

cycle is clearly less pronounced. Wolff and colleagues also note that although the older cycles do not achieve nearly the same degree of warmth as subsequently, the warm intervals represent a much greater portion of the total cycle than was the case for the past few peak interglacial times; these seem to be increasingly brief, albeit pronounced, respites from the more typical harsh, unstable climate of the 100K world⁵.

The EPICA team's recovery of undisturbed ice representing all of MIS 11 is of especial note. When this interglacial occurred, some 400,000 years ago, the slowly varying shape of Earth's elliptical orbit around the Sun was nearly circular. In this configuration, variations in the seasonal distribution of sunlight are due primarily to the tilt of Earth's axis, with little influence of the precession of the seasons around the orbit every 20,000 years. Because the Sun occupies a position that is nearer to one end of the ellipse, this precession results in the gradual cooling of northern summers over 10,000 years, as they migrate towards the more distant end of the orbit, culminating in conditions that are most conducive to year-round snow cover and the initiation of an ice age. A similar orbital configuration to that for MIS 11 holds today, and will for some time, making this interglacial a potential analogue for the natural development of Earth's climate in the future⁴. Northern Hemisphere summer now occurs when the Earth is near its farthest point from the Sun, although the nearly circular orbit raises the question of whether the resulting weak decline in northern summer insolation of today was sufficient to trigger the onset of an ice age in the past⁶.

Wolff *et al.* confirm that concentrations of the greenhouse gases CO₂ and CH₄ were also similar to pre-industrial levels during MIS 11, showing that the overall controls on incoming and outgoing radiation that drive climate were similar. Their deuterium and dust records indicate that the magnitude of the climatic response was likewise similar, and the 28,000 years of relative warmth in Antarctica is in keeping with evidence for prolonged warmth elsewhere⁶⁻¹⁰. This suggests that Earth's climate may have 'skipped a beat' when its orbit was nearly circular⁶, rather than returning to an ice age after the 10,000 years of one half-precession cycle. The new results are perhaps the best evidence yet that MIS 11 was akin to the current interglacial — except, of course, that we now have rising concentrations of CO₂ and have yet to see if 'our' interglacial might last another 20,000 years.

A priority for further investigations will be completing the gas records from air trapped in the Dome C ice. Given the complete record, it may be possible to detect an overall decline in greenhouse gases that might help to account for the long-term

deterioration of global climate. Equally important is the question of whether the earlier warm intervals were associated with lower greenhouse-gas concentrations than have been achieved within the past few cycles. Such evidence will help us to find out whether the accentuated warmth of peak interglacial intervals within the 100K world was associated with 'elevated' atmospheric greenhouse-gas levels that have been increasingly surpassed in the post-industrial era. ■

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1. EPICA community members *Nature* **429**, 623–628 (2004).
2. Dansgaard, W. *et al.* *Nature* **364**, 218–220 (1993).
3. Petit, J. R. *et al.* *Nature* **399**, 429–436 (1999).
4. Loutre, M. F. & Berger, A. *Glob. Planet. Change* **36**, 209–217 (2003).
5. McManus, J. F., Oppo, D. W. & Cullen, J. L. *Science* **283**, 971–975 (1999).
6. McManus, J. F., Oppo, D. W., Cullen, J. L. & Healey, S. L. in *Earth's Climate and Orbital Eccentricity: The Marine Isotope Stage 11 Question* (eds Droxler, A., Poore, R., Burckle, L. & Osterman, L.) 69–85 (Am. Geophys. Un., Washington DC, 2003).
7. Winograd, I. J., Landwehr, J. M., Ludwig, K. R., Coplen, T. B. & Riggs, A. C. *Quat. Res.* **48**, 141–154 (1997).
8. Poore, R. Z. & Dowsett, H. J. *Geology* **29**, 71–74 (2001).
9. Hodell, D. A., Charles, C. D. & Ninnemann, U. S. *Glob. Planet. Change* **24**, 7–26 (2000).
10. Oppo, D. W., McManus, J. F. & Cullen, J. L. *Science* **279**, 1335–1338 (1998).
11. Flower, B. P. *et al.* *Paleoceanography* **13**, 388–403 (2000).

Animal behaviour

Eavesdropping on bats

Brock Fenton and John Ratcliffe

Two investigations into bat echolocation provide striking examples of the sophistication and the possible evolutionary and ecological consequences of variability in call design.

In 1794, Lazzaro Spallanzani reported experimental results supporting his earlier proposal that bats could 'see' with their ears. The famed Georges Cuvier found the suggestion preposterous¹, however, and it took almost another 150 years for Spallanzani to be vindicated. After repeating many of Spallanzani's experiments, Donald Griffin² published the same conclusions in 1940, coining the term 'echolocation' to describe how bats use echoes of the sounds they produce to locate objects in their path. A microphone sensitive to sound frequencies above the range of human hearing, a bat detector, allowed Griffin to eavesdrop on what bats said as they flew through an obstacle course in the dark.

Today, we know that there is variation between bat species in the design of echolocation calls, which often coincides with differences in their behaviour and ecology³. Two papers in this issue, by Kingston and Rossiter⁴ and Siemers and Schnitzler⁵, advance this line of investigation further.

Kingston and Rossiter (page 654)⁴ examined the situation in a single species, the large-eared horseshoe bat (*Rhinolophus philippinensis*), which occurs from southeast Asia to Australia. They showed how echolocation signals can diverge within a species and how this divergence might promote sympatric speciation — the division of one species into two or more without a geographical barrier. This is a hot and contentious topic in evolutionary biology. In three study areas, Kingston and Rossiter found three distinct variants of large-eared horseshoe bats differing in size, echolocation calls and relatedness. The largest was almost

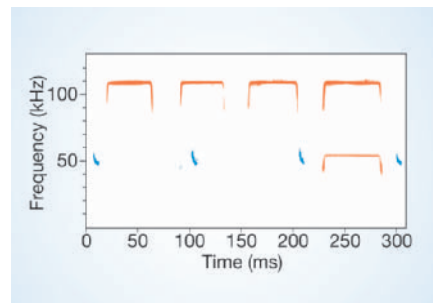


Figure 1 The two sides of the echolocation fence. These calls represent bats that separate pulse and echo in frequency (*Rhinolophus*, high-duty cycle, orange) and those separating them in time (*Pipistrellus*, low-duty cycle, blue). The high-duty calls are long, separated by short periods of silence and dominated by a single frequency; the low-duty calls are short, separated by long periods of silence and are not dominated by a single frequency. The fourth call of the *Rhinolophus* includes a lower-frequency harmonic as discussed by Kingston and Rossiter⁴. The bats foraged along the edge of a watercourse south of the Dead Sea, and the recording — made by M. B. Fenton — is unusual because it captures both types of cycle simultaneously.

twice as heavy as the smallest, and the sounds dominating their echolocation calls ranged from 27.2 ± 0.2 kHz in the largest to 53.6 ± 0.6 kHz in the smallest.

The level of detail available to an echolocating bat is a function of the wavelength of the sounds in its echolocation calls, and so differences in the frequencies that dominate its calls influence a bat's auditory scene⁶. Bats using high frequencies (shorter wavelengths) can detect smaller prey than can

bats using lower-frequency calls (longer wavelengths). Kingston and Rossiter suggest that the range of echolocation calls in one species would generate 'disruptive selection' because larger bats do not have the same access to small prey as do smaller ones. Theirs is the first demonstration of how adaptive evolution in bats, and so speciation, might have been driven through divergences in echolocation signals.

For their part, Siemers and Schnitzler (page 657)⁵ examined the behavioural consequences of differences in echolocation signals used by similar species of bats to detect prey. In a portable flight-room, they challenged flying individuals of five European species of mouse-eared bats (*Myotis* species) to detect and attack prey sitting on or close to vegetation. This is presumed to be difficult for the bats because echoes from prey could be masked by echoes — 'clutter' — from the background. Siemers and Schnitzler standardized the degree of clutter in which the bats operated, and documented their behaviour and foraging performance. The five species they used have similar hunting behaviour and are placed in the same 'foraging guild' of bats (the 'edge space aerial/trawling foragers'). The five species might have been expected to perform at the same level, but they did not.

In the tradition of Griffin and Spallanzani, Siemers and Schnitzler controlled for other cues (vision, olfaction) and demonstrated a significant relationship between the design of echolocation calls and foraging performance. Specifically, they showed that foraging performance in clutter was predictable from echolocation call design, particularly from differences in calls that had been considered minor. Their study is the first to provide empirical evidence that seemingly minor differences in call design can have real behavioural consequences. In contrast to Kingston and Rossiter, Siemers and Schnitzler show that signal designs of similar species can converge, reflecting foraging behaviour that is independent of presumed evolutionary relationships.

Individually and jointly, these two papers advance our understanding of the diversity of echolocation in bats. They have opened doors to a better appreciation of the variety of echolocation call designs, including the identification of cryptic species⁷ — that is, the discovery that what had been considered a single species really consists of two or more. Coupled with data on the enhanced echoes that some flowers return to the bats that pollinate them⁸, the new findings also allow better interpretation of insights into other pressures acting on the evolution of bats. For example, another component of the echolocation story is the listeners — other bats, or other animals that, like Griffin, eavesdrop on the calls^{9,10}. Kingston and Rossiter's work shows clearly that changes in echolocation calls can affect

not only bats' views of the world, but also the ability of one individual to communicate with another. Siemers and Schnitzler's results set the stage for examining the influence of call design on the ability of potential insect prey to detect and evade hunting bats^{9,10}.

The two studies^{4,5} used species from both sides of the bat echolocation fence. On one side, mouse-eared bats, like most bats, separate call and echo in time (low-duty cycle); on the other, horseshoe bats separate them in frequency (high-duty cycle) (Fig. 1). Both approaches to echolocation are ancient, with fossil evidence indicating that they were present in bats some 50 million years ago¹¹. The new data speak to the divergence of call design after the evolution of echolocation, but the early history of bats and echolocation remains unclear. There is plenty of opportunity in this line of research: stay tuned for the next chapter. ■

Particle physics

From the top...

Georg Weiglein

The top quark is by far the heaviest elementary particle known. A measurement of its mass with higher precision has bearing on our understanding of the fundamental interactions of nature.

The basic building-blocks of matter, as far as we know, are quarks and leptons, together with the force-carrying particles that mediate their interactions. Quarks and leptons (the latter group including the electron) are grouped in three generations; the particles in the second and third generations seem a perfect copy of those of the first generation, except that their masses are much larger. The top quark is the heaviest of all quarks and leptons, and is central to some of the most pressing questions in particle physics. For instance, why is the third-generation top quark more than 300,000 times heavier than the first-generation electron? Why are there two other quarks with precisely the same properties as the top quark but with very different masses? And what is the origin of mass itself?

Precise knowledge of the mass of the top quark and its interactions is a key ingredient in testing theory against experimental data. On page 638 of this issue¹, the DØ Collaboration report an improved measurement of the top-quark mass, using data taken at the Tevatron proton-antiproton collider at Fermilab, near Chicago. Combining this with previous measurements from DØ and its sister experiment CDF, the new world average² for the mass of the top quark is $178.0 \pm 4.3 \text{ GeV}/c^2$, where c is the speed of light (the mass of the proton expressed in these units is about $1 \text{ GeV}/c^2$). Compared with the previous world average³, the central value of the mass has shifted

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1. Griffin, D. R. *Listening in the Dark* (Yale Univ. Press, New Haven, 1959).
2. Galambos, R. & Griffin, D. R. *Anat. Rec.* **78**, 95 (1940).
3. Thomas, J., Moss, C. & Vater, M. (eds) *Echolocation in Bats and Dolphins* (Univ. Chicago Press, 2004).
4. Kingston, T. & Rossiter, S. J. *Nature* **429**, 654–657 (2004).
5. Siemers, B. M. & Schnitzler, H.-U. *Nature* **429**, 657–661 (2004).
6. Simmons, J. A. & Stein, R. A. *J. Comp. Physiol. A* **135**, 61–84 (1980).
7. Barratt, E. M. *et al. Nature* **387**, 138–139 (1997).
8. von Helversen, D. & von Helversen, O. *Nature* **398**, 759–760 (1999).
9. Pye, J. D. *Nature* **218**, 797 (1968).
10. Fullard, J. H. in *Comparative Hearing: Insects* (eds Hoy, R. R., Popper, A. N. & Fay, R. R.) 279–326 (Springer, New York, 1998).
11. Simmons, N. B. & Geilser, J. H. *Bull. Am. Mus. Nat. Hist.* **235**, 1–182 (1998).

upwards by about $4 \text{ GeV}/c^2$. The experimental error has been reduced by about 15%, sharpening our view of the underlying physics.

The role of the top quark in disentangling the fundamental principles of nature is twofold. On the one hand, its large mass makes the top quark a prime target in the search for new physics that might so far be unaccounted for. For instance, the long-hypothesized Higgs boson, which is the last missing ingredient of the standard model of particle physics, is predicted to interact with other particles with a strength that is proportional to their masses. So the physics of the heavy top quark would be significantly influenced by its interaction with the Higgs boson. On the other hand, the mass of the top quark is a key parameter in the predictions for many observable quantities. Small deviations between measurement and prediction could be a signal of new physics, so the uncertainty in the predictions that arises from the experimental error on the top-quark mass limits the sensitivity of experiment to new physics.

The values of several precisely measured quantities, as predicted by the standard model, depend on the square of the top-quark mass, M_t ; their dependence is much weaker on the as yet unknown mass of the Higgs boson (so far, experiment has excluded⁴ any mass value below $114.4 \text{ GeV}/c^2$). Therefore, in using a so-called global fit of the model predictions to all available data, an improved knowledge of M_t better constrains