

competition. At the end of the experiment, a water-saturated airstream without ethylene was passed over sclerotia inhibited from germination in both non-aerated and ethylene-treated tubes. Many sclerotia then germinated within a few days and moulds developed on the soil surface. Thus, at the levels tested, ethylene causes no permanent damage to sclerotia of *S. rolfssii* or to the mould propagules.

**Table 4** Effect of Ethylene on Germination (%) of *Sclerotium rolfssii* Sclerotia on Soil

Soil	Aerated + <i>v.p.m.</i> C <sub>2</sub> H <sub>4</sub> (500 ml min <sup>-1</sup> )	Aerated (500 ml min <sup>-1</sup> )	Non-aerated
Ashburner	0	35	0
Penrith	0	48	10*

\* Only sclerotia nearest ends of tubes germinated.

Although all soils tested were fungistatic, they showed marked differences in ability to produce ethylene. Evidence from other experiments with addition of organic amendments to soil shows that there is an interaction between nutrient levels for microbial growth and the concentration of ethylene required to maintain fungistasis. Soils rich in nutrients produce more ethylene but such soils require higher levels of ethylene to inhibit germination of fungal propagules. Thus, following the terminology of Watson and Ford<sup>2</sup>, nutrient is the main stimulator of propagule germination and ethylene the main inhibitor. The balance between the two determines whether a soil is fungistatic at any given time. This balance between stimulator and inhibitor would also explain why the addition of nutrients to soil temporarily annuls fungistasis<sup>1</sup>.

Ethylene also affects other microorganisms including bacteria, actinomycetes and nematodes in soil and, therefore, will almost certainly have a marked influence on most soil processes including turnover of organic matter and mineralisation of nitrogen. The concept of a balance between nutrient, the stimulator, and ethylene, the inhibitor, has far-reaching implications for the study of the occurrence and control of soil-borne plant diseases, especially those caused by fungal pathogens.

Chemical analyses of soils were done by the Chemistry Branch, Biological and Chemical Research Institute, Rydalmere.

A. M. SMITH

Biological and Chemical Research Institute,  
PMB 10, Rydalmere,  
NSW 2116

- <sup>1</sup> Dobbs, C. G., and Hinson, W. H., *Nature*, **172**, 197 (1953).
- <sup>2</sup> Watson, A. G., and Ford, E. J., *A. Rev. Phytopathol.*, **10**, 327 (1972).
- <sup>3</sup> Hora, T. S., and Baker, R., *Nature*, **225**, 1071 (1970).
- <sup>4</sup> Balis, C., and Kouyeas, V., *Ann. Inst. Phytopathol. Benaki, N.S.*, **8**, 145 (1968).
- <sup>5</sup> Smith, K. A., and Restall, S. W. F., *J. Soil Sci.*, **22**, 430 (1971).
- <sup>6</sup> Young, R. E., Pratt, H. K., and Biale, J. B., *Analyt. Chem.*, **24**, 551 (1952).

## Energetic Cost of Locomotion in Kangaroos

The hopping of kangaroos is reminiscent of a bouncing ball or the action of a pogo stick. This suggests a significant storage and recovery of energy in elastic elements. One might surmise that the kangaroo's first hop would require a large amount

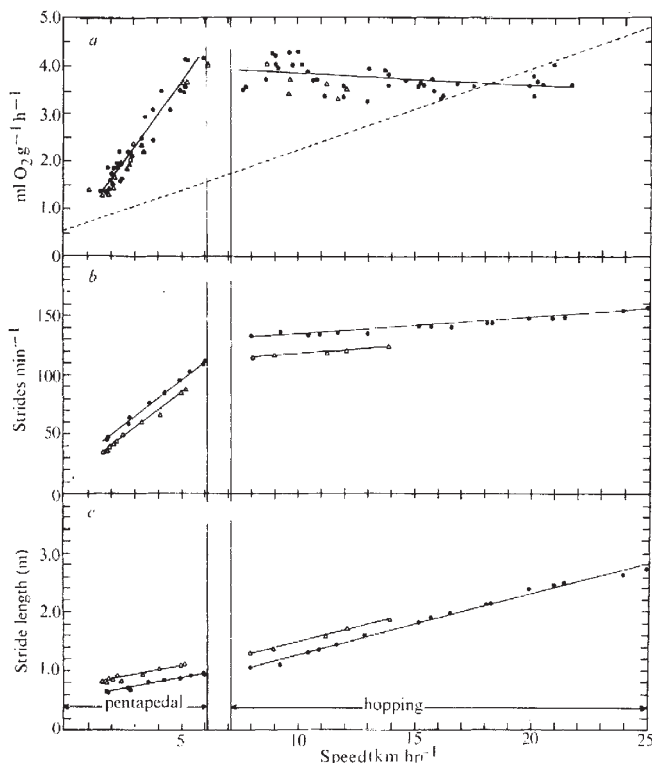
of energy whereas subsequent hops could rely extensively on elastic rebound. If this were the case, then the kangaroo's unusual saltatory mode of locomotion should be an energetically inexpensive way to move.

Recent studies on quadrupedal mammals have shown that the energetic cost of their locomotion varies in a regular manner with size, and the oxygen consumption of a running mammal can be predicted quite closely if its speed and weight are known<sup>1</sup>. This relationship between weight and energetic cost of locomotion for quadrupedal animals provides a baseline against which the energy expended by the hopping kangaroo can be compared. In this study we set out to answer the simple question: Is it cheaper for an animal to hop or to run?

Two red kangaroos (*Megaleia rufa*, 18 and 28 kg average weight, both female) were trained to hop on a treadmill (236 cm long and 76 cm wide) while wearing a lightweight ventilated face mask. Steady state oxygen consumption was measured for 5 to 20 min while they travelled at speeds from 1.0 to 22 km h<sup>-1</sup>. Air temperature was 24° C and wind speed was approximately matched to tread speed. Oxygen consumption increased to a nearly constant value after a minute of hopping at each speed and returned to the resting level almost immediately after the animal stopped. We assumed that the constant level reflected a steady state oxygen consumption and that there was no significant anaerobic metabolism since the oxygen debt observed after a run never amounted to more than 2% of the oxygen consumed during the run. Furthermore, it was clear that maximum levels of aerobic metabolism had not been reached during our experiments, for when the animal struggled we observed oxygen consumption values up to twice those observed at the highest speeds at which we were able to achieve sustained hopping. Oxygen consumption of the animal was measured by pulling room air through a mask at metered rates (300 to 340 l min<sup>-1</sup>) and measuring the difference in oxygen concentration between air entering and leaving the mask (using a Beckman F-3 paramagnetic oxygen analyser). The error involved in this procedure was determined to be less than ±2% by bleeding nitrogen into the mask at known rates (simulating the extraction of oxygen by the animal). In separate experiments stride frequencies were counted at speeds from 1.0 to 25 km h<sup>-1</sup>. Each reported observation is the mean of three half-minute counts. Stride length was calculated from stride frequency and treadmill speed.

At low speeds the kangaroo does not hop but moves by what can perhaps best be described as a 'pentapedal type' of locomotion, since the animal uses its heavy tail as a fifth leg. This type of locomotion has also been called 'slow progression'<sup>2</sup>. When moving in this manner the animal (starting with its hind feet and tail on the ground): (a) puts its front feet on the ground and pulls its tail towards the body causing the hind limbs to lift until only the rear toes are touching; (b) swings its hind limbs forward together while supporting itself on its front limbs and tail; (c) lifts its front legs off the ground; and (d) moves its front feet forward as it repeats the cycle. This form of locomotion not only looks awkward but appears to be energetically quite costly compared to quadrupedal running (Fig. 1a). Oxygen consumption increased nearly linearly as the animal increased its speed from 1 to 6 km h<sup>-1</sup> while moving pentapedally (slope 0.66; *y* intercept 0.35; correlation coefficient 0.96 for the 18 kg animal). Oxygen consumption at 6 km h<sup>-1</sup> was about twenty times the predicted standard metabolic rate<sup>3</sup>. The observed slope for the relationship between oxygen consumption and pentapedal speed was 3.9 times that predicted for an 18 kg animal running on four legs. The increase in speed while moving pentapedally was achieved primarily by increasing stride frequency (Fig. 1b) and stride length increased only slightly (Fig. 1c).

The kangaroos changed from the 'pentapedal type' of locomotion to bipedal hopping between 6 and 7 km h<sup>-1</sup>. As the animals increased their hopping speed (from 7 to 22 km h<sup>-1</sup> in the smaller kangaroo) there was a slight decline in oxygen consumption. This slight decline does not represent a maximum



**Fig. 1** *a*, Steady state oxygen consumption; *b*, stride frequency; *c*, stride length of the red kangaroo as a function of speed. The dashed line in *a* represents the oxygen consumption predicted for an 18 kg mammal running quadrupedally<sup>1</sup>. Data are from two female animals which weighed 18 kg (●) and 28 kg (△). The regression lines for oxygen consumption as a function of speed were calculated (method of least squares) using only the data from the 18 kg animal. For pentapedal locomotion,  $n=27$ , slope=0.66,  $y$  intercept=0.35, correlation coefficient=+0.96  $P<0.001$ . For hopping,  $n=39$ , slope=-0.026,  $y$  intercept=4.09, correlation coefficient=-0.40  $P<0.01$ . Stride frequency was measured separately from oxygen consumption, thus the data points in *b* and *c* do not correspond with those in *a*. The lines for stride frequency and stride length as a function of speed were fitted by eye.

sustained oxygen consumption since the animals were capable of more than doubling their metabolism above this level when they struggled. The values for oxygen consumption of the 28 kg kangaroo tended to be lower than those from the 18 kg animal (Fig. 1*a*). We were, however, unable to obtain higher speeds safely with the larger animal because our treadmill was too short.

The number of hops  $\text{min}^{-1}$ , like the oxygen consumption, was nearly the same over a wide range of speeds (Fig. 1*b*), thus the animals increased their speed primarily by increasing the distance per hop (Fig. 1*c*). The almost constant hopping frequency observed over a three-fold change in speed means that the duration of each hop is constant. The time on the ground, however, decreases and time off the ground increases. The 18 kg kangaroo with its shorter legs hopped at a higher frequency than the 28 kg animal.

Although the distance per hop increased with increasing speed, the amount of energy expended per hop was nearly constant. Thus the animals achieved greater acceleration on take-off as they moved faster, without expending more energy. This is probably due to a greater storage and recovery of energy in the elastic elements as the animals travel at higher speeds.

The tendons and ligaments in the rear limbs and the tail seem admirably suited for storage of elastic energy. The achilles tendon is an extremely large tendon (approximately 1.5 cm in diameter and 35 cm in length in a 40 kg animal which we dissected). Badoux<sup>4</sup> comments that the very long calcaneus seems to act as a lever for the tendons and ligaments of the achilles formation. As the kangaroo landed at higher speeds,

more force would be applied on this lever causing greater stretching of these elastic elements. Recovery of this stored energy on take-off might well explain the slight decline in oxygen consumption with increasing speed of hopping. It is also possible that other systems play a role in elastic storage of energy as the kangaroo hops, and the classic example of the suspensory or springing ligaments of the horse fetlock comes to mind<sup>6</sup>. Two broad sheets of tendons run along both the ventro-lateral and dorso-lateral aspects of the tail. The ventral tendons appear involved in pulling the tail towards the animal during pentapedal locomotion while the dorsal ones might be involved in elastic storage of energy during hopping.

From our data it is seen that at speeds of less than  $18 \text{ km h}^{-1}$  the hopping kangaroo expends more energy than a running four-legged animal of the same weight, but at speeds exceeding  $18 \text{ km h}^{-1}$  it appears to be cheaper to hop. Accurate measurements of speeds at which undisturbed kangaroos ordinarily travel in nature are not available. Kangaroos can, however, travel at speeds considerably faster than the maximum speeds which were possible in our studies. Most observers agree that large kangaroos can sustain speeds of  $40 \text{ km h}^{-1}$  for several km and may reach  $50\text{--}65 \text{ km h}^{-1}$  in short bursts<sup>2,6</sup>.

It is difficult to understand why large hopping herbivores are found only in Australia, since hopping appears to be such an inexpensive way to travel at high speeds. The energetics of hopping, however, may give some insight into the survival of the large hopping herbivores of Australia while their quadrupedal counterparts became extinct. Some 20,000 to 30,000 yr ago, before Palaeolithic man arrived in Australia, the marsupial fauna was much more diverse than at present. There were predators such as the marsupial lions (*Thylacoleo carnifex*) and Tasmanian wolves (*Thylacinus cynocephalus*). There were also large quadrupedal herbivores, some of which were the size of a rhinoceros, for example *Diprotodon* sp. One might speculate that the kangaroos were able to sustain higher speeds when being pursued than those other large terrestrial marsupials, as a result of the low energetic cost of hopping. This could explain how they survived the introduction of man and his dog, the dingo, while the large quadrupedal marsupials became extinct.

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TERENCE J. DAWSON\*  
C. RICHARD TAYLOR

*Museum of Comparative Zoology and  
Biological Laboratories,  
Harvard University,  
Cambridge, Massachusetts 02138*

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\* Permanent address: School of Zoology, University of New South Wales, Kensington, NSW, Australia.

<sup>1</sup> Taylor, C. R., Schmidt Nielsen, K., and Raab, J. L., *Am. J. Physiol.*, **219**, 1104 (1970).

<sup>2</sup> Windsor, D. E., and Dagg, A. I., *J. zool. Res.*, **163**, 165 (1971).

<sup>3</sup> Dawson, T. J., and Hulbert, A. J., *Am. J. Physiol.*, **218**, 1233 (1970).

<sup>4</sup> Badoux, D. M., *Acta Anat.*, **62**, 418 (1965).

<sup>5</sup> Hildebrand, M., *Scient. Am.*, **202**, 148 (1960).

<sup>6</sup> Troughton, E., *Furred Animals of Australia* (Halstead Press, Sydney, 1967).

<sup>7</sup> Tyndale-Biscoe, H., *Life of Marsupials* (Elsevier, New York, 1973).

### Reference Abbreviations

ALL abbreviations of references in *Nature* should now conform to the style of the *World List of Scientific Periodicals*, fourth ed. (Butterworth, 1963-65). Authors submitting manuscripts are asked to ensure that the references are written appropriately.