OBITUARY

Knut Schmidt-Nielsen (1915–2007)

Quests in comparative physiology.

Knut Schmidt-Nielsen, one of the all-time greats of animal physiology, died on 25 January. His influence on the subject was profound, not only through his original research but also through his books and the meetings he organized.

Schmidt-Nielsen was born in Norway but moved to the United States in 1946. Much of his finest work concerns life in deserts, where the combination of heat and drought makes survival particularly difficult. The most effective means of keeping cool depend on evaporation of precious water, either in the breath or as sweat, but kangaroo rats survive in the Arizona Desert with nothing at all to drink. They keep reasonably cool by spending the day in burrows and emerging only at night. But even at night they would lose much too much water in their breath if it were not for their remarkable noses. The air they breathe in is relatively cool and dry, but it is inevitably warmed in the body and becomes saturated with water vapour. To minimize water loss, this air must be cooled before it leaves the body to condense out most of the vapour.

With his first wife Bodil, Schmidt-Nielsen showed that the incoming air cools the surfaces of the nasal cavity, which, in turn, cool the air when it is breathed out again. He showed that the same principle operates in other mammals and birds, but is particularly effective in kangaroo rats because their nasal surfaces are enlarged by elaborate nasal bones known as turbinals. They also save water by producing exceptionally concentrated urine.

The countercurrent effect in the nose is vital to desert rodents. But it is potentially troublesome to dogs overheated by exercise, as they need to let water evaporate to cool themselves. With colleagues, Schmidt-Nielsen showed that panting dogs avoid the effect by breathing in through the nose but out through the mouth.

Unlike kangaroo rats, camels are too big to retire to burrows in the heat of the day. Working in the Sahara Desert, the Schmidt-Nielsens showed that camels avoid the water loss that evaporative cooling would incur by allowing their bodies to heat up by day and cool by night. A camel may start the morning with a body temperature of only 34 °C, but warms to 41 °C during the afternoon. This strategy would be ineffective for small animals such as kangaroo rats, because they would quickly heat up to lethal temperatures, but it works well for camels. Later, in Australia, Schmidt-Nielsen showed that camels' noses conserve water even more effectively than do those of kangaroo rats; hygroscopic surfaces dry the outgoing air.

Sea birds face a different problem: they have nothing to drink but sea water, which has a much higher osmotic concentration than their blood. In principle, they could produce urine even more concentrated than sea water, but their kidneys are not equal to the task. Instead, Schmidt-Nielsen found that glands opening into their nostrils secrete droplets of concentrated salt solution that are shed by a shake of the head.

With William Bretz, he tackled another aspect of bird physiology — the operation of their lungs. The lungs of birds are very different from those of mammals: instead of being a mass of blind-ended sacs they are formed from slender parallel tubes. Mammalian breathing is a reciprocating process; the air leaves by the same route that it came in. However, Schmidt-Nielsen and Bretz showed that airflow is one-way in bird lungs, flowing in at one end of the tubes and out at the other, and they suggested that gas exchange is enhanced by a countercurrent flow of air and blood. This would help birds to get oxygen into the blood at the high rates needed to power active flight.

In the later part of his career, Schmidt-Nielsen concentrated on the consequences for animals of differences in body size. With C. R. (Dick) Taylor and other colleagues, he measured the rates of oxygen consumption of various mammals, ranging from mice to horses, running at different speeds. They calculated the quantity of oxygen used for each kilogram of animal moving a distance of one metre, and found that this was less for larger animals, falling off in proportion to $(\text{body mass})^{-0.4}$.

Data for flying birds and swimming fish showed similar relationships to body mass, although flight is cheaper than running (for the same body mass), and swimming is cheaper still. These findings, and later work on this theme by others, have given valuable insight into the energy budgets of animals. They have also caused puzzlement (still not wholly dissipated), because they imply that the muscles of small animals work less efficiently than those of large ones.

Of his books, *Desert Animals* (1964) and *Scaling* (1984) cover Schmidt-Nielsen's two main fields of interest. His *Animal Physiology* (1960 and later editions) has been used and appreciated by countless students. *How Animals Work* (1972), my favourite among his books, is a small masterpiece. *The Camel's Nose* (1998) is his autobiography.

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Schmidt-Nielsen understood the value of bringing scientists together. Like the other participants, I benefited enormously from the series of select meetings that he and Liana Bolis arranged at delightful locations in Europe. He convened the small preliminary meeting that laid the foundation for the 1975 'Scaling Conference' in Cambridge, UK, a meeting that inspired much subsequent research. He was president of the International Union of Physiological Sciences from 1980 to 1986.

A fine bronze statue celebrating Schmidt-Nielsen's work with desert animals in particular, which is shown in the picture here, stands outside the Department of Biology at Duke University in Durham, North Carolina, where he had worked since 1952. He received many other honours, including the International Prize for Biology, presented at an impressive ceremony by the Emperor of Japan. He was nevertheless unassuming, with the slight diffidence of manner characteristic of the old-fashioned ideal of the perfect gentleman. He and his wife Margareta were among the most delightful hosts I have known. ■

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