

INSIDE JEB

High-speed dolphins burn double calories



A dolphin that participated in the study. Photo credit: Terrie Williams.

Surviving in an environment that actively impedes your progress can leave you vulnerable during an escape; couple this with the need to conserve limited oxygen reserves and the magnitude of the challenges faced by many cetaceans when threatened becomes clear. ‘Amazingly, there has been only a handful of studies that have actually measured the energetic cost of a dive for dolphins or whales’, says Terrie Williams, from the University of California Santa Cruz, USA, who is fascinated by how marine mammals balance their energy demands with their finite oxygen supply. Explaining that fleeing dolphins beat their fins continually when swimming full-out, while adopting a more leisurely burst-and-glide style during a routine dive, Williams wondered just how much energy each swimming style uses and how much energy a startled animal may use when evading peril.

Working with a team of expert trainers, Williams and her colleagues spent over 6 months training six bottlenose dolphins that had previously worked with the US Navy to participate in swimming tests that would allow the scientists to measure the metabolic costs of the different swimming styles. In the first test, the dolphins learned to swim at their most comfortable speed while pushing against a force plate in the wall of the pool as the researchers filmed the number of fin beats. In contrast, the second test required the animals to dive down 10 m wearing a fin-beat tracker and swim through a series of hoops before returning to the surface. Fortunately,

Williams was able to take advantage of the animals’ marine lifestyle to directly measure the metabolic cost of each dive by training the animals to surface in an air dome where she could record how much oxygen the animals inhaled as they recharged the oxygen stores that they had consumed while swimming. And when Williams included killer whales in the metabolic measurements, she had to build an oversized 1.7 m² respiration dome to accommodate the larger animals.

After months of patience, the team was eventually able to calculate that bottlenose dolphins consume 3.3 J kg⁻¹ stroke⁻¹ during routine swimming, but the energy consumption almost doubles to 6.4 J kg⁻¹ stroke⁻¹ when swimming their hardest. And when the team added the killer whales’ fin-beat cost to a plot including the swimming costs of bottlenose dolphins, harbour dolphins and belugas, they finally had a tool that they could use to estimate the diving costs of any cetacean.

But what are the conservation implications of the increased cost of each fin beat when whales and dolphins need to avoid danger? Loud man-made noise pollution is thought to be responsible for some mass strandings, so Williams contacted Brandon Southall, who had recorded how a Cuvier’s beaked whale reacted to 20 min of loud sonar. With the recording showing that the whale’s fin-beat pattern increased significantly from ~13.6 to ~17 strokes min⁻¹, she calculated that the startled animals would use 30.5% more energy as their metabolic rate rocketed to power the fleeing animals’ fin beats. And the whale did not recover swiftly, continuing to use the most costly fin beats for almost 2 h after the noise stopped.

‘Not all strokes are the same in terms of energy expenditure for swimming dolphins, and this has enormous implications for the cost of flight from aversive stimuli by wild cetaceans’, says Williams, adding, ‘In view of the number of cetacean mass strandings across the globe and the increase in human presence in the oceans, such data are critical. The

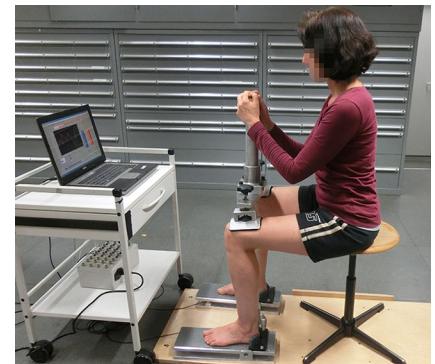
animals in our care provided that opportunity.’

10.1242/jeb.158683

Williams, T. M., Kendall, T. L., Richter, B. P., Ribeiro-French, C. R., John, J. S., Odell, K. L., Losch, B. A., Feuerbach, D. A. and Stamper, M. A. (2017). Swimming and diving energetics in dolphins: a stroke-by-stroke analysis for predicting the cost of flight responses in wild odontocetes. *J. Exp. Biol.* **220**, 1135-1145.

Kathryn Knight

Achilles tendon exercises improve elderly mobility



A member of the study performing Achilles tendon exercises. Photo credit: Gaspar Epro.

Anyone experiencing the ageing process first hand can relate to the loss of muscle strength that we experience in later life, and Gaspar Epro, from the German Sport University Cologne, explains that the tendons that connect muscle to bone also become softer and more elastic as we age. ‘This deterioration has been linked to several problems such as tendon injuries, reduced mobility and poor balance while walking’, he says. But are the effects of age inevitable or can anything be done to stave them off? Knowing that calf press exercises – where individuals flex their feet to press on, and raise, a weighted board – strengthen and stiffen the Achilles tendons of younger athletes, Epro and Kiros Karamanidis wondered whether similar exercises might also benefit the Achilles tendons of older people.

With volunteers ranging from 58 to 73 years of age who were already participating in a study of knee osteoarthritis, the team had a willing group of 21 participants that was keen to try Epro's custom-designed exercise machine to find out whether calf press exercises could build up and improve the stiffness of their Achilles tendons. After MRI scanning each volunteer's lower leg with Jonas Doerner and Julian Luetkens – to build a picture of the initial condition of their Achilles tendons – Epro and Karamanidis provided the volunteers with three exercise sessions a week for a period of 14 weeks. However, Karamanidis and Gert-Peter Brüggemann were also keen to find out whether long-term training was also beneficial, so when nine of the original participants dropped out, Epro and his colleague Andreas Mierau continued offering two training sessions a week for another year and 3 months to the remaining volunteers.

Having rescanned the volunteers' lower limbs at the end of the 14 week training session, the team was impressed to see significant improvements in the condition of their Achilles tendons: in addition to increasing the thickness (cross-sectional area) of the tendon by 6%, the tendon was 23% stiffer and 20% stronger. The exercise had also developed the calf muscle, increasing its strength by 22%. 'Most of the volunteers noticed that it was easier to walk and to keep their balance, so everyday life had already gotten slightly better during the first 2 months. And a few told me they felt way stronger, which meant that they needed to order new winter boots because their calves did not fit into the old ones anymore', says Epro with a smile.

However, when the team followed up the volunteers at the end of the 1.5 year study, the condition of the tendon had not improved any more. Epro says that he was surprised, but the lack of progress seemed to coincide with a plateau in the calf muscle strength, which may have limited the tendon's ability to improve.

Admitting that he was impressed that the cross-sectional area of tendon had increased to such an extent during initial training, Epro says, 'We were expecting that to happen rather later in the training'. And he is excited that it is possible for older people to improve their quality of life by strengthening the Achilles tendon. 'Some of the subjects were surprised and happy that they could play longer with their

grandkids and stay at the Christmas market longer before getting tired', he says.

10.1242/jeb.158659

Epro, G., Mierau, A., Doerner, J., Luetkens, J. A., Scheef, L., Kukuk, G. M., Boecker, H., Maganaris, C. N., Brüggemann, G.-P. and Karamanidis, K. (2017). The Achilles tendon is mechanosensitive in older adults: adaptations following 14 weeks versus 1.5 years of cyclic strain exercise. *J. Exp. Biol.* **220**, 1008-1018.

Kathryn Knight

Bearded dragons colour match their home territory



A bearded dragon before and after changing colour. Photo credit: Adam Elliot.

Blushing and suntanning (or sunburning) are probably the best we can hope for on a spectrum of natural skin tone change; but imagine having access to a whole palette of colours that you could change at will. While chameleons are best known for their pyrotechnic colour displays, dowdier bearded dragons (*Pogona vitticeps*) are also capable of switching between muted shades in a matter of seconds. 'There are three main potential benefits to colour change', says Viviana Cadena, from the University of Melbourne, Australia, explaining that bearded dragons probably change colour to regulate their body temperature; to communicate with the opposition while defending territory and during courtship; and to blend in with the surroundings for camouflage. But Cadena and her colleagues Kathleen Smith, Devi Stuart-Fox and John Endler wanted to understand how bearded dragons alter their colour when the shade of their surroundings changes and when the light intensity alters as a cloud passes over.

'This is important to dragons in the wild because it would affect how well they can use colour change for camouflage to avoid being spotted by a predator', says Cadena, who headed out to northwestern Victoria (near Mildura) and the red desert around

Alice Springs with Smith to collect wild bearded dragons. 'We chose these two populations because their colours and the appearance of the habitats in which they live differed the most amongst all bearded dragon populations', says Cadena, recalling that the lizards were fun to work with, but difficult to catch. 'Spotting them in the wild takes some practice, and their skin is rough and you have to hold them steady because they try to wiggle to get out of your hands', she laughs as she remembers the scratches incurred. But once the lighter (southern) and darker (northern) dragons were back in the Melbourne lab, Cadena and Smith photographed their responses to play sand (similar to the yellow sand tone near Mildura), red desert sand from Alice Springs and black sand from a local pet store. Then the scientists transferred the dragons to the yellow play sand before photographing how the reptiles responded as they varied the light from intense daylight to overcast conditions and early sunrise.

'We found that both populations of bearded dragons were able to change colour to the same extent, but this varied depending on the colour of the background we exposed them to', says Cadena, who saw that once the Mildura lizards had adjusted their colour to match their new surroundings, their hue was always yellower than the more orange-toned Alice Springs lizards. And Cadena was surprised to find that both populations were able to achieve better colour matches with their surroundings when the light was lowest. 'We think this could be because there might be a higher risk of predation at low light levels at dawn and dusk, when many predators are most active', says Cadena.

Having confirmed that that each population is capable of matching its surroundings, Cadena says, 'We believe that the differences in colouration we found between the two populations help the lizards better adapt to the looks of their own habitats'. And she and her colleagues are now eager to find out whether the reptile spectacular extends further into regions of the optical spectrum that our limited vision cannot see.

10.1242/jeb.158667

Cadena, V., Smith, K. R., Endler, J. A. and Stuart-Fox, D. (2017). Geographic divergence and colour change in response to visual backgrounds and illumination intensity in bearded dragons. *J. Exp. Biol.* **220**, 1048-1055.

Kathryn Knight

Birds do not work harder to breathe



An efficient one-way airflow system is essential for bird flight. Extracting more oxygen per breath than mammals, birds can meet the costly fuel demands of flight. However, despite the gains achieved by maximising the amount of oxygen passing through their lungs, the metabolic cost of breathing for birds could be high. Birds were thought to have to work against the weight of their flight muscles loading down the sternum as they breathe, increasing the exertion of breathing even during rest. Yet, no one had ever successfully measured the direct cost of breathing for resting birds. Intrigued by the possibility that high-altitude species may also have evolved special adaptations to minimise the cost of breathing in thin air, Julia York, from the University of British Columbia, Canada, and colleagues from Canada, USA, Peru and Australia, collected 11

species of duck (including teal and pintails) from high-altitude locations (3812 m at Lake Titicaca in Peru) and nearer sea level (~1260 m in Oregon) to measure how much effort it takes birds to breathe.

Recording the work done by a ventilator that was helping the birds to breathe while anaesthetised, York and her colleagues discovered that the respiratory systems of the high-altitude species were less rigid and more compliant than those of the species that are adapted to low-altitude living, which could have helped to reduce their breathing costs relative to their low-altitude cousins. However, when she calculated the metabolic costs of breathing for each of the species, the values fell between 1 and 3% of the basal metabolic rate – the energy required to simply keep that animal alive – which is

as low, and sometimes even lower than, the metabolic cost of breathing for other terrestrial species. And when she measured the volume of the high- and low-altitude birds' respiratory systems, they were essentially the same. So birds do not have to work harder to breathe than mammals and other non-fliers, and the high-altitude ducks had not developed larger lungs to improve their oxygen supply in thin air.

10.1242/jeb.158675

York, J. M., Chua, B. A., Ivy, C. M., Alza, L., Cheek, R., Scott, G. R., McCracken, K. G., Frappell, P. B., Dawson, N. J., Laguë, S. L. and Milsom, W. K. (2017). Respiratory mechanics of eleven avian species resident at high and low altitude. *J. Exp. Biol.* **220**, 1079-1089.

Kathryn Knight
kathryn.knight@biologists.com