INSIDE JEB

Kids are clumsy runners because they are small

Three walking children.
Photo credit: Jim Usherwood.

To the untrained eye, kids just look like scaled-down adults. But take a closer look at the way that they move and a toddler's stiff-legged waddle is completely different from an adult's fluid run. Perceived wisdom held that small children were simply immature versions of their parents: 'Some scientists see a young child appearing to walk and run uneconomically and then attribute it to being underdeveloped', explains Jim Usherwood from the Royal Veterinary College, UK. But when he took a closer look at the way children move, Usherwood questioned this dogma and suspected that he needed to take a completely new approach to try to understand the factors that account for kids' clumsy movements. He wondered whether the children's diminutive stature was responsible for their lack of grace.

Recalling that many of his friends had children of the appropriate size at the time, Usherwood and Tatjana Hubel recruited 18 children – including two of Usherwood's own daughters – ranging in age from 1.1 to 4.7 years, to find out more about their movements. Keeping the children amused with balloons and bubbles, the duo used a camera system to track the position of reflective dots placed at specific locations on the children's limbs as they moved at various speeds along a track, while also measuring the forces that they exerted on the floor. Usherwood adds, 'We were careful not to tell them what gait to use', explaining that Hubel would ask the children to either match their parent's speed, or to go faster or slower, to ensure that she did not bias their movements.

However, having collected the data, the duo then ran into trouble. No matter how hard Hubel tried, the measurements did not stack up. When she attempted to put all of them onto the same size scale – to see how well they agreed with the predictions of the simple models that account for how adults walk and run – one factor kept on confounding her calculations: time. Wracking his brains, Usherwood realised that the mechanical models – some of which are based on inverted pendulums – missed out one key physiological factor: muscle. 'You activate the muscles and there is a physiological cost to activating it', Usherwood says, but this was not accounted for in the models based solely on the physics of movement. He adds that kids' legs are shorter than adults', allowing them less time to push up and away from the ground, providing their muscles with less time to contract and generate the power that they need to move and leaving their feet on the ground for a longer proportion of each stride than the adults'. 'You can see that by watching a 3 year old running, they barely get off the ground', he says. By calculating the amount of muscle that is necessary to generate the movements, Usherwood realised that he could deal with the troublesome time factor.

Building a model that represented the moving people as a single piston that was the length of the individual's leg, Usherwood calculated the amount of muscle required to produce the power necessary to propel the individuals along at the speeds that he and Hubel had measured. This new model successfully reproduced the youngsters' and adults' movements.

So kids move the way that they do simply because they are smaller than adults and their short limbs do not have enough time to produce the high powers needed to lift them into the air when running, not because they are training to be as good as adults.

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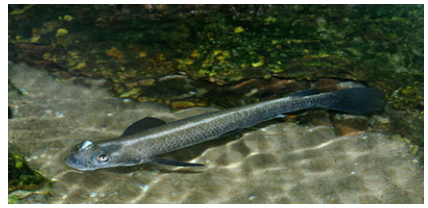
Hubel, T. Y. and Usherwood, J. R. (2015). Children and adults minimise activated muscle volume by selecting gait parameters that balance gross mechanical power and work demands. *J. Exp. Biol.* **218**, 2830-2839.

Kathryn Knight

Largescale foureyes launch jaws to feed on land



Largescale foureyes (*Anableps anableps*).
Photo credit: Quartl (own work).
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When the first fish dragged themselves out of the swamps and onto dry land, they promptly faced a problem: their mouths opened in the wrong direction. While nibbling at morsels suspended in the water is fine when your mouth opens forward, it is of little use when the surface that supports your next snack is horizontal beneath you. The first invaders would have needed flexible mouths to enjoy the nutritious feast awaiting them on the bank. Evidently, the earliest land dwellers managed to overcome the challenge and the rest is history, but Krijn Michel, Peter Aerts and Sam Van Wassenbergh from the University of Antwerp, Belgium, and Alice Gibb, from Northern Flagstaff University, USA, were curious to know more about the adaptations that may have permitted this ground-breaking life transition. 'Records for terrestrial feeding exist for… largescale foureyes', they explain, adding that the eccentrically named fish – which have specially adapted eyes that permit them to see above and below the water's surface – have been known to haul themselves onto the bank to ambush oblivious victims. In order to investigate the fish's technique for feeding on land, Michel purchased nine fish from a local supplier ready to film them in action.

However, before he could begin to dissect the fish's feeding mechanism, he needed to know more about the animal's jaw structure. Fish have many more bones in their intricate

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jaws than most terrestrial animals, so Michel carefully CT scanned the head of one of the largescale foureyes to reveal the complex architecture – including a structure known as the suspensorium (consisting of six bones that connect the jaw to the fish's skull) and the upper and lower jaws. Then, he enticed the hungry fish with a chunk of tasty brown prawn to lurch out of the water onto a ramp as he filmed the manoeuvre. He was amazed to see the fish's jaws almost leapt out of their heads, as the lower jaw rotated down by 90 deg while the upper jaw pushed forward as they engulfed the tasty treat. 'The rotation seemed to be completely dissociated from any restrictions, as if the jaw was on a dislocated joint of some sort', says Michel. And when he compared the fish's feeding technique in the water and on land, he could see that the land-feeders had to move their jaws significantly more than the fish that nibbled in the water.

But how were the largescale foureyes pulling off this remarkable feat? To get inside the fish's head, Michel built a mathematical model of the jaw structure, including a spring linking the lower and upper jaw, and then simulated how the bones might move to reproduce the fish's impressive jaw action. The simulations showed that a ligament linking the upper and lower jaws has to be flexible and placed high on the two bones to provide sufficient leverage to push and rotate the upper jaw far enough forward to snap up prey on the ground. Michel and colleagues also add that the modifications that allow the largescale foureyes' jaws to leap out of its head are in line with the jaw adaptations found in other members of the cyprinodontiform fish family that allow them to manipulate food more deftly.

10.1242/jeb.131599

Michel, K. B., Aerts, P., Gibb, A. C. and Van Wassenbergh, S. (2015). Functional morphology and kinematics of terrestrial feeding in the largescale foureyes (*Anableps anableps*). *J. Exp. Biol.* **218**, 2951-2960.

Kathryn Knight

Daphnia sniff out doom with first antennae

Daphnia longicephala without and with defensive crest. Photo credit: Linda Weiss.

Crustaceans have a reputation for vicious weapons and impenetrable defences. However, Linda Weiss from the University of Birmingham, UK, explains that one diminutive crustacean – the water flea (*Daphnia*) – fine-tunes its defences depending on which predator is in the vicinity. '*D. pulex* is able to distinguish the phantom midge larvae from fish', she says, explaining that the crustaceans remain small and inconspicuous when threatened by fish, but develop neck teeth when menaced by the voracious larvae. As water fleas select their defence strategy in response to the warning odours (kairomones) exuded by specific predators, Weiss and her colleague Ralph Tollrian from the Ruhr-University Bochum, Germany, decided to focus on the responses of developing *Daphnia longicephala* to their archenemy, the back swimmer *Notonecta glauca*. The youngsters develop a helmet-like defensive crest when threatened by the back swimmers, so the duo wondered at which stage of development the minute water fleas produce the defensive structure and how they sniff the odour that triggers the lifestyle change.

However, before Weiss and undergraduate student Julian Leimann could begin testing the developing water flea's reactions to the predator, they had to produce kairomone-scented water. 'The chemical structure of kairomones remains to be determined', says Weiss, so she isolated a few water fleas with predatory back swimmers and collected the kairomone-laced water 24 h later. Then she began testing the effects of the spiced water on the *Daphnia*.

Explaining that the crustaceans shed their shell every 24 h as they move on to the next stage of development, the duo selected youngsters at each developmental stage – from the first instar to the fifth – bathed the water fleas in kairomone water and monitored their development. Scrutinising the youngster's appearance, the duo could see that the youngest life stage (first instar) was unaffected by the warning odour. Instead, the youngsters began responding to the back swimmer's kairomones during the second instar, although they only produced the distinctive protective crest during the fourth instar. And when Weiss and Leimann tested the effects of long-term exposure to the kairomone-scented water, the youngsters did not develop larger crests.

Having confirmed that the youngsters could only respond to the distinctive warning odour once they had reached the second life stage, the duo began testing which of the crustacean's antennae were sensitive to the scent of doom by dabbing a drop of glue onto the first antennae. Knowing that the crustaceans slough off the adhesive when they moult, Weiss realised that she could temporarily inactivate the crustaceans' sense of smell at specific stages of development with a glue mask then wait to see whether the animals were able to develop a defensive crest after bathing in the kairomone. However, the duo made little headway – normal adhesives failed to set on the water flea's damp surface – until Leimann hit on the idea of using waterproof aquarium adhesive. 'This was a great moment', Weiss chuckles.

Impressively, the second instar water fleas were no longer able to produce the defensive display with the glue mask in place. However, once it became detached during the fourth instar, the water fleas responded to the warning odour again, developing defensive crests during the sixth instar 2 days later. So, the receptors for the predator's kairomones are located on the first antenna and Weiss is keen to understand how the tiny crustaceans convert the warning signal into defensive action.

10.1242/jeb.131581

Weiss, L. C., Leimann, J. and Tollrian, R. (2015). Predator-induced defences in *Daphnia longicephala*: kairomone-receptor location and timeline of sensitive phases to trait formation. *J. Exp. Biol.* **218**, 2918-2926.

Kathryn Knight

Toadfish hearing improves with age

Toadfish do not have a reputation for glamour, but what they lack in visual appeal they more than make up for with their chatty personalities: croaking, grunting and moaning like a boat horn (boatwhistle), even the tiniest fry get in on the action. But communication is pointless if there is no one there to hear the message, which made Raquel Vasconcelos from the University of Saint Joseph, China, and colleagues from the Universidade de Lisboa, Portugal – Andreia Ramos, Paulo Fonseca and Clara Amorim – wonder how closely hearing development in the vociferous Lusitanian toadfish (*Halobatrachus didactylus*) matches the development of their vocal repertoire.

Trawling for the communicative fish in the Tagus and Mira river estuaries in Portugal, the team collected animals ranging in size from dainty fry (up to 1.7–2 cm) to fully grown adults (25–35 cm) and recorded the animals' garrulous conversations. Then they shipped fish from the three oldest groups to the University of Washington, USA, where Vasconcelos, Peter Alderks and Joseph Sisneros played short bursts of sound to the animals and measured the sensitivity of the delicate hair cells in the fish's ear to the tones.

Analysing the fish's vocal repertoire, the team noticed that the animals produced single grunts and grunt trains when competing for food, while double croaks and long trains of grunts were associated with sitting alone in shelters, and large juveniles resorted to their distinctive boatwhistles when defending their territory. They also realised that the calls became more sophisticated as the fish grew older. And when they analysed the fish's sensitivity to sound, they noticed that the hearing of the large juveniles was three times more sensitive than that of the small juveniles, while the adults' and large juveniles' hearing was equally sensitive.

So the fish's hearing becomes more sensitive as their vocal repertoire expands and the team adds that learning more about the interplay between the development of the two could help us to understand how communication evolved.

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Vasconcelos, R. O., Alderks, P. W., Ramos, A., Fonseca, P. J., Amorim, M. C. P. and Sisneros, J. A. (2015). Vocal differentiation parallels development of auditory saccular sensitivity in a highly soniferous fish. *J. Exp. Biol.* **218**, 2864-2872.

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