References and Notes

1. W. C. Clark and H. F. Hunt, in *Physiological Basis of Rehabilitation Medicine*, J. A. Downey and R. C. Darling, Eds. (Saunders, Philadelphia, 1971), pp. 373–401; W. C. Clark, *Res. Clin. Stud. Headache*, in press.
2. D. M. Green and J. A. Swets, *Signal Detection Theory and Psychophysics* (Wiley, New York, 1966); W. C. Clark, *Anesthesiology* **40**, 272 (1974).
3. W. C. Clark, *J. Abnorm. Psychol.* **74**, 363 (1969).
4. C. R. Chapman, T. M. Murphy, S. H. Butler, *Science* **179**, 1246 (1973).
5. D. J. Dillon, *Proc. Am. Psychol. Assoc.* **7**, 872 (1972).
6. In an unpublished study, W. C. Clark and L. Mehl studied the effect on thermal sensitivity of a median nerve block produced by dilute (0.5 percent) Carbocaine (Winthrop). A 2.75-ml dose decreased d' from 1.60 to 0.13, while a 1.50-ml dose decreased d' from 1.53 to 1.27.
7. Board of Acupuncture Anesthesia, *Acupuncture Anesthesia* (in Chinese) (People's Publishing Society, Shanghai, ed. 1, 1972), pp. 214–215.
8. E. G. Dimond, *J. Am. Med. Assoc.* **218**, 1558 (1971).
9. R. Melzack, *Psychol. Today* **7**, 28 (1971).
10. Supported in part by NIH grants NS 09263 and FR 05650. We thank L. Mehl and E. Tupper for assistance with data collection and analysis and M. Rosengarten for the electrical determinations.

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Energy Cost of Animal Locomotion

Gold (*1*) has presented an interesting hypothesis regarding energy expenditure in animal locomotion, that the cost of a step, wingbeat, or swim stroke (in calories per gram per "step") is independent of body size and stepping (flapping, stroking) frequency. This hypothesis merits investigation; unfortunately Gold did not compare it with available information.

In order to check the specific energy cost (C) values derived by Gold, I calculated C for three animals, taking information from Tucker (*2, 3*), Brett (*4*), Gray (*5*), and Muybridge (*6*). The calculations for Table 1 may need some refinement, but of the three only the horse conforms to Gold's prediction. The hypothesis may fit for walking animals, but there are some fundamental differences in flying and swimming which indicate that Gold's hypothesis is oversimplified.

Gold regards as similar the slopes relating log C and log body mass for runners and flyers, -0.40 (*7*) and -0.227 (*2*), respectively. In allometric analysis these values would not be regarded as similar.

There is also a fundamental difference between flying and swimming. The specific energy cost can be obtained as:

$$\begin{aligned} C &= \text{energy cost} \times \text{stride length} \\ &= \text{cal g}^{-1}\ \text{cm}^{-1} \times \text{cm step}^{-1} \\ &= \text{cal g}^{-1}\ \text{“step”}^{-1} \end{aligned} \qquad (1)$$

or

$$\begin{aligned} C &= \text{metabolic rate/step frequency} \\ &= \text{cal g}^{-1}\ \text{hour}^{-1}/\text{step hour}^{-1} \\ &= \text{cal g}^{-1}\ \text{“step”}^{-1} \end{aligned} \qquad (2)$$

If Eq. 2 is used, note that the speed and tailbeat frequency ("stepping frequency") of a fish are linearly proportional (*5*), while wingbeat frequency is independent of airspeed (*3, 8*).

Finally, Gold is qualitatively correct in stating that the proportion of body mass devoted to propulsion increases from mammals to birds to fish. According to Gray (*5*), however, only 45 percent of the mass of a fish is muscle, which does not support Gold's remark that most of the body structure of the fish seems to be devoted to propulsion.

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Table 1. Values of the specific energy cost (C) in calories per gram per "step" calculated from the information available for the horse, budgerigar, and salmon are compared with the values derived by Gold (*1*).

Animal	C (cal g^{-1} "step"$^{-1}$)		Calculated/Gold's
	Calculated	Gold's derivation	
Horse (walking)	2.87×10^{-4}*	3×10^{-4}	0.96
Budgerigar (flying)	2.02×10^{-3}†	1×10^{-4}	20.2
Salmon (swimming)	1.26×10^{-4}‡	4×10^{-5}	3.15

* From (*2*), (2.61 cal g^{-1} hour^{-1})/(5 km/hour^{-1}) = 0.522 cal g^{-1} km^{-1}. From (*6*), for the horse "Eagle," (2.2 m/stride)/4 = 5.5×10^{-4} km/step; 0.522 cal g^{-1} km^{-1} $\times$ 5.5×10^{-4} km/step = 2.87×10^{-4} cal g^{-1} step^{-1}. † From (*3*), 102 cal g^{-1} hour^{-1} = 1.70 cal g^{-1} min^{-1}; dividing this by 840 wingbeats per minute gives 2.02×10^{-3} cal g^{-1} wingbeat^{-1}. ‡ From (*4*, p. 82, figure 2), 880 mg of O_2 per kilogram per hour = 8.21×10^{-4} cal g^{-1} sec^{-1}; dividing this by 78 cm/sec gives 1.053×10^{-5} cal g^{-1} cm^{-1} for 20-cm salmon. From (*5*, p. 48), the distance traveled between tailbeats is 0.6 times the length; 0.6 $\times$ 20 cm = 12 cm. Then 1.053×10^{-5} cal g^{-1} cm^{-1} $\times$ 12 cm/tailbeat = 1.26×10^{-4} cal g^{-1} tailbeat^{-1}.

References

1. A. Gold, *Science* **181**, 275 (1973).
2. V. A. Tucker, *Comp. Biochem. Physiol.* **34**, 841 (1970).
3. ———, *J. Exp. Biol.* **48**, 67 (1968).
4. J. R. Brett, *Sci. Am.* **213** (No. 11), 80 (1965).
5. J. Gray, *Animal Locomotion* (Weidenfeld & Nicolson, London, 1968), pp. 48 and 52.
6. E. Muybridge, *Animals in Motion* (Chapman & Hall, London, 1902), p. 25.
7. K. Schmidt-Nielsen, *Science* **177**, 222 (1972).
8. V. A. Tucker, *Am. J. Physiol.* **222**, 237 (1972).

14 September 1973

Calder has demonstrated that for swimming and flying the "step rule" cannot be interpreted as implying the constancy of energy expenditure for each contraction of the animal's propulsive muscles, but must be more narrowly construed to imply only the constancy of energy expenditure per characteristic length.

Herschman (*1*) has noted that the reported interspecific constancy of the strength of muscle (approximately 4 kg/cm^2), in fact, implies a constancy in the quantity of energy available per contraction per unit of muscle mass (approximately 1 cal/kg). It is instructive to combine this with Calder's observation and some rough anatomical assumptions.

If c is the derived energy cost per step (per characteristic length), then we may write

$$c \propto (m/M)n$$

where m is the mass of propulsive muscle, M is the animal's body mass, and n is the number of muscle contractions required for the animal to travel one characteristic length. The ratio of the c values for running, flying, and swimming, respectively, is 15 : 5 : 2 (*2*). For runners, a reasonable value of m/M is 0.1; for flyers and swimmers, respectively, 0.2 and 0.45 are rough values.

Taking Calder's observation that $n = 1$ is an excellent approximation for running, we find that

$$\begin{aligned} n &= 1/6 = 0.167 \quad \text{(flying)} \\ n &= 2.96 \quad \text{(swimming)} \end{aligned}$$

These are at least qualitatively consistent with Calder's demonstration that a salmon requires about two strokes to swim its own body length, whereas a budgerigar traverses about a meter, some four or five times its wingspan, per wingbeat.

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References

1. A. Herschman, *Am. J. Phys.*, in press.
2. A. Gold, *Science* **181**, 275 (1973).

21 February 1974