Part XIII

Animal Form and Function

Some species of lizard breathe better than others. The savannah monitor lizard *Varanus exanthematicus* breathes more efficiently than some of its relatives by pumping air into its lungs from the gular folds over its throat.

Real People Doing Real Science

Why Some Lizards Take a Deep Breath

Sometimes, what is intended as a straightforward observational study about an animal turns out instead to uncover an odd fact, something that doesn't at first seem to make sense. Teasing your understanding with the unexpected, this kind of tantalizing finding can be fun and illuminating to investigate. Just such an unexpected puzzle comes to light when you look very carefully at how lizards run.

A lizard runs a bit like a football fullback, swinging his shoulder forward to take a step as the opposite foot pushes off the ground. This produces a lateral undulating gait, the body flexing from side to side with each step. This sort of gait uses the body to aid the legs in power running. By contracting the chest (intercostal) muscles on the side of the body opposite the swinging shoulder, the lizard literally thrusts itself forward with each flex of its body.

The odd fact, the thing that at first doesn't seem to make sense, is that running lizards should be using these same intercostal chest muscles for something else.

At rest, lizards breathe by expanding their chest, much as you do. The greater volume of the expanded thorax lowers the interior air pressure, causing fresh air to be pushed into the lungs from outside. You expand your chest by contracting a diaphragm at the bottom of the chest. Lizards do not have a diaphragm. Instead, they expand their chest by contracting the intercostal chest muscles on both sides of the chest simultaneously. This contraction rotates the ribs, causing the chest to expand.

Do you see the problem? A running lizard cannot contract its chest muscles on both sides simultaneously for effective breathing at the same time that it is contracting the same chest muscles alternatively for running. This apparent conflict has led to a controversial hypothesis about how running lizards breathe. Called the axial constraint hypothesis, it states that lizards are subject to a speed-dependent axial constraint that prevents effective lung ventilation while they are running.

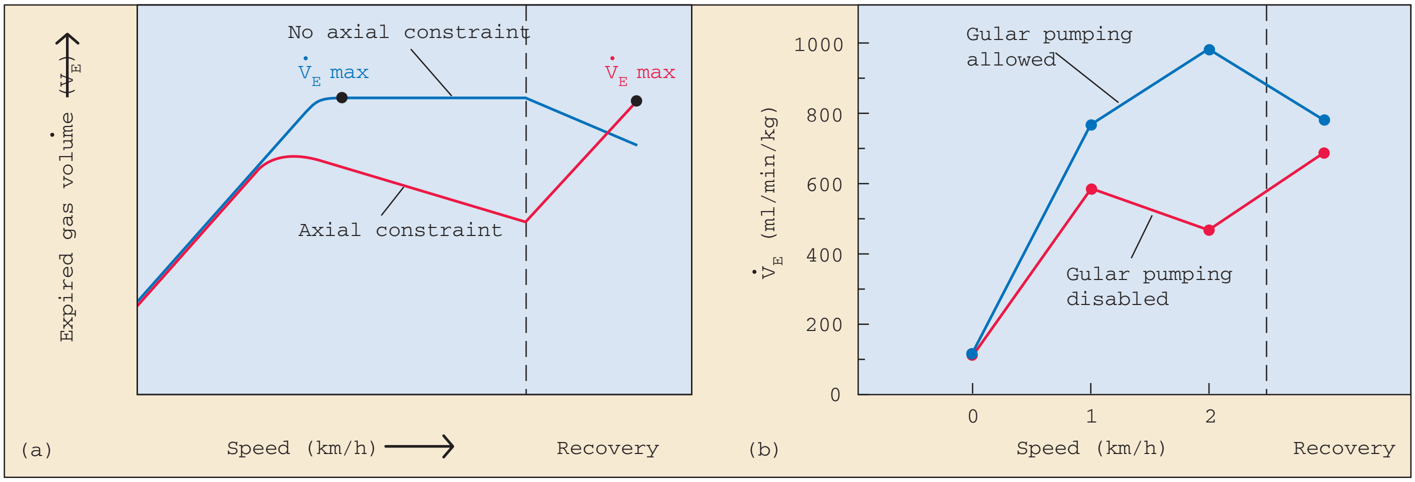
This constraint, if true, would be rather puzzling from an evolutionary perspective, because it suggests that when a lizard needs more oxygen because it is running, it breathes less effectively.

Dr. Elizabeth Brainerd of the University of Massachusetts, Amherst, is one of a growing cadre of young researchers around the country that study the biology of lizards. She set out to investigate this puzzle several years ago, first by examining oxygen consumption.

Looking at oxygen consumption seemed a very straightforward approach. If the axial constraint hypothesis is correct, then running lizards should exhibit a lower oxygen consumption because of lowered breathing efficiency. This is just what some of her colleagues found with green iguanas (*Iguana iguana*). Studying fast-running iguanas on treadmills, oxygen consumption went down as running proceeded, as the axial constraint hypothesis predicted.

Unexpectedly, however, another large lizard gave a completely different result. The savannah monitor lizard (*Varanus exanthematicus*) exhibited *elevated* oxygen consumption with increasing speeds of locomotion! This result suggests that something else is going on in monitor lizards. Somehow, they have found a way to beat the axial constraint.

How do they do it? Taking a more detailed look at running monitor lizards, Dr. Brainerd's research team ran a series of experiments to sort this out. First, they used videoradiography to directly observe lung ventilation in monitor lizards while the lizards were running on a treadmill. The X-ray video images revealed the monitor's trick: the breathing cycle began with an inhalation that did not completely fill the lungs, just as the axial constraint hypothesis predicts. But then something else kicks in. The gular cavity located in the throat area also fills with air, and as inhalation proceeds the gular cavity compresses, forcing this air into the lungs. Like an afterburner on a jet, this added air increases the efficiency of breathing, making up for the lost contribution of the intercostal chest muscles.



Effects of gular pumping in lizards. (*a*) THEORY: The axial constraint hypothesis predicts that, above a threshold speed, ventilation, measured by expired gas volume ($\dot{V}_E$–ml/min), will decrease with increasing speed, and only reach a maximum during the recovery period after locomotion ceases. Without axial constraint, ventilation should reach its maximum during locomotion. (*b*) EXPERIMENT: Monitor lizards typically show no axial constraint while running. Axial constraint is evident, however, if gular pumping of air is disabled. So, it seems that some species of monitor lizards are able to use gular pumping to overcome the axial constraint on ventilation.

The Experiment

Brainerd set out to test this gular pumping hypothesis. Gular pumping occurs after the initial inhalation because the lizard closes its mouth, sealing shut internal nares (nostril-like structures). Air is thus trapped in the gular cavity. By contracting muscles that compress the gular cavity, this air is forced into the lungs. This process can be disrupted by propping the mouth open so that, when the gular cavity is compressed, its air escapes back out of the mouth. The lizards were trained to run on a treadmill. A plastic mask was placed over the animal's mouth and nostrils and air was drawn through the mask. The mask permitted the measurement of oxygen and CO_2 levels as a means of monitoring gas consumption. The expired gas volume ($\dot{V}_E$) was measured in the last minutes of locomotion and the first minute of recovery at each speed. The speeds ranged from 0 km/hr to 2 km/hr. The maximum running speed of these lizards on a treadmill is 7 km/hr.

To disable gular pumping, the animal's mouth was propped open with a retainer made of plastic tubing. In parallel experiments that allow gular pumping, the same animals wore the masks, but no retainer was used to disrupt the oral seal necessary for gular pumping.

The Results

Parallel experiments were conducted on monitor lizards with and without gular pumping:

1. *Gular pumping allowed.* When the gular pumping mechanism was not obstructed, the $\dot{V}_E$ increased to a maximum at a speed of 2 km/hr and decreased during the recovery period (see blue line in graph *b* above). This result is predicted under conditions where there is no axial constraint on the animal (see graph *a* above).

2. *Gular pumping disabled.* When the gular pumping mechanism is obstructed, $\dot{V}_E$ increased above the resting value up to a speed of 1 km/hr. The value began to decrease between 1 and 2 km/hr indicating that there was constraint on ventilation. During the recovery period, $\dot{V}_E$ increased as predicted by the axial constraint hypothesis, because there was no longer constraint on the intercostal muscles. $\dot{V}_E$ increased to pay back an oxygen debt that occurred during the period of time when anaerobic metabolism took over.

Comparing the $\dot{V}_E$ measurements under control and experimental conditions, the researchers concluded that monitor lizards are indeed subject to speed-dependent axial constraint, just as theory had predicted, but can circumvent this constraint when running by using an accessory gular pump to enhance ventilation. When the gular pump was experimentally disrupted, the speed-dependent axial constraint condition became apparent.

Although the researchers have not conducted a more complete comparative analysis using the methods shown here, they have found correlations between gular pumping and increased locomotor activity. During exercise, six highly active species exhibited gular pumping for lung ventilation, while three less active species did not. It is interesting to speculate that gular pumping evolved in lizards as a means of enhancing breathing to allow greater locomotor endurance. The gular pumping seen in lizards is similar to the breathing mechanism found in amphibians and air-breathing fish. In these animals, the air first enters a cavity in the mouth called the buccal cavity. The mouth and nares close and the buccal cavity compresses, forcing air into the lungs. The similarities in these two mechanisms suggest that one might have arisen from the other.