FRONT MATTER: EDITORIAL



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Taking thermal physiology to where the wild things are

The afternoon summer sun beat down on us, as our subjects, 2 free-ranging male lions, lay deep in the shadows of the thick mopane grove. We were in a game reserve in southern Zimbabwe, hoping to dart these lions in order to surgically implant temperature and activity biologgers as part of a conservation physiology study. We predicted that the coolness of the night would likely soon bring these predators into the open, allowing us to dart them. But these lions had no intention of moving that evening. We knew that trying to immobilize them and carry out surgery in dense bush in the dark was too risky. There is a fine line between pushing for the ultimate data and taking the risk that leads to disaster, when working with wild and dangerous animals in their natural habitat.

Reluctantly we steered our Land Rover toward home, the disappointment palpable in our silence. Those young lions, already well known to researchers at the site who were studying their behavior, would have provided important data for our study. We would have to return on another night to try and dart them. With the unprecedented rate of rise in global temperatures associated with climate change, it is important to understand how large, iconic species, such as the African lion, might respond to hotter, drier conditions. Indeed, lion populations already are declining rapidly in many parts of Africa, and unless there are large-scale and immediate increased conservation efforts, lions are likely to disappear from many regions.¹ As apex predators, loss of lions will seriously disrupt ecosystems.

We had hoped our targeted young male lions would emerge into the open, with thoughts of a tasty steak on their minds. Lions display a unique type of "boom and bust" feeding strategy, where hours of inactivity and fasting are interspersed with high-intensity activity and large, high protein meals. Lions prefer large-bodied prey, such as buffalo, giraffe and zebra. We were particularly interested in the energetic balance of lions because our studies on antelope had revealed that large mammals do not maintain a constant body temperature in the face of insufficient food.² How the body temperatures of lions differed from those of their arid-adapted antelope prey species, and what physiological plasticity they had to buffer a changing climate, was not known.

Just as we approached camp, with my mind full of the unanswered questions we hoped to uncover during this study, the cellphone rang and our Land Rover did a u-turn back into the dark bush. Our colleague (in a Land Cruiser) had decided to take an easier track home than us, along the boundary fence. He had stumbled upon a male lion. This lion was likely the culprit that had broken through the reserve fence a couple nights previously. An assistant on our vehicle took up the spotlight position, an invaluable task for speedy night driving, as adequate lights on our old Landy were a luxury we did not have. As we approached, the lion's eyes reflected in the beam of the spotlight, and we realized that this new male was an ideal candidate for the study. He was calmly sitting in a perfect, open, relatively safe area. Luck had turned our way. As I quietly loaded a dart, the researcher leading the lion study glanced my way and whispered rhetorically, "You're happy to do this in the dark, with a small team?"

I knew perfectly well that this was an opportunity we could not afford to throw away and I was eager to get going with the surgery before the nocturnal creatures became too active.

As the white light illuminated the majestic lion, he remained calm and paradoxically placid as I fired a dart into his muscular shoulder. Once the drugs had taken effect, we strategically positioned the vehicles for optimum light and safety. We were about to carry out our first lion surgery at night. We placed one person in charge of keeping an eye out for other potentially inquisitive wild animals, including other lions, while the rest of us got on

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with the procedure. I was confident that with a good headlight, the surgery would be just as simple as it had been on antelope during the day. Also, as the cool evening breeze gently flicked the dark mane of this old lion, I was thankful that the night would make the battle against hyperthermia, common in captured wildlife, easier to win. However, what I omitted to consider was that the strong beam from my headlight would attract every flying insect between Beit Bridge and Bulawayo. Trying to maintain sterility, with a plethora of insects honing directly in on the open surgery site, was a little more taxing than I had imagined. The bugs and mosquitoes had conveniently discovered that my sterile hands were barred from swatting actions, giving them the opportunity to munch into me unabated. Thankfully, a support team of additional people arrived just in time to occupy the fulltime position of keeping the surgery site sterile.

I had done this type of surgery many times before: a small incision in the abdominal wall, insertion of a miniature data logger covered in inert wax, and a tether to secure the logger to the muscle before closing up the wound. As soon as I had completed the suturing, I could finally give a good swipe to the annoying insects. The research team fitted a tracking collar to the lion and collected some biological data and samples. I then injected the antidote and moved off to give Wilbur (as he had just been named) space, while still keeping an eye on him as he recovered from his anesthetic.

As the creatures of the dark noisily started celebrating the coolness that comes with the deepening night, I picked up a set of eyes in the beam of my spotlight. At first I thought it was another lion, but then I realized it was a buffalo with the rest of the herd in tow, also taking advantage of the cool evening air. To our relief, the buffalo did not interfere with our drowsy lion, and quietly moved off, totally unaware that a vulnerable lion lay just a few meters away. This apex predator, lying in close proximity to a prey species, made me excited to recover the data from the implanted logger. What would Wilbur's body temperature do over the course of a year while he hunted, interacted with other lions and established himself in this territory? At the end of my 12-day stay in the reserve, we had successfully implanted biologgers into 19 lions, a sample size big enough to allow us to examine differences in the physiology and behavior of lions of different sex and status (dominant and nomadic lions). I would return in a year's time to help the team recover the data loggers, so that we could examine how the animals functioned across the year, and in the face of very hot temperatures typical of the region (Fig. 1).



Figure 1. One of the collared study lions becomes drowsy as the drugs in the dart (not visible) start to take effect.

Much of what we already know about the physiology of large African mammals in hot and dry environments arises from the work of eminent comparative physiologists like Knut Schmidt-Nielsen and C. Richard Taylor. While the admirable effort by these early comparative physiologists in obtaining the data cannot be underestimated, the way in which the data were collected undermines the validity of some of the conclusions drawn from the results. Working with large, wild mammals is difficult, and was particularly so 50 y ago, so body temperatures typically were measured in tame, juvenile, or restrained animals housed in artificial laboratory environments or small paddocks. Unlike wild animals, the study animals therefore likely were deprived from engaging in normal behavior, such as interactions with other animals and microclimate selection, and their physiology may have been altered by the frequent presence of humans. Over the last 20 years, the development of biologging technology and improved game management techniques have enabled researchers to carry experiments in wild animals going about their daily business in their natural habitats. These studies have shown that the thermoregulatory responses of animals in their natural habitats often differ from those of captive animals. Laboratory experiments reveal what animals can do, while field experiments reveal what animals actually will do in the face of various stressors. Indeed, the significant contribution of behavioral thermoregulation, which is usually less costly than autonomic thermoregulation, can be measured only in free-living animals in their natural habitat.

Our research group investigates the capacity of free-living animals to cope with changed environments and the potential physiological plasticity that may contribute to their success in hotter, drier environments. One phenomenon that we have focused on is selective brain cooling. In the past, researchers studying captive and laboratory animals have suggested that species with a carotid rete are able to survive very high body temperatures because selective brain cooling protects their brains.³⁻⁵ However, our view of selective brain cooling was challenged in the mid-1990s, when the eminent German thermal physiologist Claus Jessen⁶ came to South Africa to measure brain and arterial blood temperatures for the first time in a wild animal. Working with members of our team, he was puzzled to discover that black wildebeest did not exhibit selective brain cooling when they were hottest, which was at the end of the study when they were chased and darted from a helicopter. Instead, their brain temperatures reached 42°C without apparent ill effects for the animals.⁷ When Jessen presented the results at the International Symposium on Thermal Physiology in Copenhagen in 1997, the data were criticized because a helicopter was hardly a natural stressor for an animal. So the team repeated the research, this time using the springbok as the study animal, and this time using activity data loggers to record the patterns of movement in wild animals undisturbed by humans. The data showed clearly that exercise attenuated selective brain cooling, and that the animals experienced their highest body temperatures when they engaged in intense activity.

As a result of studies in free-living animals, and through further investigation of mechanisms in laboratoryhoused animals, selective brain cooling is now understood to have a different function to that originally proposed. By cooling the hypothalamus, and hence temperature sensors that drive heat loss, selective brain cooling inhibits evaporative heat loss. It therefore helps arid-zone mammals to survive in hot environments by reducing water loss, rather than by protecting the brain from thermal damage.² When an antelope is chased by a predator, selective brain cooling is abandoned, and evaporative heat loss mechanisms are activated. In such circumstances, the animal's survival depends on rapid whole body heat loss. Although brain temperature exceeds arterial blood temperature in such circumstances, there do not appear to be consequences for wild animals. Indeed, despite the belief that the brain is the organ most sensitive to heat, during general body heating, the gut is the first organ to fail.⁴

As members of the felid family, the lions that we are studying likely also have a carotid rete. In domestic cats, however, the anatomy of the rete is somewhat different to that seen in antelope. Whether lions or any other freeliving cats have the capacity to employ selective brain cooling is not known. We did not implant temperature probes into the brains of our lions, but the technology and surgical skills exist to do so. Perhaps one day, once we know more about the body temperature patterns of free-living lions, we will investigate their capacity for selective brain cooling as the antelope they prey on do, then they too may have a mechanism that will allow them to conserve body water in hot and dry environments, like those predicted to occur more frequently now with climate change (Fig. 2).



Figure 2. Young male lions taking advantage of the surface water, Zimbabwe (permission obtained from Paul Trethowan to publish the image).

When early comparative physiologists such as Schmidt-Nielsen and Taylor first started investigating the physiological adaptations to hot and dry environments, climate change science was very much in its infancy. And, despite 2015 likely to be the hottest year on Earth ever in recorded history, some people remain unconvinced that the rise in global temperatures has been accelerated by anthropogenic influences. However, in my country, South Africa, the rising temperatures and reduction in rainfall have become glaringly obvious, particularly in areas where many of our iconic large mammals live. A series of heat waves, with maximum air temperatures well above 40°C, occurred recently in October in the world-famous Kruger National Park. Almost a year and half ago, at the 5th International Symposium on the Physiology and Pharmacology of Temperature Regulation (PPTR), delegates in the Kruger National Park were exposed to air temperatures of 36°C. That was despite the conference being held in August, a winter month! Those delegates out on the golf course (on a free afternoon) exposed to the additional heat load from solar radiation had to take care (and drink copiously) to avoid heat illness. Other delegates, viewing game animals from vehicles or relaxing at the camp, had the opportunity to cool down through air-conditioning or plunging into man-made swimming pools. The animals in the Kruger National Park were not so fortunate, although those near to our conference center could seek out the cool water of the Sabie River. During the recent October heat waves, the animals had to cope not only with even greater environmental heat loads, but also with aridity associated with drought in southern Africa. There is no doubt that many animals are severely physiologically stressed during periods of extreme heat, especially when the heat is coupled with low rainfall resulting in poor quality forage and limited or no drinking water.

What mechanisms do our wild animals have to cope in such circumstances? If we are to understand how climate change will affect animals and how best to conserve them, we need to take physiology to where the wild things are. Although field studies often are accompanied by unavoidable risks and variability, they allow us to determine what animals will do, and how they will adapt their behavior, in the face of a complex array of stressors imposed by environmental change. As a researcher wishing to influence conservation strategies, it is important for me to study lions in the field. Also, although the work is particularly challenging, watching an animal recover from an anesthetic and silently slink into the dark bush to carry on with its nighttime activities is a particular pleasure that cannot be reproduced in the laboratory.

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