wind to be 'broad-spectrum', with wind speed variation (and the energy implied in that variation) distributed more or less evenly across all frequencies.

If there is energy available in wind, then it can be tapped to do physiological work. The challenge is to understand how this can be done for the purposes of the extended physiology of burrow ventilation, particularly in the AC band. The value of an electrical analogy like the one described above is that it can sharpen the focus on just how burrows might harness transient energy in turbulent winds to do physiological work. Specifically, a credible AC mechanism for burrow gas exchange would have some means of transient-state energy storage: the equivalent of the capacitance component of the AC analogy (Fig. 1).

We have identified various mechanisms whereby burrow gas exchange operates specifically through some means of transient energy storage, and below we present evidence that these drive gas exchange in various types of burrow. We do not believe our examples exhaust the range of possibilities.

The pendelluft

Perhaps the most straightforward AC mechanism for gas exchange is the so-called pendelluft ('air pendulum') effect. The pendelluft was first described in the context of inter-alveolar patterns of microcirculation within the lungs (Feng and Poon, 1998; Lee et al., 2006; Ultman et al., 1988). In the lung pendelluft, the energy storage term resides in the lung's elastic tissues. The pendelluft can also operate at much larger scales, including burrows, but there, the mechanisms for energy storage differ. In particular, the pendelluft seems well suited to burrows that have multiple openings and that develop significant vertical gradients of air density within them. Energy storage there depends upon vertical displacements of these gradients of air density.

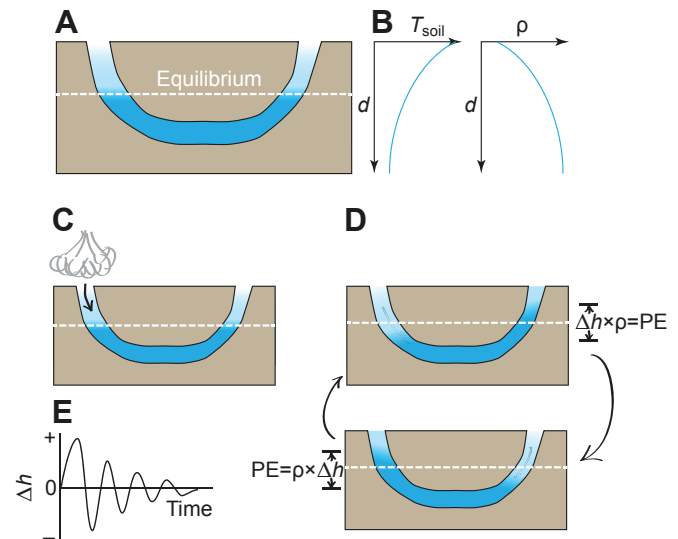


Fig. 2. Hypothetical scenario for a pendelluft in an animal burrow. (A) A cross-section through a simple U-shaped burrow, showing a stratified vertical gradient in air density indicated by shading. The dashed line is the equilibrium position of the stratified layers. (B) Hypothetical variation of the vertical distribution of soil temperature (T_{soil}) and air density (ρ) with depth (d) of a stably stratified gradient in a burrow. (C) The initiation of a pendelluft. A transient gust of air (in gray) pushes down on the stratified layer in the burrow. (D) The action of a pendelluft. A transient force on one burrow entrance displaces the stratified layer from its equilibrium position by some vertical extent, Δh . The product of Δh and density, ρ , is the potential energy (PE) that is stored in the displaced stratified layer (representing capacitance). This initiates a back-and-forth motion of the stratified air layer. (E) A pendelluft behaves as a damped oscillator as the initial displacement is dissipated as heat (representing resistance).

As a possible scenario for a burrow pendelluft, consider a simple U-shaped burrow with a depth sufficient to span a vertical temperature gradient within the soil (Fig. 2). Let us assume that superficial soil temperatures are warmer than the deep soil temperatures. If the air within the burrow is relatively stagnant, the variation of soil temperature will impose a vertical density gradient upon air within the burrow, with dense air deep in the burrow and lighter air closer to the surface: a stably stratified density gradient, in other words. If there is an animal living at the bottom of such a burrow, CO_2 will tend to accumulate there, and O_2 will be depleted.

Now imagine a transient pulse of positive pressure at one of the burrow entrances (Fig. 2). This will push down on the air at this entrance, which will, in turn, push the air upward at the other entrance of the burrow. There is now a vertical displacement of the air density gradient from its equilibrium horizontal state, with dense, heavier, air pushed upward at one burrow entrance and light air pushed downward at the other. This vertical displacement of mass from its equilibrium state constitutes stored energy. When the transient pulse of pressure passes, the energy stored in the displaced density gradient will set the air mass in motion as it seeks to return to its equilibrium horizontal orientation. Because the air in motion has mass, and therefore momentum, this will cause the density gradient to 'overshoot' its equilibrium position, just as a pendulum would overshoot its equilibrium vertical position on its return stroke. Hence, a transient pulse of pressure at one burrow entrance will set the burrow air into an oscillatory motion similar to that of a damped pendulum: a pendelluft, in short.

Zucker-Milwerger (Zucker-Milwerger, 2013) has seen this mechanism in action in artificial burrows modeled after the

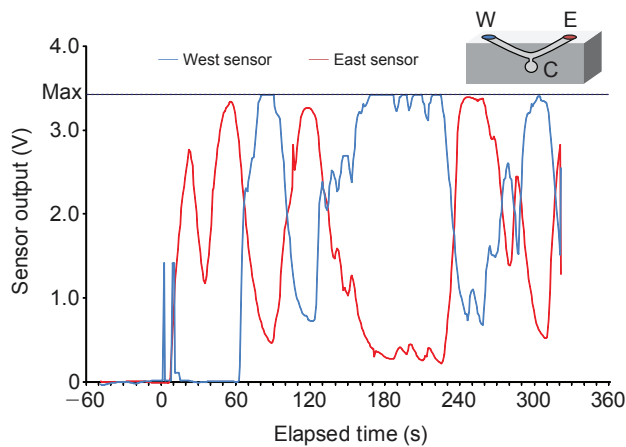


Fig. 3. A pendelluft in an artificial burrow of Sundevall's jird (*Meriones crassus*) during still conditions in the morning, showing oscillatory flow between two burrow entrances. A bolus of combustible gas tracer was injected into the nest chamber (C) at time 0. Combustible gas concentration was measured at the west (W) and east (E) burrow openings. The oscillation of the burrow air mass is evident as the anti-phase emergence of combustible gas from the burrow entrances. After Zucker-Milwerger (Zucker-Milwerger, 2013).

multiple-entrance burrows of the Sundevall's jird (*Meriones crassus*). The model burrows were full-scale U-shaped constructions with two entrances and a side chamber in the deep section mimicking the nest chamber typically built by these rodents. Burrow gas exchange was assessed by injecting a bolus of combustible gas tracer (a dilute mixture of propane and air) into the nest chamber, and then measuring its appearance at the two burrow entrances (Fig. 3). The oscillatory flow was evident as antiphase pulses of tracer gas appearing alternately at the two burrow entrances.

The actual occurrence of the pendelluft in natural burrows will undoubtedly be complicated by natural variation of vertical density gradients. These will not always be stably stratified, as was the case in the example presented above (e.g. Shorthouse and Marples, 1980). Overnight, the vertical temperature gradient in a burrow may be reversed, resulting in an unstable density gradient. Whether this obviates the importance of pendelluft exchange is not clear, however. Turnover of unstable density gradients is complicated by viscosity and constrained by the shapes and dimensions of the burrow tunnels, which can easily stabilize unstably stratified density gradients within burrow systems that are hard to disrupt. Here, a pendelluft effect could still help destratify an already unstable density gradient within a burrow. Clearly, there is much more to be learned.

Eddy capture

Another mechanism of AC energy storage involves what we call eddy capture. Turbulence usually is manifest in the generation of eddies, which are focal areas of circular motion of a parcel of air. An eddy forms when the translational momentum of a parcel of air (or any fluid) is transformed into angular momentum. The momentum has not disappeared – conservation of energy demands that it does not – but has simply been changed from translational into angular form. Thus, an eddy can be considered a storage medium for kinetic energy in wind, captured and held there as its energy is dissipated through viscosity to heat.

Turbulent winds contain an infinitude of eddies that vary widely in size and angular velocity. This distribution of eddy sizes and rotation rates is probably the source of the broad-spectrum AC

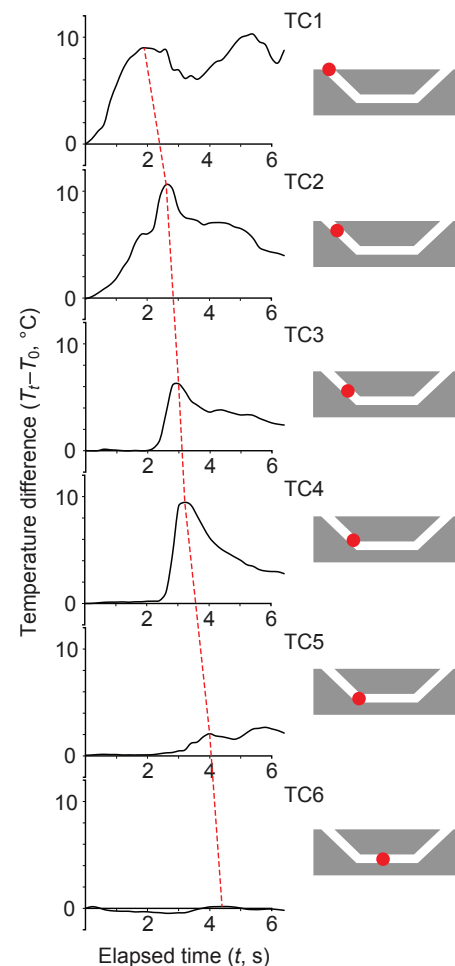


Fig. 4. An example of eddy penetration in an artificial burrow of *M. crassus*. Thermocouples (red circles) were placed at several locations (TC1, TC2, etc.) to measure air temperature in the center of the burrow lumen (right panel). Simultaneous time series of temperatures during an eddy penetration event are shown in the left panel. The progress of an eddy is shown by the temperature peaks connected by the red dashed line.

energy that is characteristic of turbulent wind. Large-scale eddies produce wind gusts and are probably responsible for the kinds of low-frequency transient pulses of energy that might pass over a burrow entrance and set a pendelluft into motion. Eddies at smaller scales may, however, be captured and penetrate downward into a burrow. In such an instance, an eddy can be a source of energy that promotes mixing of burrow air with the atmosphere.

Full-scale model burrows of Sundevall's jird (Brickner-Braun et al., 2014) provide an example of such eddy capture (Fig. 4). The air temperature of eddies frequently differs slightly from that of the ambient air, and the passage of an eddy past a point can be registered by a fast-response thermocouple as a 'blip' in temperature. Eddy capture in the model jird burrow was detected by outfitting the burrow with an array of fast-response thermocouples positioned to measure air temperature within the burrow. One can clearly see in this example the capture and migration of an eddy through the burrow in the correlated pulses of temperature. As an eddy penetrates into a burrow in this way, mixing of deep burrow air with ambient air would be the result.

Unlike the pendelluft, which requires at a minimum two burrow entrances to operate, eddy capture can operate in single-opening

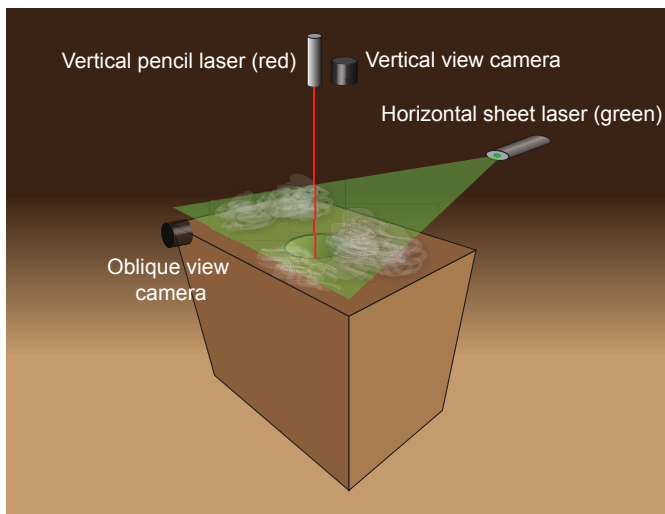


Fig. 5. Measuring smoke clearance in a single-opening burrow of the Cape skink, *Trachylepis capensis*, using laser-enhanced smoke visualization. A red pencil laser beam is projected vertically into the burrow, and a horizontal green laser sheet is projected about a centimeter above the burrow entrance. Two video cameras are used to record illuminated smoke simultaneously within and exiting the burrow. See 'Eddy capture' for details, and supplementary material Table S1 for links to movies showing the measurements in operation.

burrows. We have made an extensive set of measurements of air exchange in the burrows of the Cape skink, *Trachylepis capensis*. This lizard's burrow is a simple vertical tunnel that is typically about 4 cm in diameter and 35 cm deep, with a single opening to the surface. Usually, there is a small side-chamber at the bottom, where the lizard can rest or turn around. Otherwise, the lizard sits oriented vertically in its tunnel (personal observations, B.P.).

We studied air exchange in these burrows using laser-enhanced smoke visualization (LESV). In this method, the lizard is excluded from the burrow, and smoke is injected into the burrow. The smoke is illuminated by a laser light, in this instance a red pencil beam aimed downward into the burrow (Fig. 5). Smoke within the burrow scatters the light: the denser the smoke, the more the light will be scattered, and the brighter the illuminated smoke will appear to be. The extent of this scattering can be quantified from analysis of images taken by a camera aimed down the burrow. For these measurements, we also analyzed images from a camera positioned to view the burrow obliquely. This enabled us to visualize upward motion of smoke from the burrow, which was evident as 'jets' of illuminated smoke that were drawn upward from the burrow entrance. In some of our experiments, we also aimed a horizontal sheet of laser light (of a different color) positioned about a centimeter above the burrow entrance, and used this to illuminate turbulent eddies in the surface boundary layer (Fig. 5). Videos of these experiments in operation may be accessed from the supplementary material (see supplementary material Table S1).

One can see various interesting patterns of smoke clearance from these burrows. We offer just one example (Fig. 6). Here, clearance is multiphase, with a slow initial phase, followed by two distinct phases of smoke clearance, each faster than the last. We saw several other patterns of air clearance all from the same burrow, which suggests there is no single pattern of eddy capture and air turnover within the burrow. That there is no such general pattern is an important point. Given the chaotic nature of turbulent wind, patterns

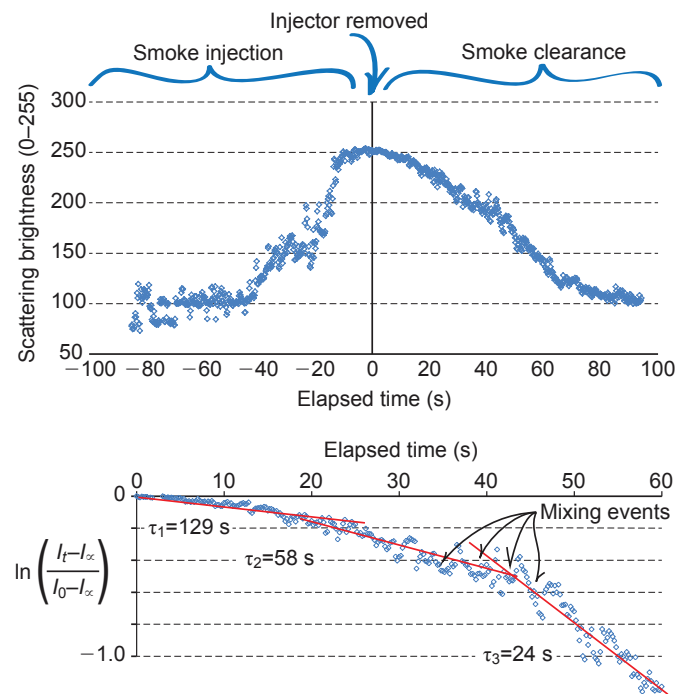


Fig. 6. Smoke clearance from a *T. capensis* burrow using backscattered light from a laser-enhanced smoke visualization experiment. The top panel plots the brightness of the backscattered laser light (256 discrete levels) from the beginning of smoke injection to its ultimate clearance from the burrow. Smoke injection is evident as an initial increase in backscattered light, and time 0 is set at the moment the smoke injector tube was removed from the burrow. The bottom panel is a semi-log plot of smoke clearance from the burrow from time 0. Clearance in this instance was three-phase, with associated clearance time constants, τ , calculated from the red regression lines. Mixing events as noted on the video recording for this clearance experiment are indicated with arrows.

of air clearance even within single burrows would be expected to be remarkably complex and variable. Video recording of the smoke clearance (see supplementary material Table S1 for link) in fact shows distinct penetration of eddies into the burrow, and this clearly influences the clearance of smoke, and hence turnover of air, within the simple burrows of these lizards. Furthermore, eddy mixing events are clearly correlated with the passage of turbulent eddies over the burrow entrance (see supplementary material Table S1 for links).

There's lots of room in AC

If animal burrows in fact function as part of a burrow builder's extended organism, these structures must have access to some external source of energy for doing physiological work. For some time, these sources of energy were thought to be steady or quasi-steady gradients in partial pressure (diffusion), air density (natural convection) or wind-induced pressure differences (forced convection). From our studies of gas exchange in burrows, it is now clear that there is, in addition, a rich dimension of AC-driven mechanisms that rely on the seemingly abundant transient sources of energy that comprise a significant part of natural wind. We have explored two of these mechanisms, pendelluft flow and eddy capture, but we believe we have by no means exhausted the range of possibilities or novel mechanisms for gas exchange. For example, burrows tend to be tubular air spaces which, given the right conditions, can be set to resonate just like an air column in an organ

pipe would. This can produce a powerful mixing of the air mass contained within the tube, a phenomenon known as Rayleigh–Taylor mixing (Ramaprabhu and Andrews, 2004). Could burrow air spaces be ventilated by such mechanisms? The broad spectrum distribution of energy in turbulent wind suggests that they might, and there is a dramatic example that they actually do, as in the whistling thorn acacia, *Acacia drepanolobium*. These trees are colonized by at least four species of ant and produce hollow galls that can act as a Helmholtz resonator (Young et al., 1996). Under the right circumstances, the galls whistle audibly, perhaps producing a burst of air turnover within the ant colony. A variety of other interesting questions also come to mind. For example, is there a correlation between burrow size and the tendency to capture eddies? Are there circumstances where an animal might create burrows that impede eddy capture? The burrows of scorpions provide a tantalizing example of this. Most scorpion burrows are characterized by abrupt turns and spirals in their tunnel passageways. Might these be eddy traps, situated not to promote but to prevent eddy capture? This might be a particular issue for scorpions that inhabit arid environments, where it would be desirable to sustain a strong separation between dry ambient air and moist air in a burrow microclimate. Actively plugging one or more of the burrow entrances as a means of controlling eddy capture or pendelluft mixing is another intriguing possibility for fruitful research (Reichman and Smith, 1990).

Not appreciating this has led to important phenomena being overlooked. For example, White et al. (White et al., 1978) observed episodic and irregular air turnover events in the single-opening nests of European bee-eaters, dug deeply as horizontal tunnels into soil banks. In light of our observations on air turnover in *Trachylepis* burrows, these episodic air turnover events were likely eddy capture events. Even though the authors remarked upon this at the time, their significance has sat obscured for nearly four decades. What else of the fascinating extended physiology of the burrow environment might we be missing?

In conclusion, we might paraphrase Richard Feynman's famous admonition that 'there's lots of room at the bottom', referring to the interesting mechanics and physics that operate at the micro- and nano-scales (Feynman, 1992). We might just as well invite our fellow physiologists to explore the ample room in the fascinating, and largely unstudied, realm of the transient world. We have tried to open a window onto that world via the mechanism of burrow ventilation. Given the chaotic nature of energy sources in the real world, the AC mode may prevail more widely there as well.

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Competing interests

The authors declare no competing financial interests.

Author contributions

J.S.T. and B.P. conceived and designed the Cape skink experiments and carried them out. J.S.T. analyzed the data. J.S.T. and B.P. wrote the paper, revised it and approved it.

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Supplementary material

Supplementary material available online at <http://jeb.biologists.org/lookup/suppl/doi:10.1242/jeb.110858/-/DC1>.

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Table S1. Links to various videos on YouTube that supplement some of the verbal descriptions of laser-enhanced smoke-visualization experiments

Title	Link	Description
<i>Trachylepis capensis</i> burrow clearance	http://youtu.be/opvtgs8X1cY	Depicts the various configurations of the laser-enhanced smoke visualization experiments described in the text.
Eddy penetration as a mechanism for burrow gas exchange	http://youtu.be/VWq64IzCO6I	Penetration of turbulent eddies into a vertical glass tube, showing the episodic nature of eddy penetration as a means of powering air turnover in a single opening vertical burrow
Using lasers to visualize boundary layer flows near animal burrow entrances	http://youtu.be/-Cisabm7vck	Depicts the ways that multicolored lasers can be used to describe the complex turbulent flows in the surface boundary layer, near the opening of the complex nest of the ant <i>Pheidole</i> spp. Details of such methods as color separation, smoke injection, and clearance.