

INSIDE JEB

Running birds prioritise safety on uneven terrain



An ostrich jogs over an obstacle runway. Photo credit: Jim Usherwood.

Anyone who does cross-country running knows how uneven the real world is, and moving animals have to constantly negotiate bumps and obstacles in their surroundings. But how does size affect the strategy that animals use when encountering objects that impede progress, and which selective pressures have driven the strategies that they use for negotiating these obstacles? Monica Daley from the Royal Veterinary College, UK, explains that an animal's posture could dramatically affect how it manoeuvres across uneven terrain. Small animals that stand with a crouched posture could use a completely different strategy from large upright animals, and Daley wondered which physical factors have driven differently sized animals to select the strategy that works best for them. Explaining that ground-dwelling birds span a mind-boggling range of sizes from heavy weight ostriches down to dainty crouched quail, Daley and her student Aleksandra Birn-Jeffrey decided to find out more about the strategies that birds ranging in size from 0.2 kg up to 117 kg use when running over a step (p. 3786).

However, sourcing many of the animals in the UK, some of which are native to the USA, was trickier than Daley had anticipated. She also recalls that working with the ostriches was particularly challenging. 'Ola [Birn-Jeffrey] hand-raised these ostriches for 2 years so that they were imprinted on humans so that they could be handled easily and weren't as dangerous', she says.

Birn-Jeffrey and Yvonne Blum then filmed the birds as they ran over steps that ranged in size from 0.1 to 0.5 times the length of their leg, and also measured the forces exerted by the birds to find out how their bodies moved as they crossed the obstacle. However, after 4 years of bird rearing, and data collection and analysis, Birn-Jeffrey discovered that all of the birds, no matter how large or whether their posture was crouched or upright, negotiated the obstacle using the same strategy. Daley admits that she was surprised. 'I thought that we would find that the small animals would crouch and extend the leg to buffer terrain variations and maintain a relatively smooth body motion', she says, adding that she had expected the larger birds to vault up on to the obstacle and down the other side. Instead, all of the birds appeared to launch themselves up on to the obstacle and crouch slightly on top of it before extending their legs as they descended back down. 'It's a compromise strategy in a sense', says Daley.

Meanwhile, Daley was also investigating the physical factors – known as task-level priorities – that influence how birds negotiate uneven terrain in collaboration with Jonathan Hurst, Christian Hubicki and Daniel Renjewski from Oregon State University, USA. The engineers built a computer model to simulate the running birds, and Daley says, 'We used the model to say, here are two alternative "task level priorities", one of them being to prioritise stability – to try to return to a steady gait as quickly as possible – or alternatively to minimise energy cost'. Simulating heavy birds with long legs and lighter birds with shorter legs, the team found that instead of evolving to prioritise stability when running over an obstacle, the birds' movements were determined by the need to move economically and avoid injury. 'What you find is that the model does something very similar to birds when you minimise energy cost and control the leg posture at the start of stance to avoid excessive leg loading', says Daley, who hopes that she and Hurst can now begin to apply the lessons learned from running birds to build stable bipedal robots.

doi:10.1242/jeb.115402

Birn-Jeffrey, A. V., Hubicki, C. M., Blum, Y., Renjewski, D., Hurst, J. W. and Daley, M. A. (2014). Don't break a leg: running birds from quail to ostrich prioritise leg safety and economy on uneven terrain. *J. Exp. Biol.* **217**, 3786–3796.

Kathryn Knight

Double pole cross-country skiing more like sliding run

Walking on snow is tough, so for centuries people have attached planks to their feet to improve movement across winter landscapes. More recently, cross-country skiing has become a popular sport, with sophisticated equipment that is painstakingly prepared before major competitions. Biomechanists Barbara Pellegrini and Chiara Zoppirolli from the University of Verona, Italy, work with top international athletes to assess and improve their performance. So, when cross-country skiers began coming to their lab at the Centre for Research in Mountain Sport and Health to optimise their performance, their colleague Federico Schena realised that they needed to learn more about the basic biomechanics of the different cross-country ski techniques. Having already shown why double poling (where only the arms are used for propulsion) is the most efficient method on flat surfaces, while diagonal stride (where skiers use both their arms and legs, pushing off at the same time with the alternate arm and leg) is most effective up hill and double poling with kick (where the skiers push off intermittently with one leg while double poling) is used to transition between the two techniques, Pellegrini, Paola Zamparo and colleagues have now turned their attention to how the different techniques relate to more conventional forms of motion, such as walking and running (p. 3910).

Fortunately, Pellegrini and her colleagues did not have to head out into icy winter conditions to assess the skiers' performance. Using roller skis and instrumented ski poles that had been designed and built by their colleague Lorenzo Bortolan, Pellegrini and Zoppirolli could measure the performance of skiers on a treadmill inclined at 2 deg and moving at 14 km h⁻¹ as they used each technique.

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The team also had access to some of the fittest cross-country skiers in Italy: ‘They are professional athletes from the military’, says Pellegrini, adding that the athletes were happy to help the scientists with their research by skiing on roller skis in the lab, as they often use them during the summer as part of their out of season training. Pellegrini and Zoppirolli measured the forces exerted through the soles of the skiers’ feet and ski poles, and also filmed the athletes with a six-camera motion-capture system to accurately reconstruct the movement of each body segment.

Analysing the foot force traces and body segment motions, the team calculated how the energy of the body’s centre of mass cycled between potential and kinetic energy while the skiers moved. They realised that when the skiers were double poling, the energy cycle closely resembled that of walkers. And when they calculated the kinetic and potential energy cycles for the skiers as they used the diagonal stride technique, the team realised that the pattern was most similar to running; however, instead of bouncing off the ground, the skiers slid. The team also investigated how much work the skiers had to do to overcome the effects of friction, and discovered that the roller skiing athletes were using 17% of their energy when diagonal striding and 24% when double poling with kick. However, double poling (without kicking) was the most costly technique of all: those skiers used 32% of their energy to overcome friction, and Pellegrini estimates that this could rocket to as much as 81% in bad snow conditions.

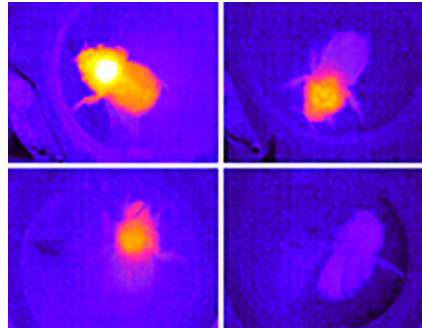
‘The quantification of the work required against friction for the different techniques will allow us to establish whether double poling is abandoned when friction increases and the skier makes the transition to double pole with kick or diagonal stride’, says Pellegrini. She is also optimistic that understanding that diagonal sliding is more similar to running than to walking could help novices to learn faster.

doi:10.1242/jeb.115378

Pellegrini, B., Zoppirolli, C., Bortolan, L., Zamparo, P. and Schena, F. (2014). Gait models and mechanical energy in three cross-country skiing techniques. *J. Exp. Biol.* **217**, 3910–3918.

Kathryn Knight

Bumblebees ration energy use when oxygen is low



Thermal images of bees taken at different O₂ levels. Photo credit: Glenn Tattersall.

Life is easy when the temperature is right and there is enough food, oxygen and water to satisfy demands. But as soon as temperatures fluctuate wildly or an animal ventures beyond its usual terrain, stresses can accumulate and survival can be tough. Life at high altitude can be particularly challenging: not only is it cold but also oxygen is scarce, making it harder for animals to meet their metabolic demands. ‘Most insects... have a relatively low critical P_{O₂}, or partial pressure of oxygen, below which they cannot maintain metabolic rate’, explains Ed Dzialowski. He adds that warm-blooded animals also suffer when oxygen is depleted, with some species allowing their body temperature to fall in a bid to conserve energy: all of which puts bumblebees in an intriguing position. Bumblebees are one of the few insects that actively raise their body temperature above that of their surroundings, which made Dzialowski and his colleagues, Glenn Tattersall, Stewart Nicol and Peter Frappell, wonder how hot bumblebees would cope if oxygen was scarce (p. 3834).

The team rounded up bumblebees near to the University of Tasmania – where the insects are an invasive pest – and took them to the lab ready to monitor the insects’ body temperatures as the oxygen levels dropped. Inserting a microscopic thermocouple (thermometer) into the thorax of some of the insects and monitoring the surface temperature of others with a thermal imaging camera, the team varied the oxygen supply between 5 kPa O₂ (~5% oxygen) and 20 kPa O₂ (~20% oxygen) and monitored each insect’s temperature, metabolic rate (through CO₂ production) and breathing

pattern. ‘Working with the bumblebees was relatively easy’, recalls Dzialowski, although the team had no control over when, or whether, an individual bee would warm up; some of the insects never did.

Analysing the temperature traces of the bumblebees that did get hot, the team could see that the insects fared well at normal oxygen levels (20 kPa O₂), maintaining a temperature of 35.5°C (9.5°C above their surroundings), and only dropping to 31.6°C at 10 kPa O₂. However, when the insects’ oxygen supply was reduced to 5 kPa O₂, their temperature plummeted to 27.3°C. The insects’ metabolism was also limited by oxygen availability and plunged at 5 kPa O₂. And, instead of increasing the rate at which they pump the abdomen when the oxygen supply was reduced – to increase oxygen delivery to the tissues through the tracheole (breathing tube) system – the insects’ pumping rate fell from 327 breaths min⁻¹ at 20 kPa O₂ to 152 breaths min⁻¹ at 5 kPa O₂.

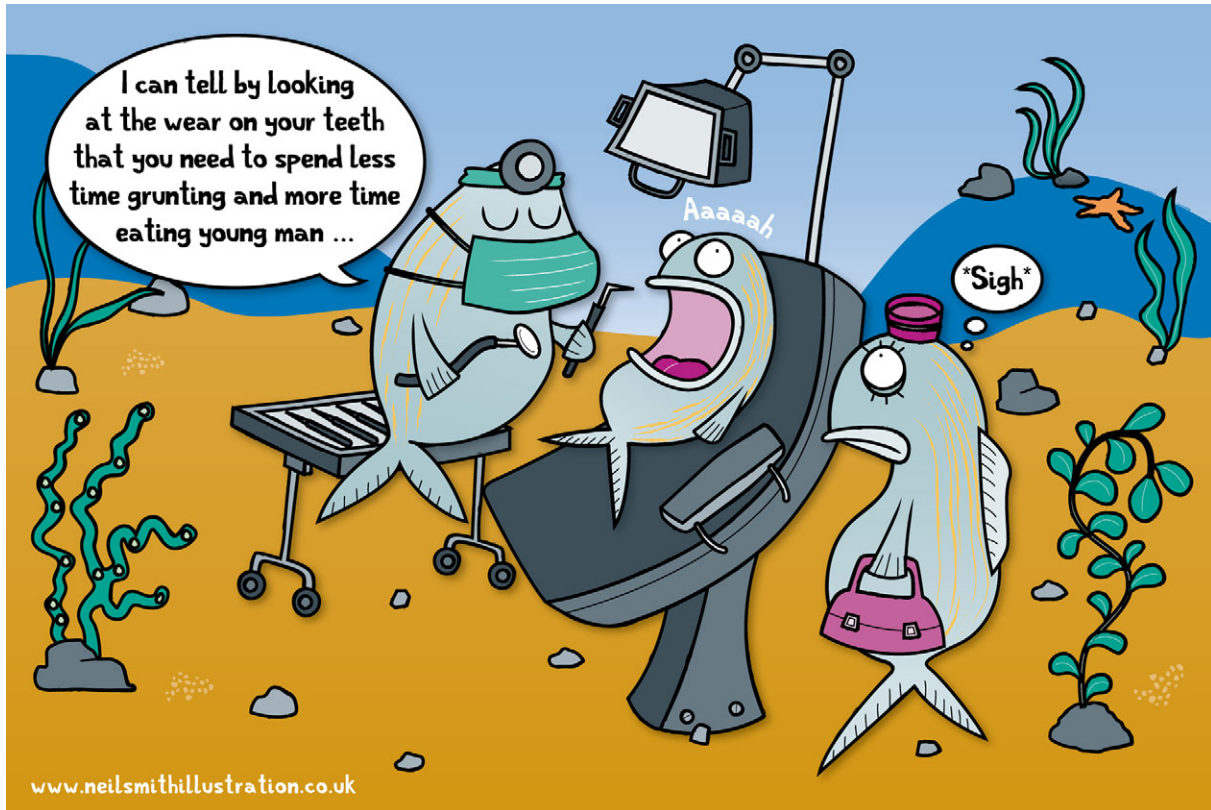
So, bumblebees are able to raise and control their body temperature remarkably well down to oxygen levels that are as low as half normal oxygen (10 kPa O₂). However, when oxygen is scarce (5 kPa O₂), they are unable to maintain an elevated body temperature, although they recover the ability quickly when oxygen returns to normal. Explaining that there are two alternative mechanisms that might prevent bees from regulating their temperature in low oxygen – they could either decrease their temperature set-point, lowering their energy demands and abdominal pumping rates, which would result in decreased heat production, or they might be unable to produce enough energy to elevate their temperature because oxygen is low – the team suspects that the systems that regulate heat production and oxygen delivery by abdominal pumping are tightly coordinated to reduce energy expenditure when there is little oxygen. ‘Bumblebees are excellent at rationing energy use in association with energy availability’, concludes Tattersall.

doi:10.1242/jeb.115394

Dzialowski, E. M., Tattersall, G. J., Nicol, S. C. and Frappell, P. B. (2014). Fluctuations in oxygen influence facultative endothermy in bumblebees. *J. Exp. Biol.* **217**, 3834–3842.

Kathryn Knight

French grunts grind teeth



Many fish are not as toothless as they may first appear. Far back in their throats they carry a second set of jaws – the pharyngeal jaws – equipped with tooth plates studded with teeth that are tailored to each species' own specific diet. Many species are also believed to grind their teeth together to make distinctive calls, but as Frédéric Bertucci and colleagues from the Universities of Liège and Antwerp, Belgium, explain, the relationship between the teeth and any sounds produced by their owners is often only anecdotal: 'Studies focusing on the possible role of pharyngeal jaws in sound production remain rare', they say. Intrigued by the abrupt scratching sounds produced by the French grunt (*Haemulon*

flavolineatum) when alarmed, the team set about recording the fish's calls, testing their hearing and making high-speed X-ray movies of the fish's heads to find out exactly how the grunts produce the distinctive sounds (p. 3862).

The team found that the grunts produced by the fish were pitched at around 700 Hz; however, their hearing sensitivity was strongest at 300 Hz, suggesting that they weren't specifically tuning into the distress calls of their own species. Next, they scrutinised the high speed movies, where they could clearly see the teeth from the top jaw rasping across those of the lower jaw. And when the team took a close look at the

structure of the grinding teeth with scanning electron microscopy, they found that the enamel was slightly worn. They suggest that the fish use the same grinding motion that they use to pulverize food to produce their grunting sounds, and say, 'Sound production is probably an exaptation of the food-processing mechanism in this species'.

doi:10.1242/jeb.115386

Bertucci, F., Ruppé, L., Van Wassenbergh, S., Compère, P. and Parmentier, E. (2014). New insights into the role of the pharyngeal jaw apparatus in the sound-producing mechanism of *Haemulon flavolineatum* (Haemulidae). *J. Exp. Biol.* **217**, 3862–3869.

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