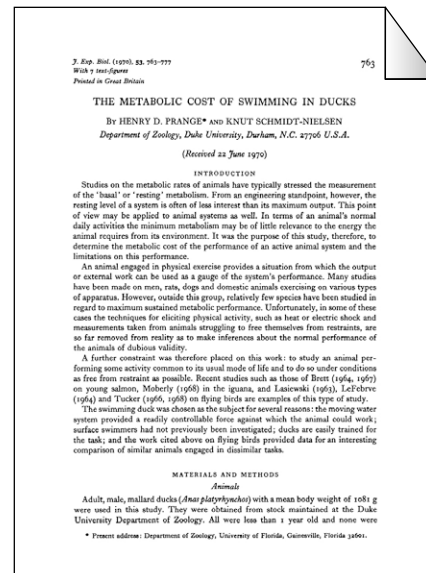


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JEB CLASSICS

FIRST IN THE MEASURE OF ENERGETICS IN A SWIMMING TETRAPOD



Gerald Kooyman discusses Henry Prange and Knut Schmidt-Nielsen's 1970 paper entitled: 'The metabolic cost of swimming in ducks.'

A copy of the paper can be obtained from <http://jeb.biologists.org/cgi/content/abstract/53/3/763>

What is the nature of a classic paper? It can be a result of a single discovery that has extensive connections with several fields of research, but more often it is a result of several characteristics such as 'thoroughness of the method, and that the method is new and it takes a subject in a novel direction' (Heinrich, 2007). The Henry Prange and Knut Schmidt-Nielsen paper of 1970 represents, to my knowledge, the first published report on the study of energetics and flow properties of swimming aquatic tetrapods (Prange and Schmidt-Nielsen, 1970). This was a subject whose time was soon to come, thanks to the subsequent enactment of the Marine Mammal Protection Act two years later. With growing interest in the energetic demands of the large populations of Arctic and Antarctic birds and mammals, it was time to begin measurements. Numerous studies were emerging on diving physiology of these two groups. The lynchpin for understanding the physiology and behaviour of aquatic animals was their cost of transport while at sea. One of the ways to move forward on these questions was by means of laboratory experiments similar to those of Prange and Schmidt-Nielsen.

Their report was simply titled 'The metabolic cost of swimming in ducks':

nothing vague or fancy. Yet, it was thorough in execution and in answering the questions that were raised. Similar studies had been published and were underway dealing with fish (Brett, 1964) and flying birds (Tucker, 1966). Also, a bit more obscure was the work of Wohlschlag on respiratory metabolism of swimming Antarctic fish (Wohlschlag, 1964). He measured oxygen consumption while the fish swam in a Plexiglas, doughnut-shaped chamber, which was rotated at various speeds and immersed in a water bath at -2°C . I have personal, frozen hands-on experience with these studies as a technical assistant to 'Curly' Wohlschlag. But the simplicity of the Prange and Schmidt-Nielsen experiments was brilliant. They used an everyday animal, out of the backyard, that was easily and cheaply trained to perform the required tasks.

The Prange and Schmidt-Nielsen experiments utilised tame and trained mallard ducks in a racetrack-configured water treadmill where they could set a range of speeds appropriate for the ducks. They addressed questions about the mechanics of the bow wave and its relationship to swim speed. They dealt with the problem of turbulence both in the experimental apparatus, and compared their observations in the flume with those of surface swimming ducks on ponds. Considering all of these elements, I would put their study in the category of an inspiration and a model for many who try to think of an experiment that will have influence. They took us beyond the interests of comparative physiology in resting metabolic rate to the more contextual issue of the cost of living in natural conditions.

For me, one of the most satisfying aspects of their work was the comparison of their results with their observations of wild ducks on a pond. They showed that the cost of transport ($\text{kJ kg}^{-1} \text{h}^{-1}$) against swimming speed (m s^{-1}) formed a U-shaped curve in which the lowest cost of transport was at 0.5 m s^{-1} . This matched closely to the preferred swimming speed of ducks on a pond. It illustrated a practical application of the laboratory experiments by showing us what animals in the wild preferred and what that metabolic cost was. This confirmed that some of the energy measurements made in the laboratory are valid for estimation of energy needs of animals in the wild from their behaviour.

There was much interest in knowing more about the energetics of swimming animals described in the major review of

locomotion by Schmidt-Nielsen two years after the Prange and Schmidt-Nielsen paper (Schmidt-Nielsen, 1972), and also a clear need for more work on this subject. Except for the presentation on salmon and a few other fishes in the review, the only other animals represented were in the theoretical discussion of the dolphin and the swimming duck paper. Another paper by Prange in 1976 (Prange, 1976) and a monograph on the hydrodynamics and energetics of fish propulsion by Paul Webb (Webb, 1975) followed the Schmidt-Nielsen review. Reports on swimming energetics then remained quiet until the 1980s when at least seven important papers came out in *The Journal of Experimental Biology* alone, and four more stars in locomotion and energetics began to shine. Robert Blake published a book on fish mechanics (Blake, 1983). Pat Butler began reporting on diving energetics and cardiovascular responses in swimming and diving ducks (Woakes and Butler, 1983). Frank Fish began his studies on a variety of aquatic mammals from the bottlenose dolphin to the platypus (Fish, 1984; Fish et al., 1983; Fish et al., 1988). Terrie Williams first published on swimming metabolism and hydrodynamics in the mink (Williams, 1983), followed by a report of drag measurements of seals trained to be towed around a ring-tank by their teeth (Williams and Kooyman, 1985). On the personal side, I was attracted to the Physiological Research Laboratory at Scripps Institution of Oceanography in part because of the ring-tank and holding tanks designed and built in 1965 under the direction of Per F. Scholander for the express purpose of studies on marine tetrapods. It took 10 years for me to gain the funding to launch such studies, but some of the results, in addition to the Williams study, included similar work on sea lions conducted by Steve Feldkamp, one of my graduate students (Feldkamp, 1987). Going beyond in-place water flumes that were standard laboratory items, Boris Culik constructed a portable water flume large enough to accommodate penguins. He took it to Antarctica to obtain important data on the food needs of penguins (Culik et al., 1994).

What we learnt from laboratory studies, and continue to learn from the sophisticated instrumentation now being applied in field

studies, is that swimming animals travel on the cheap. Some, especially penguins, have near-perfect hydrodynamic bodies that reduce drag to a minimum. Divers often get a free ride when gliding during descent and ascent or when in a burst-and-glide mode. In short, research since the 1970s confirms what Schmidt-Nielsen (Schmidt-Nielsen, 1972) speculated about in his review paper: that swimming is the most economical means of locomotion.

From the 1990s to the present there has been a move away from studying how marine animals swim in the laboratory to field work on free-ranging, wild animals. With the development and use of microprocessors imbedded in submersible dive recorders in the late 1980s, it has become possible to measure a host of variables similar to what Prange and Schmidt-Nielsen did with their ducks in the water flume or treadmill. Today, these instruments are attached to penguins, seals and even the largest of whales, ranging hundreds of miles out to sea and diving to depths of thousands of metres. Perhaps the capstone of this steady flow of papers is a recently published report that Schmidt-Nielsen would have dearly appreciated because of his own research on scaling. Based on numerous measurements from complex submersible recorders, called bio-loggers, that were attached to a variety of penguins, Katsufumi Sato has scaled swim variables to body mass and shown a relationship to minimum cost of transport (Sato et al., 2009).

In summary, the Prange/Schmidt-Nielsen paper was the first in an investigation of locomotion in aquatic tetrapods in what has become an important field of research in comparative physiology. They set a standard for thoroughness in their experiment that is a guide to all investigators conducting such projects. The discipline has evolved from work in the laboratory to the utilisation of bio-loggers for field work in which the variables measured range from time and depth to a Global Positioning System (GPS) for location of the animal on the planet. Furthermore, some investigators go along for the ride, so to speak, capturing a visualisation of what the animal is seeing including a forward-looking camera or 'Cittercam' within the

device (Davis et al., 1999; Marshall et al., 2007).

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References

- Blake, R. W. (1983). *Fish Locomotion*. Cambridge: Cambridge University Press.
- Brett, J. (1964). The respiratory metabolism and swimming performance of young sockeye salmon. *J. Fish. Res. Board Can.* **21**, 1183-1226.
- Culik, B. M., Wilson, R. P. and Bannasch, R. (1994). Underwater swimming at low energetic cost by pygosealid penguins. *J. Exp. Biol.* **197**, 65-78.
- Davis, R., Fuiman, L., Williams, T., Collier, S., Hagey, W., Kanatous, S., Kohin, S. and Horning, M. (1999). Hunting behavior of a marine mammal beneath the Antarctic fast ice. *Science* **283**, 993-996.
- Feldkamp, S. D. (1987). Swimming in the California sea lion: morphometrics, drag and energetics. *J. Exp. Biol.* **131**, 117-135.
- Fish, F. E. (1984). Mechanics, power output and efficiency of the swimming muskrat (*Ondatra zibethicus*). *J. Exp. Biol.* **110**, 183-201.
- Fish, F. E., Innes, S. and Ronald, K. (1983). Swimming dynamics of the harp seal and ringed seal. *Amer. Soc. Zool.* **23**, 906.
- Fish, F. E., Innes, S. and Ronald, K. (1988). Kinematics and estimated thrust production of swimming harp and ringed seals. *J. Exp. Biol.* **137**, 157-173.
- Heinrich, B. (2007). The origin of insect thermoregulatory studies. *J. Exp. Biol.* **210**, 177-179.
- Marshall, G., Bakhtiari, M., Shepard, M., Tweedy, J., III, Rasch, D., Abernathy, K., Joliff, B., Carrier, J. and Heithaus, M. R. (2007). An advanced solid-state animal-borne video and environmental data-logging device ('Cittercam') for marine research. *Mar. Technol. Soc. J.* **41**, 31-38.
- Prange, H. D. (1976). Energetics of swimming of a sea turtle. *J. Exp. Biol.* **64**, 1-12.
- Prange, H. D. and Schmidt-Nielsen, K. (1970). The metabolic cost of swimming in ducks. *J. Exp. Biol.* **53**, 763-777.
- Sato, K., Shiomi, K., Watanabe, Y., Watanuki, Y., Takahashi, A. and Ponganis, P. J. (2009). Scaling of swim speed and stroke frequency in geometrically similar penguins: they swim optimally to minimize cost of transport. *Proc. R. Soc. B* **1515**, 1-8.
- Schmidt-Nielsen, K. (1972). Locomotion: energy cost of swimming, flying, and running. *Science* **177**, 222-228.
- Tucker, V. A. (1966). Oxygen consumption of a flying bird. *Science* **154**, 150-151.
- Webb, P. W. (1975). Hydrodynamics and energetics of fish propulsion. *Bull. Fish. Res. Board Can.* **190**, 1-159.
- Williams, T. M. (1983). Locomotion in the North American mink, a semi-aquatic animal. I. Swimming energetics and body drag. *J. Exp. Biol.* **103**, 155-168.
- Williams, T. M. and Kooyman, G. L. (1985). Swimming performance and hydrodynamic characteristics of the harbor seal (*Phoca vitulina*). *Physiol. Zool.* **58**, 576-589.
- Woakes, A. J. and Butler, P. J. (1983). Swimming and diving in tufted ducks, *Aythya fuligula*, with particular reference to heart rate and gas exchange. *J. Exp. Biol.* **107**, 311-329.
- Wohlschlag, D. E. (1964). Respiratory metabolism and ecological characteristics of some fishes from McMurdo Sound. In *Antarctic Research Series I, Biology of the Antarctic Sea, vol. I* (ed. M. O. Lee), pp. 33-62. Washington, D.C.: American Geophysical Union.