still operate in each segment separately, but with a reduction in the relevant mutation rate, U, by a factor of three in the case of $\phi6$. This may be important: it permits an increase in the total genome size for a given per base mutation rate[4]. It is known that sex will restore the health of a lineage of protozoa that is senescing after a period of enforced chastity[7]. It would be interesting to know whether, in an experiment similar to that described by Chao, the transferred lines would still decline in fitness if there was an occasional opportunity for segment reassortment between different lines, perhaps at the end of each growth cycle. □

John Maynard Smith is in the Department of Biology, University of Sussex, Brighton BN1 9QG, UK. Sean Nee is in the AFRC Unit of Ecology and Behaviour, Department of Zoology, University of Oxford, South Parks Road, Oxford OX1 3PS, UK.

1. Muller, H.J. *Mut. Res.* **1**, 2–9 (1964).
2. Felsenstein, J. *Genetics* **78**, 737–756 (1974).
3. Chao, L. *Nature* **348**, 454–455 (1990).
4. Pressing, J. & Reanney, D.C. *J. molec. Evol.* **20**, 135–146 (1984).
5. Haigh, J. *Theor. Populat. Biol.* **14**, 251–267 (1978).
6. Nowak, M. & Schuster, P. *J. theor. Biol.* **137**, 375–395 (1989).
7. Bell, G. *Sex and Death in Protozoa. The History of an Obsession* (Cambridge Univ. Press, 1988).

METABOLISM

How to fuel a hummingbird

Jared M. Diamond

FLYING hummingbirds face the problem of fuelling the highest known rates of aerobic metabolism among vertebrates. Migratory hummingbirds have the additional problem of building up large fat deposits (10 per cent of their body mass for each day of premigratory fattening) to meet the energy demands for their long migratory flights. How do they balance the contradictory requirements of fuelling their foraging while conserving fuel for migration? A study by Suarez *et al.*, published in *Proceedings of the National Academy of Sciences* (**87**, 9207–9210; 1990) yields the answer: the birds rely on different energy stores for the two activities.

Hummingbirds' high metabolic rates stem from the fact that they (together with bumblebee bats) are the smallest endothermic vertebrates, and that their preferred foraging mode of hovering is energetically expensive. Suarez *et al.* chose as their study species the Rufous hummingbird, of western North America, which migrates 3,000 km between its summer and winter grounds. To identify the metabolic fuel being used at any instant, Suarez *et al.* measured the respiratory quotient (RQ, the ratio of CO_2 produced to O_2 consumed), which is lower for fat oxidation (0.70) than for carbohydrate oxidation (1.00). The authors induced hummingbirds to hover at an artificial nectar dispenser functioning as a flow-through gas mask, and thereby determined the RQ during a single bout of foraging.

Fasted resting birds yielded an RQ of 0.72, showing that fat is then the main fuel. The RQ rose to 0.81 during the first bout of hover-feeding after a fast, then to 1.0 during subsequent bouts. These values mean there is a shift in energy source from fat to carbohydrate during foraging.

Why? The reason is that hummingbirds must build up fat stores for migration by synthesizing fatty acids from the sugar ingested in nectar. Burning the sugar itself during foraging not only spares fat stores but also avoids the inefficiency of synthesizing fatty acid from glucose and then burning the fat. Migrating hummingbirds, however, have no choice except to burn fat, because of its higher calorie yield per

B & C Calhoun/Bruce Coleman

IMAGE UNAVAILABLE FOR COPYRIGHT REASONS

The hummingbird — hovering close to the metabolic limit.

gram than carbohydrate and because of the need to save weight in flight.

Hummingbird liver and flight muscle contain enough glycogen to support metabolism for only five minutes of flight. By keeping bouts of foraging well under this time limit, the birds can fuel their foraging by glycogen reserves that they replenish from sugar, and can spare their fat stores. Their use of fat after a long fast may be necessitated by exhaustion of glycogen.

Supporting these record-high metabolic rates requires hummingbirds to be jam-packed with metabolic machinery. They top all other animals by large margins in their rates of intestinal glucose absorption, hepatic fatty acid biosynthetic capacity (over ten times that of mammals), and muscle levels of hexokinase and carnitine palmitoyltransferase. Comparison of the capacity of these latter two enzymes for glucose and fatty acid oxidation, respectively, with actual fuel consumption rates during flight shows a capacity to correspond closely to consumption — that is, there is little excess capacity or safety margin.

This comparison is all the more interesting in light of current discussions of the evolutionary design of metabolic machinery. C.R. Taylor and E. Weibel (*Respiration Physiol.* **44**, 1–10; 1981) coined the term 'symmorphosis' to refer to the concept that linked steps in physiological systems should have capacities matched to each other and to prevailing natural loads — if design efficiency were the overriding criterion. Such a framework begs the question of how much safety margin, if any, is designed into physiological systems. Typically, there seems to be a 100 per cent safety margin for nutrient transporters in the mammalian intestine (R. Ferraris and J. Diamond *A. Rev. Physiol.* **51**, 125–141; 1989), but very little if any for the hummingbird enzymes studied by Suarez *et al.* Perhaps hummingbirds have reached a design limit imposed by the difficulty of packing any more enzymes into their flight muscles, where conditions must already have virtually reached standing-room-only at the molecular level. □

Jared M. Diamond is in the Department of Physiology, University of California Medical School, Los Angeles, California 90024, USA.