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Inside JEB

ELEPHANTS HALF RUN WITHOUT BOUNCE


Norman Heglund

Most animals don't think anything of breaking into a run: they switch effortlessly from walking to a high-speed bouncing run. But what about elephants? Their sheer size makes it impossible for them to bounce up at high speeds. So how are fast elephants moving: are they running or walking? At a first glance, fast-moving elephants look as if they are walking, according to John Hutchinson from the Royal Veterinary College, UK. But closer analysis of elephant footfall patterns by Hutchinson suggested that speedy elephants' front legs walk while their hind legs may trot. Norman Heglund from the Université catholique de Louvain, Belgium, realised that the only way to resolve the conundrum was to measure the immense forces exerted on the animals by the ground as they move (p. 694).

To measure these forces, Heglund had to construct and calibrate an 8 m long, elephant-sized force platform from sixteen 1 m^2 force plates. Crating the 300 kg force plates, cameras and computers in Belgium and shipping the equipment to the Elephant Conservation Centre in Lampang, Thailand, Heglund, Joakim Genin, Patrick Willems, Giovanni Cavagna and Richard Lair built a reinforced concrete foundation and assembled the force plate platform ready to measure the enormous ground reaction forces generated by the animals.

Encouraged to move by their mahouts, 34 elephants ranging from an 870 kg baby up to a 4 tonne adult moved over the force platform at speeds ranging from a 0.38 $m\,s^{-1}$ stroll to a 4.97 $m\,s^{-1}$ charge. Based on the force measurements, Genin was able to reconstruct the movement of each animal's centre of mass and found that the elephant's movements are extremely economical. Consuming a minimum of 0.8 $J\,kg^{-1}\,m^{-1}$, an elephant's cost of transport is 1/3 that of humans and 1/30 that of mice.

Heglund explains that the elephant's cost of transport is low because the animal's step frequency is higher than expected. They also improve their stability by keeping an average of two feet on the ground even at high speeds, and three at lower speeds. Combining these approaches, the elephant's centre of mass bounces less than other animals', reducing the giant's cost of transport.

Next Genin calculated the way that each animal recycles potential energy into kinetic energy to find out whether they run. According to Heglund, running animals continually recycle potential energy stored in tendons and muscles into bouncing kinetic energy – just like a pogo stick – while walking animals convert potential energy at the start of a stride into kinetic energy as they step forward – much like an inverted swinging pendulum. By tracking how elephants cycle potential energy into kinetic energy over the course of a stride, the team could distinguish whether the high-speed animals were running or walking.

Plotting the potential and kinetic energy of the elephants' centres of mass over the course of many strides at different speeds, the team could see that the elephants were walking like an inverted pendulum at low speeds, but as they moved faster, the kinetic and potential energy plots shifted to look like those of runners. However, when the team analysed the movements of the elephant's centre of mass, they could see that it almost maintained a constant level as the animal shifted its weight from one side to the other, but bobbed down and up like a runner's during the second half of the stride.

So the elephants were running by one measure but not by another and it seems that the forelimbs trot while the hind limbs walk at higher speeds. 'High-speed locomotion in an elephant doesn't fall nicely into a classic category like a run or a trot. It really depends on your definition of "run",' says Heglund.

10.1242/jeb.042879

Genin, J. G., Willems, P. A., Cavagna, G. A., Lair, R. and Heglund, N. C. (2010). Biomechanics of locomotion in Asian elephants. *J. Exp. Biol.* **213**, 694-706.

HUMAN'S HEEL FIRST GAIT IS EFFICIENT FOR WALKING

Most running mammals totter along on their toes. In fact, toe running is far more efficient than landing heel first like humans. Yet when it comes to long distance endurance running, humans are some of the best-adapted animals for clocking up the miles, despite landing heel first. So, why have we stuck with our


David Carrier

inefficient heel first footfall pattern when the rest of our bodies are honed for marathon running? This paradox puzzled Nadja Schilling and Christoph Anders from the Jena University, Germany, and Christopher Cunningham and David Carrier from the University of Utah, USA, until they began to wonder whether our distinctive heel first gait, inherited from our ape forefathers, might be an advantage when we walk. The team put young healthy volunteers through their paces to find out why we walk and run heel first (p. 790).

Measuring the amount of oxygen consumed as their human subjects walked, the team asked the volunteers to walk in one of three different ways: normally, with the heel contacting the ground first; toes first, with the heel slightly raised so that it didn't contact the ground; and up on tip-toes. Then the scientists asked the athletes to repeat the experiments while running heel first and with their heels slightly raised. Calculating the amount of energy required to run and walk, the team found that walking with the heel slightly raised costs 53% more energy than walking heel first, and walking on tip-toe was even less economical. However, there was no difference between the runners' efficiencies when they ran with flat feet and up on their toes.

Our 'heel first' gait makes us incredibly efficient walkers, while both postures are equally efficient for runners. Human walkers burn roughly 70% less energy than human runners when covering the same distance. However, this efficiency would be completely wiped out if we switched to walking on our toes. 'Our ability to walk economically may largely be the result of our plantigrade [heel first] posture,' says Carrier.

But why is heel walking so much more efficient than walking on our toes? To find out, Carrier and his colleagues asked volunteers to run and walk at various speeds in the three postures while recording electrical activity in their muscles to see if the heel first walkers were saving energy by using their muscles differently from toe first walkers. The team also measured the volunteers' metabolic cost of standing on their toes, to find out if increasing stability saved energy, and the forces exerted by the ground on the volunteers' bodies, in case they were reduced in any way that could result in an energy saving.

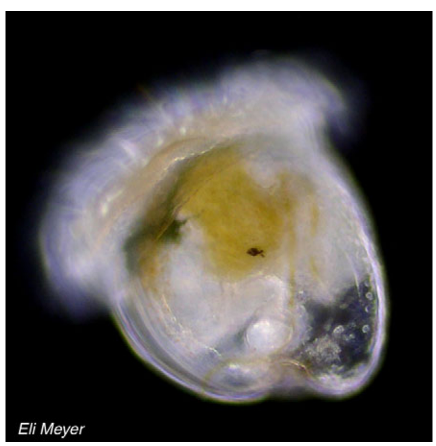
Analysing the results, the team realised that we lose less energy as our heels collide with the ground than we do when we walk toes first. Landing heel first also allows us to transfer more energy from one step to the next to improve our efficiency, while placing the foot flat on the ground reduces the forces around the ankle (generated by the ground pushing against us), which our muscles have to counteract, resulting in another energy saving.

So we still use our ancestor's heel first gait because it makes us better walkers and Carrier adds, 'Given the great distances hunter-gatherers travel, it is not surprising that humans are economical walkers'.

10.1242/jeb.042887

Cunningham, C. B., Schilling, N., Anders, C. and Carrier, D. R. (2010). The influence of foot posture on the cost of transport in humans. *J. Exp. Biol.* **213**, 790-797.

RIBOSOME AND MAINTENANCE GENES AFFECT OYSTER SIZE


Eli Meyer

Some families grow fast and big, while others will always be smaller than average, but what are the genetic causes of these striking growth differences? Curious to find out, Eli Meyer and Donal Manahan from the University of Southern California decided to discover which genes regulate oyster growth and size by investigating the genes expressed in four families of Pacific oyster. Screening 4.5 million cDNAs from the two fast and two slow growing families, the duo identified 34 genes that seem to play a major role in determining whether oyster larvae grow large or small (p. 749).

Comparing the gene sequences with databases of known genes, Meyer and Manahan discovered that over half of the genes that affected the size of oyster larvae are involved in protein synthesis and maintenance. Seventeen of the genes turned out to be components of the ribosome, the enormous protein complex that translates mRNA into proteins, but when the duo looked at the expression patterns of these genes, they did not find that the expression levels were altered in the fast growing oysters. Instead, they found imbalances in the expression ratios of individual ribosome components. Meyer and Manahan suspect that oyster families with these imbalances grow more slowly because they waste energy disposing of excessive ribosomal components.

Proteins involved in general protein maintenance also turned up in the fast and slow growing oysters, with faster growing oysters producing peptidylprolyl isomerase, a protein involved in protein folding, while a subunit of the proteasome, which degrades proteins, was expressed significantly more in fast growing larvae than in slower growing larvae.

Looking at other genes whose expression influenced the oyster larvae's sizes, the duo discovered two membrane proteins, caveolin and fasciclin, and a protein that is known to regulate feeding activity in other molluscs known as small cardioactive peptide precursor protein.

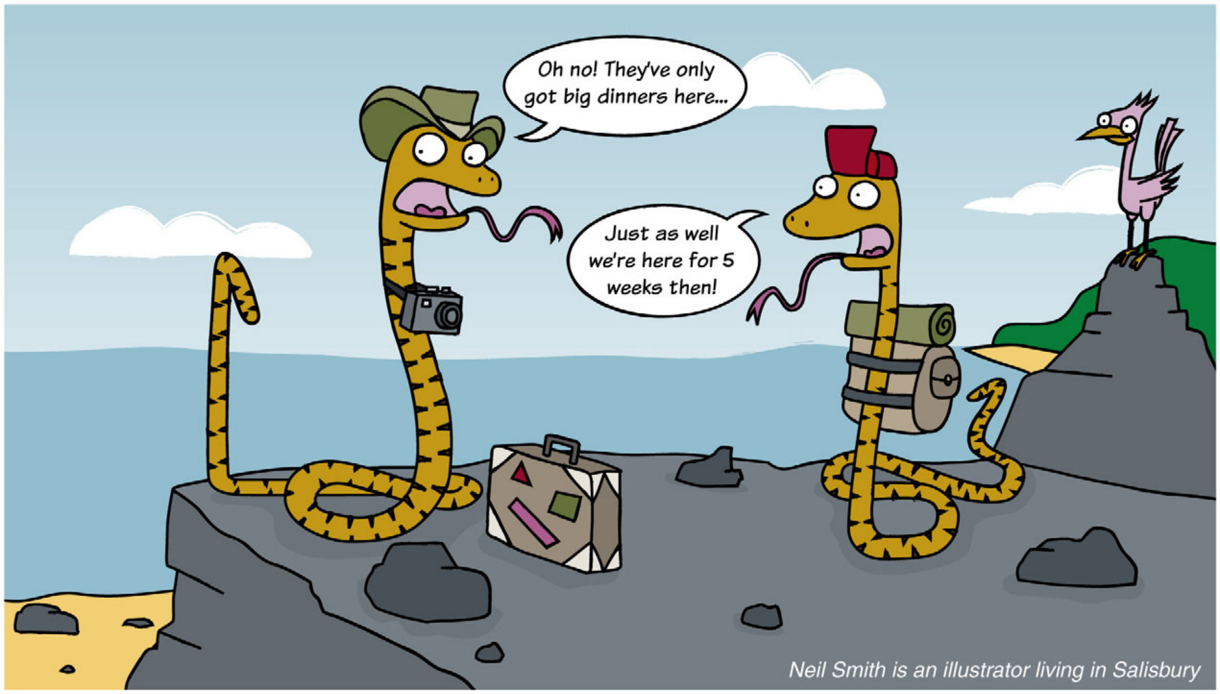
Proteins involved in energy metabolism also turned up in Meyer and Manahan's screen, including genes expressing proteins found in the larvae's energy generating mitochondria, and two nuclear genes that have mitochondrial functions.

Having outlined various genes that play a role in determining oyster larvae size, Meyer and Manahan suggest that it may be possible to identify genes that could indicate larval growth rates, as the expression patterns of some of the genes are directly proportional to the mollusc's growth rates.

10.1242/jeb.042846

Meyer, E. and Manahan, D. T. (2010). Gene expression profiling of genetically determined growth variation in bivalve larvae (*Crassostrea gigas*). *J. Exp. Biol.* **213**, 749-758.

COSTS CAUSE SNAKES TO LOSE HEAD PLASTICITY



Flexibility is often the key to success, and the ability to adjust to new environments often makes the difference between a new colony's survival and oblivion. Fabien Aubret from the Station d'Ecologie Expérimental du CNRS à Moulis and Richard Shine from the University of Sydney explain that, 'adaptive developmental plasticity confers obvious benefits,' but in well-established colonies, this ability to adjust is often lost. For example, when Australian tiger snakes occupy a new habitat they are initially able to adjust the size of their heads to match larger prey. But as time passes the head expansion becomes hard wired into their DNA, young are born with large heads and they lose their developmental plasticity. So why do they lose this ability? Aubret and Shine wondered whether the snakes pay a high fitness cost as a price for their plasticity. The duo decided to measure the consequences of the snake's versatility on their fitness to find out why they lose the ability to adjust head size (p. 735).

Collecting two groups of newly hatched Australian tiger snakes, Aubret and Shine fed small mice to one group and larger meals to the other so that the first group developed small heads and the second group larger heads. Then, when the snakes were 255 days old, they changed the snakes' diets so that they were all on large lunches (from 46.7% to 95.9% of each snake's mass) and filmed the snakes as they attempted to get their meals down.

While the small-headed snakes struggled to swallow their larger meals, they eventually adjusted the size of their heads after 33 days to swallow the large snacks with ease. But what price did the snakes pay for the adjustment?

Measuring the reptiles' growth the duo realised that the growth rates of the small-headed snakes were reduced significantly while their heads enlarged because the reptiles missed meals while it was difficult for them to feed. However, Aubret and Shine explain that once the small-headed snakes had expanded their heads, they were better able to swallow large lunches and their growth rates accelerated to make up for the disadvantage they had faced earlier in life.

So the young of early settlers do incur costs as they adjust their head size, making it beneficial for subsequent generations to hard wire the adaptation into their DNA and this explains why well-established colonies lose the plasticity to remodel their heads.

10.1242/jeb.042853

Aubret, F. and Shine, R. (2010) Fitness costs may explain the post-colonisation erosion of phenotypic plasticity. *J. Exp. Biol.* **213**, 735-739.

Kathryn Knight
kathryn@biologists.com