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- Jagasia, R., Grote, P., Westermann, B. & Conradt, B. *Nature* **433**, 754–760 (2005).
- Daniel, N. N. & Korsmeyer, S. J. *Cell* **116**, 205–219 (2004).
- Hengartner, M. O. *Nature* **407**, 770–776 (2000).

- Karbowsky, M. & Youle, R. J. *Cell Death Differ.* **10**, 870–880 (2003).
- Frank, S. *et al. Dev. Cell* **1**, 515–525 (2001).
- Kinchen, J. M. & Hengartner, M. O. *Curr. Top. Dev. Biol.* **65**, 1–45 (2004).
- Parrish, J. *et al. Nature* **412**, 90–94 (2001).
- Horvitz, H. R. *Cancer Res.* **59**, 1701s–1706s (1999).
- Labrousse, A. M., Zappaterra, M. D., Rube, D. A. & van der Bliek, A. M. *Mol. Cell* **4**, 815–826 (1999).

Evolutionary biology

The power of natural selection

Andrew P. Hendry

Adaptation by natural selection is the centrepiece of biology. Yet evolutionary biologists may be deluding themselves if they think they have a good handle on the typical strength of selection in nature.

The one constant in our world is change — change often wrought by our own devices. In consequence, some of the populations and species with which we cohabit have difficulty persisting. Yet organisms should be able to adapt to changing environments, as they have done for billions of years, diversifying into a bewildering array of environments. But extinctions are also a prominent feature of the past. Were these lost organisms unable to adapt to change? If so, are the rapid changes now being driven by humans too much for adaptation to combat? At the heart of these questions is the power of natural selection to bring about evolutionary adaptation in natural populations. Writing in *Evolution*, Joe Hereford and colleagues¹ bring this matter into stark relief.

The primary mechanism of adaptive evolution is natural selection, whereby organisms possessing traits that improve their evolutionary ‘fitness’ — their survival and reproduction — contribute more genes to subsequent generations. Yet perceptions of the power of selection have recently swung at the end of a pendulum. Charles Darwin felt that “natural selection will always act very slowly, often only at long intervals of time, and generally on only a very few of the inhabitants of the same region at the same time”². If Darwin was right, natural selection should be almost imperceptible, and adaptation must require “the long lapse of ages”². This perception held sway for more than a century before it was challenged by a series of empirical studies — most famously those showing dramatic changes in the coloration of peppered moths during industrialization³. These studies inspired a wave of interest in actually measuring selection and adaptation in natural populations.

By the mid-1980s, enough studies had accumulated for John Endler to profitably review them in his classic book *Natural Selection in the Wild*⁴. Reviews of this sort typically collate and combine selection estimates for a variety of traits and studies so as to address general questions about the strength

of selection (Box 1). Endler’s review heralded a shift in our perceptions when he emphasized that “strong selection is not rare and may even be common”⁴, basing this conclusion largely on the observation that some studies documented quite strong selection.

Another way to infer the power of selection is to actually measure evolutionary changes in natural populations^{5,6}. Studies taking this approach often document substantial changes over short time intervals, suggesting that natural selection does indeed have the power to drive rapid adaptation. Darwin was too modest, it seemed, about the power of his idea.

Fast-forward to 1998, when I joined a discussion group led by Joel Kingsolver at the University of Washington. This group set about analysing all studies of natural selection published since Endler’s book.

Burdened by the practical needs of graduating, I soon bowed out of the project and did not see the results until 2001. Surprisingly, it seemed that Endler’s conclusions had swung the pendulum too far back when Kingsolver *et al.* emphasized that “directional selection on most traits and in most systems is quite weak”⁷. This conclusion was largely based on the observation that most estimates of selection were non-significant and centred around zero. A particularly worrisome finding was that most studies did not have sufficient statistical power to detect typical strengths of selection^{7,8}. Perhaps the pendulum should swing all the way back to Darwin: natural selection really is weak in nature, except in exceptional situations.

Enter Hereford *et al.*¹, who argue that previous reviews did not have objective criteria by which to judge whether selection was weak or strong. They suggest that this problem can be resolved if selection estimates for individual traits are standardized to allow comparison with the expected strength of selection on fitness itself (Box 1). Selection on fitness, they argue, provides a clear benchmark for strong selection. In reviewing many of the same studies as Kingsolver *et al.*, Hereford *et al.* conclude that selection estimates are, on average, 54% as strong as selection on fitness (31% after correction for a statistical bias). In their view, these values represent “extremely strong selection overall” and “such large estimates clearly cannot be representative of selection on all traits”¹. They then consider reasons for why current estimates of selection might be biased.

These results¹ raise some perplexing questions. Principal among them is the

Box 1 Measuring selection in natural populations

On the small island of Daphne Major in the Galapagos Islands, Peter and Rosemary Grant and colleagues⁹ measured the beak size of all medium ground finches (*Geospiza fortis*, pictured) before a drought. The abundance of seeds (particularly soft seeds) decreased during the drought and finch mortality was high. When the drought ended but before reproduction started, the Grants determined the beak size of all surviving finches.

The difference in mean beak size from before to after the drought is one measure of the strength of selection (*S*). A related measure is the selection gradient, β , which



can be obtained by dividing *S* by the variance for the trait (β can also be obtained from a regression of the trait on a measure of fitness, in this case survival). Selection estimates can be standardized by dividing *S* or multiplying β by the standard deviation of the trait. β is additionally useful because it can account for correlations among traits. The

standardized strength of selection on beak depth during the drought was $S = 0.63$ and $\beta = 0.53$. That is, selection favoured large beaks because such beaks could crack the harder seeds that remained.

Endler⁴ and Kingsolver *et al.*⁷ compiled standardized *S* or β values for many studies and traits. Hereford and colleagues¹ took a similar approach, except that β values were standardized by the mean for the trait, rather than its standard deviation. Hereford *et al.* argue that the benefit of standardizing selection by the mean is that the corresponding value for fitness should be 1. **A.P.H.**

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apparent paradox that typical studies of selection do not have the statistical power necessary^{7,8} to detect selection that appears unrealistically strong¹. Unfortunately, this paradox will not be resolved simply by accumulating more data of the same ilk, as all reviews identify problems with our current methods^{1,4,7,8}. How, then, are we to obtain a good handle on the true power of selection in nature?

Evolutionary biologists will have to resolve this uncertainty by determining how best to measure and judge the strength of selection, and by conducting more robust studies of selection. Meanwhile, we are only deluding ourselves that we have a good handle on the typical power of selection in nature. Once we do, we can begin to

investigate how humans are changing selection pressures, and whether populations and species will be able to adapt accordingly. ■

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1. Hereford, J., Hansen, T. F. & Houle, D. *Evolution* **58**, 2133–2143 (2004).
2. Darwin, C. *On the Origin of Species* (John Murray, London, 1859).
3. Kettlewell, H. B. D. *The Evolution of Melanism: The Study of a Recurring Necessity* (Oxford Univ. Press, 1973).
4. Endler, J. A. *Natural Selection in the Wild* (Princeton Univ. Press, 1986).
5. Hendry, A. P. & Kinnison, M. T. *Evolution* **53**, 1637–1653 (1999).
6. Stockwell, C. A., Hendry, A. P. & Kinnison, M. T. *Trends Ecol. Evol.* **18**, 94–101 (2003).
7. Kingsolver, J. G. *et al. Am. Nat.* **157**, 245–261 (2001).
8. Hersch, E. I. & Phillips, P. C. *Evolution* **58**, 479–485 (2004).
9. Grant, P. R. & Grant, B. R. *Evolution* **49**, 241–251 (1995).

Planetary science

Saturn's mixed magnetosphere

Fran Bagenal

When interplanetary shock waves hit the Cassini spacecraft and then Saturn in January 2004, it presented a unique opportunity to study the planet's magnetosphere and to compare it with that of Earth.

Saturn can be considered as the geometric mean of Earth and Jupiter in terms of the strength and extent of its magnetic field. Three papers in this issue — by Clarke *et al.*¹, Kurth *et al.*² and Cray *et al.*³ — describe the response of Saturn's magnetosphere to changes in the solar wind as observed by NASA's Cassini spacecraft and the Hubble Space Telescope (HST). The authors conclude that some aspects of the behaviour of Saturn's magnetosphere are similar to the behaviour of Earth's magnetosphere, some to that of Jupiter's and some are unique. Studies of Saturn's magnetic field and how it is driven by the solar wind are interesting in their own right, but they also allow researchers to compare different planetary magnetospheres and to test our understanding of Earth's system by applying the same principles to different conditions.

Earth's magnetic field forms a cavity in the solar wind — the stream of electromagnetic radiation and charged particles that flows outwards from the Sun. Earth's magnetosphere extends roughly 10 times the planet's radius towards the Sun and many hundreds of Earth radii away from the Sun, in a 'magnetotail' stretching downstream of Earth in the solar wind. Jupiter is much larger than Earth (by a factor of 11), and its magnetosphere is also vast, extending 50–100 jovian radii on the dayside, with a magnetotail that stretches out to its orbit distance. Saturn's magnetosphere (Fig. 1, overleaf) is an intermediate case, extending about 20 Saturn radii towards the Sun (Saturn's radius is 9.4 times that of Earth).

Most of the material in Earth's magnetosphere is a plasma of protons and electrons that has leaked in from the solar wind. By contrast, the magnetospheres of Jupiter and Saturn are mainly fed by plasma sources of heavy ions from their satellites.

The three papers^{1–3}, beginning on page 717, describe observations of magnetosphere dynamics at Saturn. In Earth's magnetosphere, plasma circulates in a flow pattern that is primarily driven by the coupling of the planetary magnetic field to the solar wind. Within about 15° of the poles, Earth's magnetic field is directly connected to the solar wind. At lower latitudes the magnetic field topology is closed, with magnetic field lines connected at both ends to the planetary dynamo. At the outer boundary of the magnetosphere — the dayside 'magnetopause' — small regions of closed magnetic field couple to the solar magnetic field (which is swept towards the planet by the solar wind) in a process called magnetic reconnection. Once coupled to the solar wind, these tubes of magnetic flux are swept back over Earth's poles and down the magnetotail where they reconnect to closed field lines — as they must, to conserve the total magnetic flux from the planet.

The stresses associated with this process of coupling solar wind and magnetosphere drive electrical currents between the magnetopause and the ionosphere (the ionized upper part of the planet's atmosphere), leading to radio and auroral emissions. The terrestrial aurorae form in rings around Earth's magnetic poles, at the boundaries



100 YEARS AGO

What mutation is in biology, conversion is in psychology, and revolution in sociology. It may be said that to assume such parallels is merely to beg the question, but I think that the apparent parallelism cannot be without significance... If the supposed analogy is a valid one, it appears to follow that mutability is due to the same general causes as ordinary variability (just as change of opinion and reform are due to the same general causes as conversion and revolution), but that there is this difference — mutability represents an explosion of energy, as it were, in a given direction, and therefore differs from ordinary variation somewhat as the firing of a gun differs from the explosion of a loose heap of powder... [T]he chance of mutations succeeding from the first is comparatively remote, though such a thing is quite possible; but since they are the result of general causes, the sort of changes the mutations exhibit are likely to come about in due course, just as the sort of changes represented by a revolution are likely to prevail ultimately, though the revolution itself may appear to fail. T. D. A. Cockerell
From *Nature* 16 February 1905.

50 YEARS AGO

Amazon Head-Hunters. By Lewis Cotlow. The author of this book is a New York insurance broker whose hobby is travelling in lands inhabited by primitive races... Between 1940 and 1949 he made several expeditions to the north-west of the South American continent... These are the areas inhabited by the Choco, Colorado and Yagua Indians, and include also the very isolated country of the Jivaro Indians, who are especially known for their custom of drying and shrinking the heads of their enemies... Mr. Cotlow was able to become very friendly with several of their chiefs, and they informed him of the number of heads which they had taken during their lives. He brings out forcibly the fact that the relatives of a man slain in battle are in honour bound to kill his killer and to shrink his decapitated head. The relatives of this victim must retaliate in the same manner, so that inter-community warfare is almost continuous. The author describes fully the method of shrinking a head. Unfortunately, he did not actually see it carried out, since at the time of the raid he was stricken with dysentery.
From *Nature* 19 February 1955.