

An increase in the magnitude of the electric charge,  $Q$ , with  $c$  and  $G$  remaining constant, implies a reduction in the area of the event horizon. By contrast, a decrease in the speed of light,  $c$ , would lead to an increase in event-horizon area. Thus the two contending alternatives for an increase in  $\alpha$  produce opposite outcomes as far as black-hole entropy is concerned.

It could be argued that a reduction in event-horizon area implies a violation of the generalized second law of thermodynamics, and so the fundamental electric charge therefore cannot increase. However, before we can be secure in that interpretation, several conditions must be satisfied. The black hole will radiate heat into its environment through the Hawking process, and, as  $Q$  changes, the temperature will also change. For the second law of thermodynamics to be violated, the black hole must not raise the entropy of the environment by more than its own entropy decreases. This condition is readily satisfied by immersing the black hole in a heat bath of equal temperature and allowing the heat radiation to change isentropically as the charge varies.

Furthermore, equation (3) is based on standard gravitational theory. In a non-standard theory that involves varying  $e$  or  $c$ , the formula for the area of the event horizon might differ<sup>12</sup>. Also, the Hawking process may be modified in a way that alters the relationship between temperature, entropy and event-horizon area. Equation (3) must then be considered as an approximation of the limit of small variation of 'constants'. However, it is unlikely that minor modification of equation (3) will reverse the sign of the relationship between charge and event-horizon area.

Moreover, in the standard theory there is a maximal electric charge, given by  $Q^2 = M^2$ , above which the event horizon disappears and the black hole is replaced by a naked singularity. A modified theory might alter the value of this maximal charge, but there will still be a limit above which any increase in charge will create a naked singularity, violating the cosmic-censorship hypothesis<sup>13</sup>.

Our arguments, although only suggestive, indicate that theories in which  $e$  increases with time are at risk of violating both the second law of thermodynamics and the cosmic-censorship hypothesis. Thus, black-hole thermodynamics may provide a stringent criterion against which contending theories for varying 'constants' should be tested.

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3. Webb, J. K. *et al. Phys. Rev. Lett.* **87**, 091301 (2001).
4. Murphy, M. T. *et al. Mon. Not. R. Astron. Soc.* **327**, 1208–1222 (2001).
5. Barrow, J. D. *Phys. Rev. D* **59**, 043515 (1999).
6. Magueijo, J. *Phys. Rev. D* **62**, 103521 (2000).
7. Sandvik, H. B., Barrow, J. D. & Magueijo, J. *Phys. Rev. Lett.* **88**, 031302 (2002).
8. Bekenstein, J. D. *Phys. Rev. D* **25**, 1527–1539 (1982).
9. Barrow, J. D. & Magueijo, J. *Phys. Lett. B* **443**, 104–110 (1998).
10. Bekenstein, J. D. *Phys. Rev. D* **9**, 3292–3300 (1974).
11. Hawking, S. W. *Phys. Rev. D* **13**, 191–197 (1976).
12. Magueijo, J. *Phys. Rev. D* **63**, 043502 (2001).
13. Penrose, R. *Rev. Nuovo Cimento* **1**, 252–276 (1969).

Kinematics

## Gliding flight in the paradise tree snake

Most vertebrate gliders, such as flying squirrels, use symmetrically paired 'wings' to generate lift during flight, but flying snakes (genus *Chrysopelea*) have no such appendages or other obvious morphological specializations to assist them in their aerial movements<sup>1–6</sup>. Here I describe the three-dimensional kinematics of gliding by the paradise tree snake, *Chrysopelea paradisi*, which indicate that the aerial behaviour of this snake is unlike that of any other glider and that it can exert remarkable control over the direction it takes, despite an apparent lack of control surfaces.

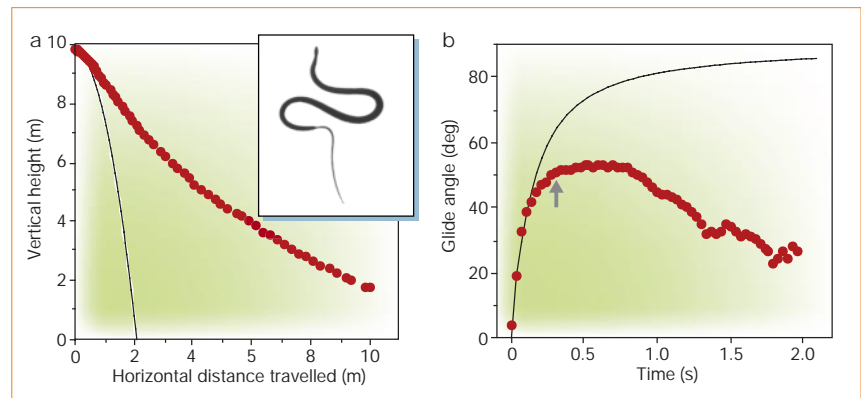
I determined the full three-dimensional gliding trajectory of wild-caught *C. paradisi*, a southeast Asian arboreal colubrid. Snakes were videotaped and photographed jumping from a horizontal branch at the top of a 10-metre-high tower in an open field at the Singapore Zoological Gardens. Two video cameras were positioned to record in stereo, allowing the three-dimensional coordinates

of the head, midpoint and vent of the snake to be monitored throughout its trajectory.

*C. paradisi* prepares for take-off by hanging from a branch, with the anterior body looped into a 'J' shape. The snake jumps by accelerating up and away from the branch, straightening the body and dorsoventrally flattening it from head to vent. Its body width roughly doubles, with the ventral surface acquiring a slightly concave shape. As the snake gains speed while falling, the body pitches downwards and the head and vent are brought towards the midpoint to form an 'S' shape in the horizontal plane. The snake begins to undulate laterally, starting with the anterior body. The flight trajectory shallows (Fig. 1) as lift is generated. Throughout the trajectory, its body posture changes in a characteristic way during each undulatory cycle.

In a typical glide, the snake took off with a maximum upward acceleration of  $14.4 \pm 0.8 \text{ m s}^{-2}$  (mean  $\pm$  s.e.m.) and horizontal velocity of  $1.7 \pm 0.1 \text{ m s}^{-1}$  ( $n=7$  for both) when fully airborne. During mid-glide, the snake undulated at a frequency of  $1.3 \pm 0.1 \text{ Hz}$ , with a wave height (peak to trough) of  $33 \pm 2\%$  snout–vent length ( $n=7$  for both). The airspeed (the speed along its trajectory) and sinking speed were  $8.1 \pm 0.2$  and  $4.7 \pm 0.5 \text{ m s}^{-1}$  ( $n=8$ ), respectively. The glide angle late in the trajectory was  $31 \pm 3^\circ$  ( $n=8$ ), although the glide angle continued to change throughout.

*C. paradisi* is surprisingly adept at aerial manoeuvring. In contrast to many fliers, *C. paradisi* turns without banking. Instead, turns are initiated by movement of the anterior body, and occur only during the half of the undulatory cycle when the head is moving towards the direction of the turn. In one sequence, a snake (snout–vent length, 47 cm;



**Figure 1** Representative glide trajectory of *Chrysopelea paradisi* (snout–vent length, 64 cm; mass, 27 g). **a**, Aerial trajectory, not including take-off sequence. *Chrysopelea* data points (red) are unsmoothed three-dimensional midpoint coordinates, projected in a lateral plane and sampled at 30 Hz. The wing loading, determined from the ventral silhouette of the aerial snake, is  $26 \text{ N m}^{-2}$ . The angle of attack of the anterior body ranges from  $5^\circ$  to  $60^\circ$ . Black curve, theoretical path of a projectile launched with the same initial velocity as the snake. The snake exits from the field of view of the cameras before landing. **b**, Glide angle through time for this same trajectory (red). Glide angle is the angle between the local trajectory and the horizon. The glide angle starts near zero, reflecting the snake's initial horizontal velocity, and then deviates from the theoretical projectile (black) early in the trajectory, roughly where the snake starts undulating (arrow). The glide angle levels off in the ballistic dive at about  $53^\circ$ , then decreases at a rate of  $22^\circ \text{ s}^{-1}$ . Both the glide angle and the airspeed change throughout the trajectory, indicating that equilibrium was not reached in this sequence.

1. Webb, J. K. *et al. Phys. Rev. Lett.* **82**, 884–887 (1999).  
2. Songaila, A. & Cowie, L. L. *Nature* **398**, 667–668 (1999).

mass, 11 g) avoided a tree in mid-glide by turning at an angular velocity of  $0.84 \text{ rad s}^{-1}$ .

Despite its unconventional flight behaviour, *C. paradisi*'s aerial performance is on a par with that of other gliders. Its best glide ratio (the ratio of horizontal distance gained to height lost) is 3.7, which is comparable with that of flying squirrels (*Petaurista petaurista*, 4.7)<sup>7</sup>, flying lizards (*Draco melanopogon*, 3.7)<sup>8</sup> and flying frogs (*Rhacophorus nigropalmatus*, 2.1)<sup>9</sup>. *C. paradisi* is thus potentially capable of using aerial locomotion effectively to move between trees, chase aerial prey or avoid predators.

*C. paradisi*'s aerial lateral undulation is a modified form of a more typical ophidian terrestrial locomotion, although in air the frequency is one-third lower (relative to the same snake;  $n=4$ ) and the amplitude is higher. The timing of the start of lateral undulation in relation to the shallowing of the trajectory suggests that lateral undulation helps to generate the snake's lift. Aerial locomotion in snakes is probably more complicated than terrestrial locomotion because gliding involves lateral undulation while simultaneously maintaining a concave ventral shape; to my knowledge, this combination of movement and postural regulation is not known to occur together in any other snake and probably requires specialized neuromuscular control.

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- Daly, M. *Bombay Nat. Hist. J.* **12**, 589 (1899).
- Flower, S. S. *Proc. Zool. Soc. Lond.* **16** May (1899).
- Wall, F. J. *Bombay Nat. Hist. Soc.* **18**, 227–243 (1908).
- Vaughn-Arbuckle, K. H. *J. Bombay Nat. Hist. Soc.* **56**, 640–642 (1959).
- Pendlebury, H. M. *Bull. Raffles Mus.* **5**, 75 (1931).
- Heyer, W. R. & Pongsapipatana, S. *Herpetologica* **26**, 317–319 (1970).
- Scholey, K. D. in *Biona Report 5, Bat flight – Fledermausflug* (ed. Nachtigall, W.) 187–204 (Fischer, Stuttgart, 1986).
- McGuire, J. *Phylogenetic Systematics, Scaling Relationships, and the Evolution of Gliding Performance in Flying Lizards (genus Draco)*. Thesis, Univ. Texas, Austin (1998).
- Emerson, S. B. & Koehl, M. A. R. *Evolution* **44**, 1931–1946 (1990).

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COMMUNICATIONS ARISING

Nitrogen cycle

## What governs nitrogen loss from forest soils?

Nitrogen is lost as dissolved organic compounds in stream waters from unpolluted South American forests, but it is lost mainly as inorganic nitrate in streams flowing from North American forests that suffer nitrogen deposition from the atmosphere<sup>1</sup>. From this it has been inferred that the standard thinking about

how nature deals with nitrogen in soils and waters<sup>2</sup> needs to be re-evaluated and that the conventional wisdom of how nitrogen is absorbed and released by plants<sup>3</sup> must be wrong. We disagree, however, on the grounds that there are other, more likely interpretations of the new results<sup>1</sup>.

How nature deals with nitrogen depends greatly on temperature. Rye-grass plants supplied with equal concentrations of ammonium and nitrate take up an increasing proportion of ammonium as the temperature becomes cooler<sup>4</sup>. Plants are equipped with transport mechanisms for a variety of nitrogen-containing organic solutes<sup>5</sup> and they can absorb small organic molecules such as amino acids in northern temperate forests with cool temperatures<sup>6</sup>.

This flexibility might have evolved because the microbes responsible for releasing soil organic nitrogen as ammonium, and for converting the ammonium to nitrate, become less active as the temperature falls: the conversion to nitrate is inhibited<sup>7,8</sup> at 3–5 °C. This implies that the cooler the average temperature is, the more important it becomes for plants to be able to manage without nitrate and to utilize nitrogen compounds that have not been fully processed by the soil microbes.

The mean annual temperatures at the sites of the South American forest studies<sup>1</sup> were quite low (4–11 °C) so plants there might well have absorbed small nitrogen-containing organic molecules. But the dissolved organic nitrogen found in forest streams does not prove this: 'dissolved' was defined<sup>1</sup> as passing through a filter of pore size smaller than 1 µm and would therefore have included molecules up to 1,000 times larger than those taken up by plants, together with colloidal organic matter and bacteria<sup>9</sup>.

The 'dissolved' organic nitrogen is probably in those streams for the simple reason that it is not needed. A forest ecosystem with no input of nitrogen would evolve to recycle usable nitrogen, inorganic or organic, and to minimize its loss in streams. But very large organic molecules and colloidal organic matter are not usable by plants. The significance of the 'dissolved' organic nitrogen in those streams is not that these are the forms of nitrogen that the forest uses, but that they are the forms that it does not recycle because it cannot use them. These results do not call for a re-evaluation of our thinking about how nature deals with nitrogen in soils and waters because they are what we would expect from our current understanding of the situation.

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- Perakis, S. S. & Hedin, L. O. *Nature* **415**, 416–419 (2002).
- van Breemen, N. *Nature* **415**, 381–382 (2002).

- Pearce, F. *New Scientist* **11** (26 January 2002).
- Clarkson, D. T. & Warner, A. J. *Plant Physiol.* **64**, 557–561 (1979).
- Williams, L. E. & Miller, A. J. *Annu. Rev. Plant Physiol. Plant Mol. Biol.* **52**, 659–688 (2001).
- Persson, J. & Näsaholm, T. *Ecol. Lett.* **4**, 434–438 (2001).
- Anderson, O. E. *Soil Sci. Soc. Am. Proc.* **24**, 286–289 (1960).
- Tyler, K. B. *et al. Soil Sci.* **87**, 123–129 (1959).
- Herbert, B. E. & Bertsch, P. M. in *Carbon Forms and Functions in Forest Soils* (eds Kelly, J. A. & McFee, W. W.) 63–88 (Soil Sci. Soc. Am., Madison, Wisconsin, 1995).

*van Breemen replies* — The predominance of organic nitrogen in stream waters and soil solutions is no proof of plant uptake of organic nitrogen, and could indeed be brought about by the uptake of only inorganic nitrogen, as Addiscott and Brookes claim and standard thinking would have it. Nor did I suggest otherwise<sup>1</sup>. Yet I maintain that "some standard thinking about how nature deals with nitrogen in soils and waters needs to be re-evaluated".

Standard thinking is best summarized by published diagrams of the terrestrial nitrogen cycle — with one exception<sup>2</sup> that I know of, such representations in recent soil-science textbooks<sup>3–6</sup> ignore two features of the nitrogen cycle that have come to light: dissolved organic nitrogen as a potentially important loss term for soil nitrogen<sup>7</sup>, and the apparently widespread ability of plants (including crop plants) to take up dissolved organic nitrogen<sup>8,9</sup>.

Addiscott and Brookes suggest that dissolved organic nitrogen reaching stream water is rather inert. Maybe so, but it has hitherto been largely ignored and we know little about it. The free amino acids present in low concentrations in soil and stream waters probably reflect a small, dynamic pool<sup>8</sup> on the way from a large pool of dissolved high-molecular-mass organic nitrogen to microorganisms, plants or ammonium. Plants might get a better share of that pool than we once thought.

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- van Breemen, N. *Nature* **415**, 381–382 (2002).
- Fisher, F. F. & Binkley, D. *Ecology and Management of Forest Soils* 3rd edn (Wiley, New York, 2000).
- Brady, N. C. & Weil, R. R. *The Nature and Properties of Soils* 12th edn (Prentice Hall, Upper Saddle River, New Jersey, 1999).
- Singer, M. J. & Muns, D. N. *Soils: An Introduction* 4th edn (Prentice Hall, Upper Saddle River, New Jersey, 1999).
- Rowell, D. L. *Soil Science, Methods and Applications* (Addison Wesley Longman, Harlow, UK, 1995; reprinted 1997).
- Miller, R. W. & Gardiner, D. T. *Soils in our Environment* 8th edn (Prentice Hall, Upper Saddle River, New Jersey, 1998).
- Perakis, S. S. & Hedin, L. O. *Nature* **415**, 416–419 (2002).
- Lipson, D. & Näsaholm, T. *Oecologia* **128**, 305–316 (2001).
- Persson, J. & Näsaholm, T. *Ecol. Lett.* **4**, 434–438 (2001).

**Editorial note:** See also addendum from S. S. Perakis and L. O. Hedin on page 665 of this issue.