INSIDE JEB

Mystery of broadbills' wing song revealed



An adult male African broadbill at the Ngorongoro Crater, Tanzania. Photo credit: Alexander Kirschel.

Waking up to the bubbling melody of a dawn chorus is one of life's simple pleasures, but not all birds indulge in vocal displays of virtuosity. Some, like hummingbirds, produce exotic buzzing sounds as their wing feathers oscillate while they bustle around. Fascinated by several wing-singing species, Richard Prum and Christopher Clark from Yale University, USA, were keen to expand their repertoire of birds that produce song with their feathers. 'We knew broadbills were reported to make fantastic sounds', says Clark. But it was unclear how the klaxon-like 'brreeeeet' emitted as they make territorial circular flights was produced – and the only way to find out was to film the birds in their natural surroundings. Clark explains that this only became feasible when Prum met Alexander Kirschel from the University of Cyprus at a conference. 'Alex had extensive experience with field work in East Africa and knew places to try to find the birds', explains Clark, so the trio teamed up with Louis Hadjioannou and headed to Uganda in 2011 in search of African broadbills and their close cousins, rufous-sided broadbills.

However, Clark admits that locating African broadbills in the Kibale region of Uganda was particularly gruelling, recalling that the team was on the verge of abandoning the search after days of fruitless effort when they turned down a particularly muddy track: 'All of a sudden we heard one', he laughs, remembering how the team then had to retrace their

steps to collect the cumbersome highspeed camera before filming two of the elusive animals. 'That's all we found that we could film', he laments, although the team had more success locating rufous-sided broadbills. 'They only live in lowland Congo jungle and there was only one patch of this type of habitat in Uganda', says Clark, recalling the treacherous drive to the Semliki National Park. There, the team was fortunate to film one bird for 45 uninterrupted minutes as it displayed enthusiastically in the undergrowth. 'It was the type of angle that documentary filmmakers would fall all over themselves for', chuckles Clark.

Analysing the movies back in the lab, Clark saw that each pulse of sound was produced during the wing downbeat, with the wing tips moving at speeds of 16 m s⁻¹ as the 8th, 9th and 10th primary feathers bent at high speed. However, when Clark tried to reproduce the sounds by positioning those feathers in a wind tunnel, they only ever produced whispers and nothing that sounded like the wing song. 'I spent a long time trying to get those feathers to make sound', says Clark. It was only when he mounted an intact wing in the tunnel that the secret was revealed. Positioning the wing as if it was flying and blowing air over it at speeds up to 17 m s^{-1} , Clark was amazed to see the 6th and 7th primary feathers begin to flutter and make sound. 'We had been testing the wrong feathers the whole time!' exclaims Clark, adding that when he tested the 6th and 7th primary feathers individually they fluttered and sounded like the birds in the jungle.

Kirschel and Hadjioannou then returned to Africa in 2013, where they trapped three African broadbills, carefully trimmed off the tips of the 6th and 7th primary feathers and found that the birds no longer produced a klaxon-like call, sounding more like a ratchet instead. So, broadbills produce their distinctive territorial wing song when the 6th and 7th primary wing feathers flutter in the wind, adding them to Darwin's roll-call of birds that produce 'instrumental music' with their feathers.

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Clark, C. J., Kirschel, A. N. G., Hadjioannou, L. and Prum, R. O. (2016). Smithornis broadbills produce loud wing song by aeroelastic flutter of medial primary wing feathers. J. Exp. Biol. 219, 1069-1075.

Kathryn Knight

The Company of Biologists

Famished bee larvae cope better with starvation in later life



A honeybee drinking water. Photo credit: Christofer Bang.

The agricultural belt of the USA is in the midst of an environmental disaster. Populations of honeybees (*Apis mellifera*) that pollinate food crops in the USA and Europe are being decimated and there is no clear single culprit. Until recently, parasites, pesticides and climate change were thought to be the contributors to the insects' demise, but now another factor is becoming apparent: malnutrition. 'Most of the research focuses on adult bee nutrition', says Ying Wang from Arizona State University, USA. However, little was known about the effects that malnutrition in early life could have on the adults. Starvation early in life is often detrimental, but it can prepare non-social animals, such as other insects, birds and mammals, for occasions when food is scarce when older. However, social bee larvae rarely experience starvation; they are usually reared in a stable environment with a reliable food supply. Could honeybees capitalise on the experience of shortages as larvae to prepare for times of scarcity when adults?

Teaming up with Osman Kaftanoglu, Wang isolated some of the wax comb where the larvae develop — from the nurse bees so that the 5th instar larvae went unfed for 10 h before allowing the nurses to resume feeding their charges. Then, after the larvae completed development and emerged as adults, Wang measured the bees' physical condition, how keen they were to feed and how well the adults survived over a 3 day period, while Colin Brent measured their hormone levels.

Collating the results, Wang found that although the bees that had been starved as larvae were initially smaller than those that had not been starved, they gained weight faster and after 6 days they were the same size as the bees that were well nourished. And the bees that had been starved during development survived better than the bees that had been well fed. Most surprisingly, the adult bees that had been starved while young coped better when food was scarce than the bees that had been well fed: 'They had higher glycogen stores, were less sensitive to sugar (meaning that they were seeking higher quality food) and they had higher juvenile hormone levels, which is a hormone that helps them to respond to stress', says Wang. The bees that had experienced deprivation during development were better prepared to survive starvation in later life, contrary to Wang's expectations.

But Wang and her colleagues Gro Amdam, Jacob Campbell, Robert Page and Jon Harrison were curious to find out whether the metabolism of bees that had been starved was permanently changed by the experience, or whether they would respond metabolically when challenged by famine. Collecting more adult bees that had been starved as larvae and measuring their metabolic rate while they were deprived of food, Wang and Campbell saw that the bees were able to reduce their metabolic rate, in contrast to bees that had not been starved as larvae. And when Wang measured their blood glucose levels, the bees that had been starved as youngsters maintained higher glucose levels than their sisters that had been well fed when young. The team also realised that the bees that had experienced larval starvation were better able to switch from using sugars for fuel to other materials, such as fats and proteins. So, the bees that had experienced starvation as youngsters had modified their metabolic response and survive starvation better as adults. Wang concludes, 'Our studies present the first evidence that social organisms can have the ability to predict and adapt to

future stress. Using this mechanism, we may be able to increase bee resistance to different stressors in the near future'.

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Wang, Y., Kaftanoglu, O., Brent, C. S., Page, R. E., Jr and Amdam, G. V. (2016). Starvation stress during larval development facilitates an adaptive response in adult worker honey bees (*Apis mellifera* L.) *J. Exp. Biol.* **216**, 949-959.

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Kathryn Knight

Hermaphrodite fish change sex to cut costs



A mangrove rivulus fish. Photo credit: Frederic Silvestre.

For most species, reproduction is simple: boy meets girl and the rest is history. But mangrove rivulus (Kryptolebias marmoratus) cut directly to the chase: 'This fish has the unique ability of "selfing" [where the fish reproduce sexually with themselves]', says Mark Garcia from the University of Alabama, USA. The majority of the fish in rivulus populations are hermaphrodite – maintaining both male and female reproductive tissues in a single ovotestis with only a small percentage of males making up the numbers. But, this fish also has another talent. When the temperature rises, they can change sex from hermaphrodite to male and do away with their ovarian tissue – although they only embark on this radical alternative when the costs of maintaining a hermaphrodite lifestyle exceed those of being male. So far, the only factor that is known to trigger the fish's transition is high temperature. 'We were interested in understanding the differences between the sexes so that we can better predict the point at which it

would be favourable for them to transition from hermaphrodite to male', says Garcia.

To find out more, Garcia and his colleagues collected 40 hermaphrodites and 40 males from the labs' 4400-strong rivulus colony. Monitoring the fish's sex hormone levels and several physical characteristics (including the size of their gonads and the amount of fat they possessed), in addition to measuring their metabolic rate, aggression levels and how daring the fish were, the team found that the hermaphrodites were more aggressive. but took fewer risks than the males. In addition, the hermaphrodites' metabolic rates were higher than those of the males and they invested more energy in maintaining their large ovotestis. In contrast, the males carried more fat, were generally larger than the hermaphrodites and had higher levels of the estradiol and 11-ketotestosterone sex hormones.

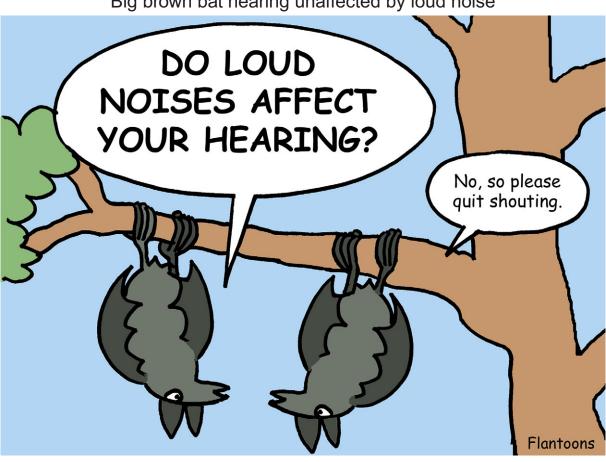
The researchers suspect that the hermaphrodites invest more energy in maintaining their reproductive organs than the males, and they suggest that the hermaphrodites transition to become male when the cost of maintaining their expensive ovotestis exceeds the benefits of selfing. In addition, they speculate that increased competition for resources could be a factor that increases the fish's costs when there are large numbers of hermaphrodites in the population. However, they admit that they are unsure why the males' estradiol levels are so high, as the hormone can be involved in feminising some species, but they add that it can also be essential for the maintenance of testicular tissue in some circumstances.

The team says, 'Our findings provide an excellent opportunity to explore why exposure to high temperatures during adulthood mediates the transition between sexes', and Garcia hopes to learn more about the impact of the fish's metabolic budget on their decision to change sex.

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Garcia, M. J., Ferro, J. M., Mattox, T., Kopelic, S., Marson, K., Jones, R., Svendsen, J. C. and Earley, R. L. (2016). Phenotypic differences between the sexes in the sexually plastic mangrove rivulus fish (*Kryptolebias marmoratus*). *J. Exp. Biol.* 219, 988-997.

Kathryn Knight



Big brown bat hearing unaffected by loud noise

Everyone knows how your hearing is muffled after a noisy concert or working with heavy power tools, and terrestrial mammals are more susceptible to the temporary hearing loss associated with intense noise than fish or birds. But how does the hearing of the only airborne mammals - bats - bear-up in the perpetual noise that they generate as they echolocate to navigate their surroundings? Do they also suffer a reduction in hearing sensitivity while hunting in groups or when emerging from their roosts in great noisy swarms, when the noise can reach up to 140 dB SPL (sound pressure level)? Andrea Simmons, Kelsey Hom, Michaela Warnecke and James Simmons from Brown University,

USA, decided to measure how the hearing of big brown bats (Eptesicus fuscus) is affected by exposures to loud noise [152 dB SEL (sound exposure level)] ranging in frequency from 10 to 100 kHz for an hour.

After measuring the normal hearing thresholds of bats, the team exposed the animals to an hour of loud noise and then repeated the hearing measurements 20 min, 2 h and 1 day later. Impressively, the bats suffered little, if any, hearing loss. 'Our results are consistent with the hypothesis that big brown bats are less susceptible to noise-induced hearing losses than expected on the basis of broadband noise exposure data from other mammals', say Simmons and her team. They add, 'This decreased susceptibility may be related to the unique demands of echolocation, which requires foraging and navigating in the midst of intense noise soundscapes', and they hope to learn how the bats protect their hearing in noisy situations that would temporarily deafen other mammals.

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Simmons, A. M., Hom, K. N., Warnecke, M. and Simmons, J. A. (2016). Broadband noise exposure does not affect hearing sensitivity in big brown bats (Eptesicus fuscus). J Exp Biol. 219, 1031-1040.

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