

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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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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*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"<sup>2</sup>.

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