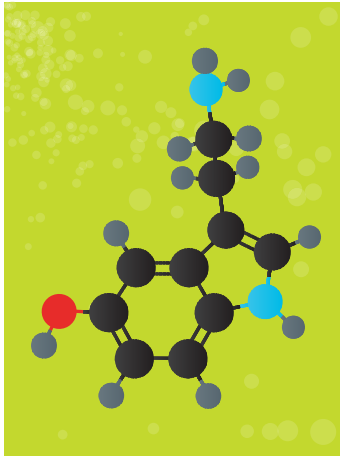


OUTSIDE JEB

Sex makes Mongolian gerbils better dads

PATERNAL CARE



Humans are fairly familiar with the idea of dads providing care to young children. However, paternal care is actually rare across vertebrate species. Instead, infanticidal behaviours, where dads show aggression towards young, are common. In rodents like the Mongolian gerbil, dads switch between slaughtering the youngsters of other parents and caring for their new-borns. Without this switch, dads would hurt their own young. Ana Martínez and colleagues at the National Autonomous University of Mexico used a combination of behavioural and physiological studies to investigate how the rodents make the switch from assailants to great fathers.

First, the researchers determined whether social factors trigger the gerbil's transition from aggressive attacker to paternal carer. Martínez and colleagues chose males that were aggressive towards pups and paired them with females to mate. The team then tested the males' reactions to pups over the course of the females' pregnancies and after the birth of their young.

After mating, the gerbils were great dads, even though the pups that were given to them were not their own offspring. This suggests that sex is one social factor that triggers paternal behaviours. Unexpectedly, however, the effects of sex were short lived: males living with

pregnant partners bit any pups introduced into their cages. Fortunately, the males transformed into nurturing fathers after the birth of their own young and their paternal behaviours continued well after the delivery, despite the fathers not having sex. This suggests that there is probably another social factor besides intercourse, such as the birth, which induces paternal behaviours.

Next, the researchers looked to hormones associated with parenting, such as oestrogens and androgens, to understand the mechanism regulating the switch to caring papa. They measured circulating blood testosterone levels and quantified the density of both oestrogen and androgen receptors in three brain areas commonly associated with maternal behaviours in rodents: the medial preoptic area, the medial amygdala and the olfactory bulb.

They discovered that the testosterone levels were higher in all of the males that were gentle with pups versus males that bit the little ones. This was not surprising as injection of aggressive males with testosterone in a previous experiment had caused the aggressive behaviour to stop. This suggests that increases in circulating testosterone play a role in initiating the switch from infanticidal to paternal behaviours.

Additionally, Martínez and her colleagues observed that the densities of the oestrogen and androgen receptors were higher in every brain area examined in the gentle fathers, suggesting that oestrogenic and androgenic pathways might play a role in regulating the caring switch. The increased density of androgen receptors in the new parents that were great dads, but had not had sex recently, further supports the idea that androgen receptors in these brain areas are directly associated with paternal behaviours and not just copulation.

So, social factors, like intercourse, might increase testosterone levels in the blood to initiate male parental care. While previous studies have shown the effects of testosterone on male parenting, this is the first study to show that androgen and

oestrogen receptor densities in the brain are connected to the transition from murderer to doting father. It seems that sex makes for better dads and the androgenic and oestrogenic pathways in the brain hold the key.

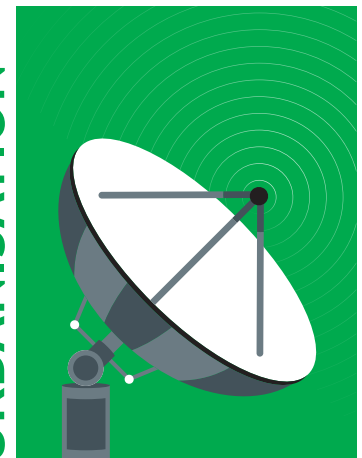
doi:10.1242/jeb.192690

Martínez, A., Arteaga-Silva, M., Bonilla-Jaime, H., Cárdenas, M., Rojas-Castañeda, J., Viguera-Villaseñor, R., Limón-Morales, O. and Luis, J. (2019). Paternal behavior in the Mongolian gerbil, and its regulation by social factors, T, ER α , and AR. *Physiol. Behav.* **199**, 351–358.

Gina Mantica (0000-0001-5329-3896)
Tufts University
gina.mantica@tufts.edu

How Kermit got streetwise

URBANISATION



On a recent flight to visit family, my son loudly announced to the entire plane that he needed to pee. It wasn't his lack of modesty, but rather the fact that he was wearing headphones and had lost the reference of his own voice to modulate his volume. Although his amusing mistake was easily remedied, many animals face a similar problem due to encroaching urbanization. Traffic and people are noisy and so, to be heard, urban animals act like my son and make more noise themselves. This matters because animals use their calls to communicate: I'm here, I'm sexy, I'm tough, etc. And getting it wrong might mean not getting the girl or, even worse, getting eaten. But how capable are animals of adjusting their calls to match

local conditions? In a fascinating new study by Wouter Halfwerk from the Vrije Universiteit Amsterdam in The Netherlands and his international colleagues, the answer is that ‘it depends’.

Túngara frogs in Panama face a trade-off between sex and death. While males use calls of varying levels of complexity to attract females to mate, these same calls attract the attention of predatory bats and blood-sucking midges. Over millennia, frogs have evolved strategies to balance this trade-off, but they haven’t had millennia to deal with their shrinking habitat. Cities have grown where trees were harvested, and frogs have had to adapt to these changing conditions.

To quantify the differences that túngara frogs face between life in forests and urban areas, Halfwerk and his colleagues measured light and noise intensity in the two locations. As expected, cities are brighter and louder. But, rather than getting stressed out by city life, the urban frogs are apparently more relaxed. And for good reason, because cities have fewer bats and midges. Thus, released from the risks of death, city frogs can focus on sex! They call more, produce calls with greater complexity and they continue to call when they are approached by eavesdropping scientists, in contrast to forest frogs that clam up without much provocation. These changes are not only permissible but also necessary. The simple calls of forest males don’t cut it in the city; urban females aren’t impressed. By contrast, forest females swoon over the complex calls of urban males. City males are apparently sexier everywhere.

When the country mouse in Aesop’s fable traveled to town to dine with his city cousin, he was frightened by dogs and returned to the safety of the country. No such luck for country frogs; the forest is a den of dangers. So how do city frogs fare when returned to the forest? Surprisingly, rather than getting eaten, city frogs dial down the complexity of their calls to match the increased risks of the forest. In other words, city living has selected for flexible frogs whose behavior is conditioned by risk.

It isn’t known whether call flexibility has any downsides in the forest. But if not, Halfwerk and his team worry that forest frogs may be doomed if increasing urbanization brings túngara frogs from the

forest and the city into more frequent contact. This, unfortunately, seems likely.

doi:10.1242/jeb.192674

Halfwerk, W., Blaas, M., Hijner, N., Trillo, P. A., Bernal, X. E., Page, R. A., Goutte, S., Ryan, M. J. and Ellers, J. (2018). Adaptive changes in sexual signalling in response to urbanization. *Nat. Ecol. Evol.* doi:10.1038/s41559-018-0751-8

Daniel E. Rozen (0000-0002-7772-0239)
Leiden University
d.e.rozen@biology.leidenuniv.nl

Parenting is hot work for blue tits



The amount of energy that an animal can burn could be limited by the food available in its environment, or how well its body can digest and utilize nutrients. Additionally, because energy metabolism characteristically produces warmth, it has been suggested that some animals have difficulty in offloading excess body heat, which could instead cap their ability to work. High body temperatures can be disastrous, particularly in birds and mammals, in which temperature is normally tightly regulated. This problem is particularly acute when animals are provisioning their growing offspring, when the amount of work a parent can perform has direct consequences for their reproductive success.

In earlier work on rodents in the lab, researchers demonstrated that lowering environmental temperature or shaving body fur – two interventions that increase the ability of the parents to dissipate heat – increases the amount of work that a parent can perform, allowing them to raise larger pups. This supports the concept that, ordinarily, offloading heat is a real

constraint on breeding success. In order to perform the first experiment to see whether this principle holds in the wild, Andreas Nord and Jan-Åke Nilsson, both based at Lund University, Sweden, at the time, set their focus on blue tits, a charismatic and agile Eurasian bird species. Working in the southern Swedish countryside during the blue tit nesting season, the duo trimmed the breast feathers of both parents of some nests to reveal their bare skin. This meant that the birds offloaded more heat, which the researchers verified with a thermal camera. They compared the surface body temperature of these birds with that of birds that had not lost any feathers and found it was on average 6.6°C higher (40.4 versus 33.8°C), potentially resulting in 50% greater heat loss from the breast surface. The pair also took internal body temperature measurements and showed that trimmed parents maintained a 0.4°C lower core body temperature (42.7 versus 43.1°C). But what effect would this difference in body temperature have on the birds’ foraging habits?

Nord and Nilsson tagged the birds with uniquely coded transponders and rigged their nest boxes with sensors to record how often they went on feeding excursions. If overheating normally handicaps activity – which the authors predicted – they believed trimmed birds would be capable of making more foraging trips. All of the parents made over 400 trips per day to find food for their chicks yet, surprisingly, the feather-trimmed group made no more trips than the birds with intact plumage.

However, when the duo looked at the body condition of both the parents and their chicks, they saw that the feather-trimmed adults only lost half the weight of untrimmed birds (0.19 versus 0.46 g) during the nesting period. More strikingly, their chicks grew longer wings. Interestingly, in the nests that were tended by females in their first breeding season, the trimmed birds raised chicks that were also over 25% heavier than normal. However, the females that were in their second breeding season reared chicks that were the usual weight, suggesting that experience may partially mitigate the costs of overheating.

Nord and Nilsson saw that when heat dissipation was facilitated, the blue tits became more successful parents, which suggests they normally have difficulty offloading heat. Given that the feather-

trimmed blue tits weren't making additional foraging trips, the pair suggest that the trimmed parents can prioritize food quality over quantity. Soberingly, this observation indicates how heat waves – an increasingly frequent occurrence in the current period of climatic instability – may render breeding birds particularly vulnerable.

doi:10.1242/jeb.192708

Nord, A. and Nilsson, J. Å. (2018). Heat dissipation rate constrains reproductive investment in a wild bird. *Funct. Ecol.* **33**, 250–259.

William Joyce (0000-0002-3782-1641)
Aarhus University
william.joyce@bios.au.dk

Stretch-induced force bursts simplify stick insects' leg swing



Are animals' graceful movements bestowed on them by a nervous system that controls all details of motion? When most animals swing their legs during

walking, their nervous system typically activates muscles on one side of the leg joint to bring the leg forward and, as the leg is about to touch the ground, activates muscles on the opposite side of the joint to slow down the leg. However, stick insects may have simplified this strategy. Their nervous system only provides the initial input to accelerate the leg and provides no input to slow the limb down. Arndt von Twickel and colleagues at the University of Cologne, Germany, wondered how stick insects could pull off this stunt. From their previous work, the team had learned that stick insect muscles are able to produce a burst of force when stretched, without any neural activation, so they hypothesized that a burst of force – produced when the muscles that slow down the leg are stretched – could provide the brake power without the necessity for additional input from the nervous system.

The team chose to study how the force production of muscles around the stick insects' femur–tibia joint – analogous to a human knee joint – controls the leg movement during the swing phase of walking. In the first step in their analysis, the team measured the force burst generated by the flexor muscle, which could provide a brake on movement of the femur–tibia joint, when stretched by the extensor muscle on the other side of the joint. To do this, they manoeuvred the joint over angles ranging from 20 to 140 deg at speeds of up to 1200 deg s⁻¹, which are typical of the movements performed by a stick insect during a stride.

By looking at the burst of force generated by the stretched flexor muscle during the swinging motion, the team found that

faster speeds and larger movement ranges increased the force burst. The muscle also generated the maximal force when the leg was bent at about 110 deg, reaching values that were more than 10 times greater than the team expected. This suggests that the flexor muscle could supply the brake power to slow down the leg during swing.

To understand further how the force could contribute to movement control during a swing manoeuvre, the team combined their observations with computer simulations to calculate the forces from the extensor and flexor muscles and determine their effect on the swing movement. The simulation showed that the force burst elicited by the flexor muscle when passively stretched by the extensors was enough to slow down the femur–tibia joint. This suggests that the burst of force from stretched flexor muscles could allow the stick insects' simple control strategy.

Passively induced stretch forces could also provide a straightforward control mechanism for other small animals, because their relatively light limbs are very sensitive to bursts of force, possibly allowing muscles to relieve the nervous system of its otherwise detailed control when the animals move.

doi:10.1242/jeb.192666

von Twickel, A., Guschlbauer, C., Hooper, S. L. and Büschges, A. (2018). Swing velocity profiles of small limbs can arise from transient passive torques of the antagonist muscle alone. *Curr. Biol.* **29**, 1–12.

Jan Stenum (0000-0002-0088-8703)
University of Massachusetts Amherst
jstenum@umass.edu