

Inside JEB is a twice monthly feature, which highlights the key developments in the *Journal of Experimental Biology*. Written by science journalists, the short reports give the inside view of the science in JEB.

Inside JEB

RUNNING COSTS



If you're going to challenge a central dogma, you've got to be prepared to defend your stance. Which is exactly what Richard Marsh from Northeastern University, Boston, does in this issue of *The Journal of Experimental Biology*. So what is the dogma that Marsh and his team have challenged? That the energetic cost of the swing phase in walking and running is negligible. Perceived wisdom held that the leg muscles supporting a walker's body weight while in contact with the ground accounted for the energetic cost of walking, but Marsh and his team challenged this in 2004 with a novel technique looking at blood flow to muscles. This approach suggested that muscles involved in swinging the leg account for 25% of the energetic cost. Having come to this unexpected conclusion, Marsh had to test further. He needed to somehow isolate the cost of swinging the leg from the cost of supporting the body. He decided to measure the metabolic cost and blood flow in running guinea fowl when carrying a weight on their backs, and weights near their feet, to see which muscles worked most during walking and running.

First the team designed a backpack that allowed the birds to carry lead weights on their backs without interfering with their breathing. They also designed lead bands for the birds' lower legs, before setting the animals running on a treadmill. David Ellerby, Havalee Henry and Marsh then measured the animals' metabolic rates while running freely, running in their backpacks, and running with the lower leg weights at speeds ranging from $0.5\text{--}2\text{ m s}^{-1}$. The team also filmed the running birds to see whether the loads hampered their running gaits and to calculate the mechanical energy required to swing the extra weight at the ends of their legs (p. 2050).

Analysing the metabolic readings from the running guinea fowl, the team realised that the birds' metabolic rate only increased by 17% when bearing the 333 g load on their

back. Marsh explains that it had been believed that the increase in metabolic rate was directly proportional to the extra load. But the 333 g weight was 23% of the bird's mass; guinea fowl were running more economically than expected.

Teaming up with Jonas Rubenson, the scientists analysed the extra mechanical work required to move the bird's weighted legs, expecting that the majority of the extra work would be done while swinging the weighted legs. But they soon realised that only 60% of the increased work was required to swing the leg weights. 40% of the increased work was unexpectedly performed while the foot was in contact with the ground. Scrutinising the bird's running technique, the team realised that the bird began to accelerate the extra weight forward while the foot was still in contact with the ground, increasing the mechanical energy of the stance phase more than expected.

Curious to know which leg muscles contributed most as the birds laboured with their leg and back loads, Marsh and Ellerby returned to the blood flow monitoring technique to investigate which leg muscles came into action when the birds ran with, and without, their weights (p. 2064). Injecting the birds with coloured microscopic spheres that became lodged in tiny capillaries, the team were able to monitor which muscles received increased blood flow as they worked harder by recording the quantity of beads trapped in muscles. Injecting the birds with different coloured beads (depending on whether the birds were running freely, running with the backpack, or running with the ankle weights) the team could clearly see which muscles had the highest blood flow and metabolic demands during each running test. The team noticed that 12 muscles were involved in supporting the bird's weight when carrying the 333 g backpacks. However, three of those leg muscles accounted for 70% of this metabolic increase. Which probably explains why the backpacked birds are unable to run much faster than 1.5 m s^{-1} ; the three supporting muscles were already working close to their peak, and couldn't support the birds at faster speeds.

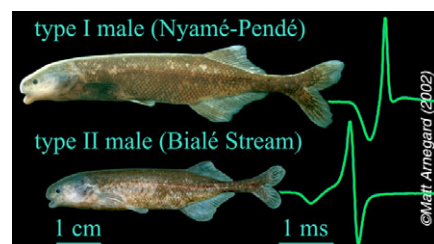
The team also noticed that the same three major stance muscles functioned as extensor muscles across several joints when supporting the extra weight. Marsh suspects that this could account for the birds' remarkably economic gait, as the muscle provides support and propulsion without wasting energy at other joints.

Looking at the blood flow in the leg muscles of the birds running with ankle weights, the team found that muscles involved in swinging the leg increased their blood flow by 58% while the muscles active in the stance phase of a stride increased their blood flow by 42%, agreeing well with the team's earlier mechanical measurements. It seems that the energetic cost of running is much more complex than had been originally thought.

10.1242/jeb.02303

Marsh, R. L., Ellerby, D. J., Henry, H. T. and Rubenson, J. (2006). The energetic costs of trunk and distal limb loading during walking and running in guinea fowl *Numida meleagris*. I. Organismal metabolism and biomechanics. *J. Exp. Biol.* **209**, 2050-2063.
Ellerby, D. J. and Marsh, R. L. (2006). The energetic costs of trunk and distal-limb loading during walking and running in guinea fowl *Numida meleagris*. II. Muscle energy use as indicated by blood flow. *J. Exp. Biol.* **209**, 2064-2075.

SPOT THE DIFFERENCE



When Matt Arnegard joined Carl Hopkins' electric fish lab in 1998, Hopkins thought that two of the fish types he was working with (type I and type II) formed two different species. Arnegard explains that Hopkins drew this conclusion because African electric fish of the same species communicate with a single kind of electric pulse, called an Electric Organ Discharge (EOD), and appear only to mate with fish

that emit the same EOD. Both of the fish types that Hopkins was working with had distinctive EOD signatures. But when Arnegard began looking closely at genetic markers from each of the fish, it was clear that the relationship between the two groups was more complex. Despite their apparent signal differences, the fish were genetically indistinguishable. What was going on? Were the type I and type II fish the founding fathers of two new, as yet undescribed, species, or were they both members of the same species, with one group on the verge of evolutionarily diverging from the other? Puzzled, the team decided that they needed to know more about the enigmatic fish. Arnegard decided to test how the two fish types responded to electric discharge 'calls' from their own, and the other group (p. 2182).

Arnegard and Hopkins left their Cornell lab and set off for the fishes' home in the Ivindo River Basin, deep in the heart of Gabon's rain forest. After a 14 hour drive over rainy-season dirt tracks to the Institut de Recherche en Écologie Tropicale, Arnegard and a team of local fishermen were ready to begin trapping both fish types to see how they responded to each other's electric discharges. Arnegard recalls that trapping the fish was relatively straightforward. By tracking the animals in the river with an electrode attached to an oscilloscope, Arnegard could distinguish whether he was catching type I or type II males.

Recording the males' responses to a choice of type I and type II female EODs, Arnegard realised that the type II males chose to ignore the type I female's EODs, but vigorously attacked the electrode simulating a type II female's EOD, replying with their own electric chirrup; type II males were well attuned to EODs from their own females. But the type I males' responses were less clear-cut. They seemed unable to distinguish between type

I and type II female EODs, responding enthusiastically to both. Type II males seemed to be more selective in their EOD responses than type I males.

More surprisingly, Arnegard realised that the type I males were significantly larger than the type II males. He explains that collecting fish during the mating season allowed him to clearly differentiate youngsters from mature males, and when he compared adult males from both groups, it was clear that type I males were on average 20% longer than the type II males. The differences between the two fish types were more than EOD deep.

Returning to Cornell, Arnegard teamed up with neurophysiologist, Scott Jackson, to test how the fishes' Knollenorgan EOD receptors responded to the individual EOD signatures. Recording Knollenorgan electrical activity as he played EODs to the fish, Arnegard found that the receptors responded to both type I and type II EODs, but generated different response patterns to each signal, allowing the fish to discriminate EODs of their own type from other's EODs.

Having found that type II fish are smaller than type I fish, and respond most strongly to EODs of their own type, Arnegard explains that it is possible the type I and type II fish could be on the brink of diverging into distinct species, but he is anxious to test this possibility further. He says that 'this could be a very interesting evolutionary snapshot', adding 'whatever evolutionary pressures are behind the size difference are probably linked to the signal difference'.

10.1242/jeb.02301

Arnegard, M. E., Jackson, B. S. and Hopkins, C. D. (2006). Time-domain signal divergence and discrimination without receptor modification in sympatric morphs of electric fishes. *J. Exp. Biol.* **209**, 2182-2198.

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PRIMATES PREFER TO AMBLE



Pete Jeffs is an Illustrator living in Paris

When most creatures speed up from a gentle walk, they eventually slip into a trot, and finally a run or gallop at top speed. But quadrupedal primates never seemed to break into a trot on course for a high-speed gallop. According to Daniel Schmitt and his colleagues from Duke University and the University of Alberta, the animals seemed to switch gear from a walk to a gallop with little or no transition between the two extremes. Curious to know which gaits primates adopt at intermediate speeds, Schmitt and his co-workers put primates, ranging in size from 70 g to 25 kg, through their paces to see which gait the animals selected (p. 2042).

Filming the primates, the team gathered clear evidence that the animals rarely broke into a trot, and almost always preferred to 'amble' at intermediate speeds. And when the team mathematically modelled the primate's gait, they realised that the ambling gait significantly reduced the amount that the animal's body bounced up and down. Analysing the mathematical model, Schmitt and his colleagues found that the gait that generated the minimum body-bounce in the mathematical model corresponded well with the ambling gait that the animals preferred at intermediate speeds.

Schmitt suggests that primates amble in preference to trotting to retain stability while rushing through trees. 'Ambling may also be part of a set of basal adaptations associated with the origin of primates 65 million years ago' says Schmitt.

10.1242/jeb.02302

Schmitt, D., Cartmill, M., Griffin, T. M., Hanna, J. B. and Lemelin, P. (2006). Adaptive value of ambling gaits in primates and other mammals. *J. Exp. Biol.* **209**, 2042-2049.

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