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Inside JEB

HEADBANGING TERMITES SEND OUT SMOKE SIGNALS



Communicating over long distances is difficult; for example, the sound of our voices can rarely be heard or understood further away than 100 m. Yet, long before the invention of the telephone or e-mail, humans were successfully communicating over hundreds of kilometres. Take, for example, the Great Wall of China, where soldiers alerted each other of an impending attack using smoke signals. Although this remarkable ability to communicate over long distances is said to be unique to humans, Wolfgang Kirchner and PhD student Felix Hager, from the University of Bochum, Germany, found out that some species of termites have also mastered the skill (p. 3249).

Kirchner explains that the African termite, *Macrotermes natalensis*, forms large colonies in subterranean mounds and operates on a caste system. The workers use the mound's maze of corridors to access the outside world to forage for food. As these outdoor excursions can take them over 10 m away from their colony, they are accompanied by another caste – the soldier termites. In addition to protecting them, these soldiers will drum home warnings of an impending attack to the distant colony should a hungry aardvark appear.

Kirchner's initial work on termites' long-distance warnings began in the Ivory Coast but because of the political situation he decided travel to South Africa with Hager to carry on his work. As termites are difficult to find outside their colonies, the duo opened up the central chamber of a termite mound and used high-speed cameras to capture in detail how soldiers warn others of unwelcome intrusions. They saw the soldiers raising their heads upwards before bashing them into the ground at speeds of 1.5 m s^{-1} . Using carefully embedded accelerometers to detect vibrations, the duo found that the *M. natalensis* termites drummed their heads rapidly, 11 times per second. Each head bang generated vibrational pulses where the ground vibrated with acceleration amplitudes up to 0.7 m s^{-2} ; this

approximately corresponds to a 70 nm movement at a frequency of 500 Hz.

'Once we had described the signal, the next step was to look at signal perception – what intensity does the signal have to have in order to be recognisable for another individual?' says Kirchner. To do this, they carefully placed termites into Petri dishes and measured their responses over a range of vibrational frequencies and displacements. They found the termites were most sensitive to frequencies around 500 Hz, as long as the movement of the dish's surface was more than 0.012 m s^{-2} (the equivalent of a miniscule 1–2 nm movement).

Satisfied that the soldiers were producing a vibrational signal that other termites could pick up, Kirchner says: 'We looked at how a signal is transmitted from the individual into the soil, how much is it attenuated with distance and how fast can it travel physically.' Mimicking a vibration pulse and placing accelerometers at set distances away from the signal, the team found that the vibrational wave could travel up to 171 m s^{-1} . They found that the vibrations were attenuated by 0.4 dB cm^{-1} and calculated that after just 40 cm the ground would no longer vibrate enough for other termites to pick it up. However, drumming signals can be picked up at much further distances. Kirchner concludes that the only way this could occur is if there's social transmission of the signal. He likens it to a game of Chinese whispers, where one termite passes on the message to the next, and so forth. Only, in this case, the message is not distorted and it's drumming loud and clear – danger ahead!

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Hager, F. A. and Kirchner, W. H. (2013). Vibrational long-distance communication in the termites *Macrotermes natalensis* and *Odontotermes* sp. *J. Exp. Biol.* **216**, 3249-3256.

Nicola Stead

SINGING GOBIES USE THEIR PECS

During the reproductive season, many fish species will use sound to communicate with one another, sending out calls to warn off rivals and serenade potential suitors. Although it may seem surprising to think of singing fish, it is actually quite common amongst fishes, as Eric Parmentier from the Université de Liège, Belgium, points out: 'When studies began on fish sound production, scientists thought they were lucky when they found a fish that was able to make sounds, but in the future I think we will be lucky if we find a fish that is not

able to make sound.' Parmentier explains that, in fact, fishes have evolved many different ways to produce sound, from grinding their teeth to drumming their swim bladders, and he even jokes that this huge diversity keeps him in his research job. In his latest study, he turns his attention to the Gobiidae family, explaining that gobies are well known for their mating melodies but that the mechanism has remained elusive (p. 3189).

In the late winter of 2010 and 2011, with the help of several lab members, Parmentier travelled to Brittany, France, to capture the rock goby, *Gobius paganellus*. Back in the lab, the team selected aggressive males and introduced them to another fish. They filmed the encounters at 200 frames s⁻¹ and captured any sounds using a hydrophone. Looking over the videos, Parmentier and his colleagues saw that the gobies seemed to be nodding their heads in time with their pulsed calls. 'We were really happy', recalls Parmentier, 'because we thought the mechanism was at the level of the head'.

So how could this nodding produce sound? 'We thought that the fish was able to take water into the mouth and [by nodding the head] change the pressure in the buccal cavity, helping the water to vibrate the bones', explains Parmentier. To test their idea, the team cut part of the flap that covers the gills, which allowed water to leak out of the mouth cavity. They were disappointed to find that the gobies still produced noise. What's more, Parmentier had supplemented his Brittany catch with *G. paganellus* gobies caught in Venice with the help of Stefano Malavasi from the University Ca'Foscari Venice, Italy. Parmentier and Malavasi found that the Italian calls were more tonal than the French calls, but more importantly the Italian gobies didn't bob their heads up and down in time with the sound – yet more evidence that the head movements were not necessary for sound production.

Back at square one, the team decided to investigate the anatomical features in more detail. During the dissections, Parmentier noticed that the gobies were morphologically very similar to the Cottidae family of fish. Parmentier explains that cottids are thought to use their pectoral girdle (a bony structure supporting their pectoral fins) to make noise. It was too risky to cut the muscles associated with the pectoral girdle without completely damaging the fish, so the team carefully inserted tiny electrodes into the associated muscle to measure its activity during sound production. 'We saw there was a perfect correlation between the sound production

and the activity of the muscle', recalls Parmentier. Speculating on the muscle's role in the gobies' songs, Parmentier says: 'The muscle is going to push and pull the pectoral girdle, so I suppose that friction somewhere between the girdle and the ligaments, or bones, produces the sound.' There is still more work to be done, and it remains a mystery how the French and Italian fish produce different types of calls, but we are certainly one muscle closer to understanding sound production in gobies.

10.1242/jeb.091728

Parmentier, E., Kéver, L., Boyle, K., Corbisier, Y.-E., Sawelew, L. and Malavasi, S. (2013). Sound production in *Gobius paganellus* (Gobiidae). *J. Exp. Biol.* **216**, 3189-3199.

Nicola Stead

NO OXYGEN? SHUT DOWN YOUR F₁F₀-ATPASE

Thomas Jackson



Mitochondria are our bodies' powerhouses, and to efficiently produce energy, *via* aerobic respiration, they use the enzymatic activities of four different protein complexes (I to IV) to pump hydrogen ions across the inner mitochondrial membrane. The H⁺ ions will then flow back into the mitochondria, down their concentration gradient, *via* a fifth complex, which drives ATP production, where the H⁺ ions are then accepted by oxygen to make water. 'Without oxygen, animals have to move to anaerobic respiration, which yields a much lower level of ATP. So their balance between ATP supply and demand is greatly affected', explains Gina Galli, from the University of Manchester, UK. The absence of oxygen (anoxia) can be disastrous, as can be seen in pathologies such as stroke or heart attacks, but for some animals, such as the red-eared slider turtle, anoxic periods are just a normal part of life. So, as part of her postdoc in Jeffrey Richards' lab at the University of British Columbia, Canada, Galli decided to find out what we can learn from anoxia tolerant turtles (p. 3283).

Galli already knew some of the tricks turtles employ during periods of anoxia: 'They have the ability to shut down all the cellular processes in their bodies that consume a large amount of ATP, but we wanted to see if that was also the case at the level of the mitochondria.' To investigate this possibility, she divided 26

turtles into two groups. One group was kept in normal, normoxic water conditions while the other group was submerged in water devoid of oxygen for 2 weeks. Galli then isolated cardiac fibres from the turtle's hearts and placed individual fibres into tiny respirometer chambers, equipped with oxygen-sensing electrodes. Galli could then measure the fibres' aerobic respiration capacity by how much oxygen was depleted. To measure the capacity of the individual complexes I–IV, Galli used specific drugs to inhibit each complex. Overall, she found that the aerobic capacity at complexes I–IV was reduced in the cardiac fibres from anoxic turtles.

Next, Galli wondered whether this reduction in aerobic capacity was caused by a reduction in the enzymatic activity of each complex. To test this, Galli supplied tissue samples with substrates that were unique to each complex, one by one, and measured how much product was produced. To her surprise, Galli found that each of the complexes from anoxic turtles was working at the same rate as complexes from normoxic turtles. Perplexed, Galli wondered whether the apparent reduction in aerobic capacity was perhaps just due to a decrease in the total number of mitochondria in cardiac cells from anoxic turtles. However, anoxic and normoxic cardiac fibres were able to produce the same amount of citrate (*via* the unique mitochondrial enzyme citrate synthase), suggesting that total mitochondrial levels were the same in the two conditions.

So, Galli decided to test the enzymatic activity of the fifth and final complex, also known as the F₁F₀-ATPase, and found its enzymatic activity was indeed shut down. Suddenly, everything fell into place – shutting down this complex would reduce flow through complexes I–IV but not their enzymatic activities. In addition, shutting down this complex has clear benefits, as Galli explains: 'When there's no oxygen, the F₁F₀-ATP synthase will start consuming ATP to keep that H⁺ gradient going. It starts to chew up all of the available ATP; it will eventually lead to ATP depletion and that's one of the biggest contributors to cellular breakdown.' Recent studies have shown that, in mammals, drugs inhibiting this final complex do protect tissues against anoxia, but it seems that turtles have known the secret all along!

10.1242/jeb.092064

Galli, G. L. J., Lau, G. Y. and Richards, J. G. (2013). Beating oxygen: chronic anoxia exposure reduces mitochondrial F₁F₀-ATPase activity in turtle (*Trachemys scripta*) heart. *J. Exp. Biol.* **216**, 3283-3293.

Nicola Stead

MANAGING OXYGEN LEVELS: DIVE DEEP OR STAY SHALLOW?



How long can you hold your breath for? Californian sea lions can hold their breath for up to 10 min during foraging dives. But how do they do it? To investigate, Birgitte McDonald from the Scripps Institution of Oceanography, USA, decided to measure oxygen saturation in the venous blood. She explains that, at rest, venous blood is about 78% saturated with oxygen after supplying the body with oxygen, but wondered how much it decreased during dives (p. 3332).

With the help of her postdoctoral supervisor, Paul Ponganis, McDonald captured seven lactating sea lions off the coast of California and inserted an electrode into the vena cava vein of anaesthetised sea lions, enabling her to measure partial pressure of oxygen (a measurement of oxygen levels). Equipped with this partial pressure of oxygen data logger and a time depth recorder, McDonald released the sea lions back into wild.

After recovering the equipment, McDonald converted all her measurements into percentage oxygen saturation. McDonald saw marked differences in oxygen depletion patterns between shallow and deep dives. During shallow dives lasting less than 3 min, oxygen saturation levels went down to anywhere between 10 and 80%. After a shallow dive, the sea lions didn't always replenish their blood oxygen stores back to 78% and in some cases dived down with only 15% saturation, which may explain why some appeared to have very low saturation levels.

McDonald found that at the beginning of a deep dive, the sea lions increased their venous oxygen saturation more than for a shallow dive, in some cases reaching up to 95% saturation. She explains that it is possible that arterio-venous shunts exist that allow saturated arterial blood, fresh from the lungs, to bypass tissues and

oxygenate the venous blood. By shunting this arterial blood they would maximise their blood oxygen storage before a dive. During the dive there was near-complete oxygen depletion, and after resurfacing, unlike after a shallow dive, the sea lions remained at the surface for longer periods to replenish their oxygen stores. In conclusion, McDonald's data suggest that sea lions know when they're going to dive deep or remain shallow and alter their oxygen management strategies accordingly.

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McDonald, B. I. and Ponganis, P. J. (2013). Insights from venous oxygen profiles; oxygen utilization and management in diving California sea lions. *J. Exp. Biol.* **216**, 3332-3341.

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