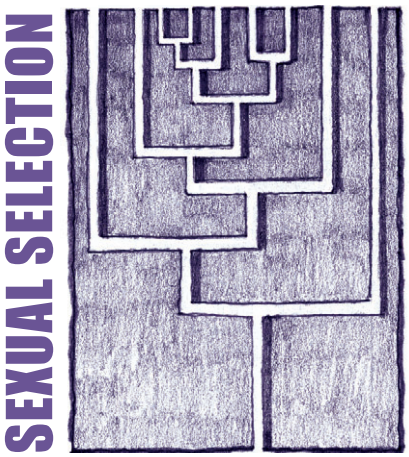
Keeping track of the literature isn't easy, so Outside JEB is a monthly feature that reports the most exciting developments in experimental biology. Short articles that have been selected and written by a team of active research scientists highlight the papers that JEB readers can't afford to miss.

Outside JEB




## SEXUAL SELECTION CONSTRAINS ADAPTATION

Thinking about baker's yeast, we tend to focus on its useful side, notably as an invaluable aid in producing fluffier bread. It's easy to forget that it also has a sex life. In the haploid stage, two mating types are produced, which can be viewed as essentially analogous to the two sexes in vertebrates like ourselves. As soon as two sexes are present, the way is open for sexual selection, where organisms can out-reproduce others if they are better at securing more or superior mates. Sexual selection is known to drive the evolution of a multitude of reproductive traits, but it has also been argued that this evolutionary force could be involved in both increasing and decreasing diversity. By driving isolation, new species may be formed but it may also push populations towards the edge. The dangerous context of flirting with extinction could be exacerbated further when environmental conditions change, especially if change occurs too rapidly. In research published in *Biology Letters*, Luke Reding and colleagues addressed these themes experimentally using the technique of experimental evolution.

The team exposed populations of *Saccharomyces cerevisiae* to two different intensities of sexual selection by manipulating sex ratio. They then contrasted these sexually selected lines with asexual populations. Weak and strong sexual selection were generated by setting up populations in which the ratio between mating types was either balanced or skewed. Skewing the ratio increased competition among the spores of the more common mating type. To examine adaptation rates, all populations were allowed to evolve for some 250 generations exposed to a stressful high-salt environment in a glucose-containing medium. Population responses were also monitored under conditions where glucose was replaced with sucrose (representing an additional challenge, as digestion requires production of the enzyme invertase). The authors performed an ambitious series of assays testing population fitness, mating propensity between populations (subjected to the same sexual selection treatment) and extinction risk.

The team found that populations evolving under strong sexual selection were less able to adapt to the harsh salty conditions in comparison to their counterparts exposed to other treatments. This reduced performance under duress is possibly a consequence of shifting resources towards greater investment in mating pheromones in order to increase attractiveness when competition is magnified. This finding is particularly noteworthy because we know that being sexual rather than asexual usually allows faster adaptation. Strikingly, this benefit seems to disappear if sexual selection is too strong. Similar results emerged regardless of whether the medium fed to populations contained glucose or sucrose. Interestingly, the study also revealed a trend suggestive of emerging reproductive isolation between populations exposed to strong sexual selection. Crosses between individual lines subjected to strong sexual selection tended to have a lower success rate. So the action of sexual selection might also increase divergence between populations, thus promoting diversity.

Stepping back to view the bigger picture, these promising results confirm that sexual selection can be an agent of evolutionary change and may shape biodiversity in various biological systems. Environmental change can clearly act in conjunction with population-level characteristics such as sex ratio. This, in turn, shows that we urgently need a greater understanding of such interactions, especially in the context of fast-moving climate change.

10.1242/jeb.090225

**Reding, L. P., Swaddle, J. P. and Murphy, H. A.** (2013). Sexual selection hinders adaptation in experimental populations of yeast. *Biol. Lett.* **9**, 20121202.

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## KINDERGARTEN FOR COWBIRDS

In most species, social skills develop long before sexual maturity. In kindergarten, children are already learning the basics of playing nicely; share your toys and don't hit others. These early social skills are important for interacting and cooperating with colleagues throughout life, but does mastery of these kindergarten skills also translate to better courtship skills? Do those that share their toys more generously in kindergarten have better success on the dating scene as adults?

Gregory Kohn, Andrew King, Rebekka Dohme, Gwendwr Meredith and Meredith West from Indiana University investigated this phenomenon in the brown-headed cowbird, *Molothrus ater*. Brown-headed cowbirds are brood parasites, and so juveniles typically form flocks together, rather than interacting extensively with mature birds. However, brown-headed cowbirds still learn several key social abilities as juveniles. In particular, they learn to play nicely with others by using a head-down display, where one bird will bow towards another brown-headed cowbird, and invite the other bird to make close physical contact. Like sharing toys or giving a hug, this affiliative gesture lets birds form closer social bonds. In their study, the authors predicted that juvenile cowbirds would vary in their social skills, and some birds would initiate more of these displays, while others would initiate fewer. The authors predicted that the juveniles that had better social skills would then display better courtship skills as adults, and would be better at maintaining a stable relationship with a potential mate, than those with poorer social skills as juveniles.

To examine consistency of social skills as juveniles, the authors captured 12 male and 12 female juvenile brown-headed cowbirds and brought them back to the laboratory for the autumn and winter. To explore whether birds would be more likely to interact with familiar partners, the birds were divided into two aviaries for a month in the autumn, and then reunited for the remainder of the autumn and winter. The authors made daily recordings of the aviary throughout, noting all of the head-down displays, and which birds were involved. Finally, to examine how juvenile social skills related to adult courtship skills, daily recordings were made of both male courtship and female response to the courtship during the subsequent breeding season.

The researchers found that females typically initiated head-down displays with other females, while males were equally likely to initiate displays with both males and females. They also found that once the two flocks were reunited, the birds were more likely to initiate head-down displays with the birds they were familiar with. Individual females were consistent in the number of head-down displays that they initiated, with some females reliably initiating more head-down displays than others. Within the males, however, there was no pattern, and all males initiated similar numbers of displays. In the spring, the females that initiated higher numbers of head-down displays received more attention from males, and formed more stable partnerships with males than the females that initiated lower rates of these displays as juveniles. However, there was no relationship between juvenile social skills and adult courtship skills for males. Thus, for females, initiating close social relationships with other females as juveniles predicts courtship skills with males as adults. It appears that at least for female brown-headed cowbirds, everything they need to know, they learn in kindergarten.

10.1242/jeb.081620

**Kohn, G. M., King, A. P., Dohme, R., Meredith, G. R. and West, M. J.** (2013). Robust autumn social attributes predict spring courtship skills in juvenile female brown-headed cowbirds, *Molothrus ater*. *Anim. Behav.* doi: 10.1016/j.anbehav.2013.01.009

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## CELL DEATH TRIGGERS LIFE IN MUSCLES

During muscle development and regeneration, the threadlike myofibres that make up mammalian skeletal muscles emanate from the progressive fusion of progenitor cells, called myoblasts. Some details of the underlying signalling pathway involved in myoblast fusion are known, but the early triggers have remained elusive. In a ground-breaking study recently published in *Nature*, a team of scientists from the University of Virginia, USA, led by Kodi Ravichandran came to the startling conclusion that cell death provides a signal that promotes myoblast fusion.

Myoblast fusion involves two proteins (ELMO/Dock180) known to activate the Rac G protein, which in turn induces reorganization of the actin cytoskeleton. Exposure of phosphatidylserine (PS) on the outer leaflet of the myoblast's plasma membrane enhances myoblast fusion. Strikingly, all these molecules are also known to be involved in programmed cell death (apoptosis), specifically in the clearance of apoptotic cells by phagocytosis. During this process, PS exposed on the surface of apoptotic cells acts as a signal to phagocytic cells. PS is then recognized by the G protein-coupled receptor BAI1 and is transmitted in an ELMO/Dock180/Rac-dependent manner to induce remodelling of the cytoskeleton and engulfment of apoptotic cells.

Given the usage of similar pathways in myoblast fusion, the scientists from Virginia wondered whether cell death might be linked to myoblast fusion in a much more direct fashion. They designed a series of sophisticated experiments using myoblast cell cultures that allowed them to induce and quantify myoblast fusions under various experimental conditions.

First, the team focused on the expression of BAI1, which they indeed detected in

myoblast cells. Moreover, after they experimentally induced myoblast fusion in the cell culture, they found that BAI1 transcript levels were significantly elevated compared with the control, suggesting a role of BAI1 in myoblast fusion. Motivated by this finding, they went on to artificially overexpress the *BAI1* gene in myoblasts. They observed that myoblast fusion was enhanced in these BAI1-overexpressing cells, and furthermore demonstrated that this effect is dependent on ELMO/Dock180 and Rac proteins, as overexpression of a mutant BAI1 version, lacking the docking site for ELMO, failed to enhance fusion. The team also tested their hypothesis *in vivo* using mice lacking a functional version of the *BAI1* gene. In line with their hypothesis, the team found that the myofibres obtained from *BAI1*-deficient mice were smaller than in control mice and that muscle regeneration was negatively affected.

The team knew from their previous work that a significant number of myoblasts undergo apoptosis during myoblast fusion, so they tested whether blocking either PS signalling or apoptosis would affect myoblast fusion. They added PS-masking proteins or inhibitors of apoptosis to the cell culture and then induced myoblast fusion. Intriguingly, blocking either PS signalling or apoptosis impaired myoblast fusion. By adding back apoptotic cells of different origins, they rescued fusion, suggesting that various types of apoptotic cell can trigger myoblast fusion.

Ravichandran's team has provided compelling evidence that a known cell death signal, PS signalling through BAI1, induces myoblast fusion. But how apoptosis aids fusion and how very similar pathways can result in phagocytosis in some cells and fusion in others remains to be elucidated. Further insights into the underlying mechanism may help to develop new strategies for muscle regeneration in sports and medicine.

10.1242/jeb.081638

**Hochreiter-Hufford, A. E., Lee, C. S., Kinchen, J. M., Sokolowski, J. D., Arandjelovic, S., Call, J. A., Klibanov, A. L., Yan, Z., Mandell, J. W. and Ravichandran, K. S.** (2013). Phosphatidylserine receptor BAI1 and apoptotic cells as new promoters of myoblast fusion. *Nature* **497**, 263-267.

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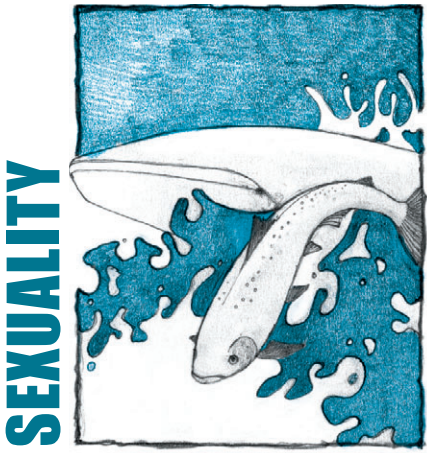


## (HOMO)SEXUALLY ACTIVE FISH ARE SEXIER TO FEMALES

Homosexuality occurs in most animal species, from insects to mammals, and it is more common amongst males. But how could homosexual behaviour have evolved if same-sex copulations do not result in offspring and should therefore decrease fitness? Furthermore, copulation tends to be an energetically costly activity for both parties involved and even though it tends to be less so for males than for females, the fact remains that even male–male homosexuality appears to be a waste of energy and gametes. The truth though, is that exclusive homosexuality is rarely present in non-human animals, and most males that engage in homosexual encounters also mate with females. Could it be possible, then, that male homosexual behaviour leads to an increase in subsequent success with female mates? If this were the case, homosexual behaviour would have a direct positive effect on fitness.

When it comes to mate choices, females of the live-bearing fish *Poecilia mexicana* like to copy their female friends. That is, seeing a male consorting with someone else makes him a more desirable mate and they are more likely to mate with him later, probably because copulation in itself is an indication of male quality; but would the effect of this fishy voyeurism be different if the sexual participants were both males? A recent paper by David Bierbach and his colleagues from the University of Frankfurt in Germany provides insight into the secret sexual lives of bisexual male fish and the aphrodisiac effects of their sexual escapades on their heterosexual mates.

There are two types of *P. mexicana* males; drab, small males, and big, colourful ones. Not surprisingly, females generally prefer the larger, more handsome suitors. Before copulations, males of the species engage in a pre-mating behaviour called 'nipping', in which a male makes oral contact with either the female's genital opening or the male's copulatory organ depending on the sex of his chosen mate. To test the hypothesis that male–male sexual behaviour increases male attractiveness to females, Bierbach and his team presented females with a digital animation of either a drab male 'nipping' on another male or a drab male 'nipping' on a female. The team then determined whether the female bias for colourful males had changed based on the behavioural interactions they had observed.

The results of these experiments showed that females that had watched the drab males 'nipping' at either other males or females increased their preference towards these drab males. The aphrodisiac effect on the females was similar whether they had watched videos of homosexual or heterosexual interactions suggesting that, for males, sexual encounters, even if they are homosexual, will increase their fitness by increasing their chances of later finding a female mate.

In their study, Bierbach and his colleagues provide insight into the evolution of homosexual behaviour. So, what adaptive benefits could homosexual behaviour confer to individuals for it to be so ubiquitous across the animal kingdom? Well, this study doesn't talk about other animals but if you are a little ugly *P. mexicana* male and can't seem to find a female date, mating with another male might increase your chances of scoring a nice fertile female down the road.

10.1242/jeb.081646

**Bierbach, D., Jung, C. T., Hornung, S., Streit, B. and Plath, M.** (2013). Homosexual behaviour increases male attractiveness to females. *Biol. Lett.* **9** 20121038.

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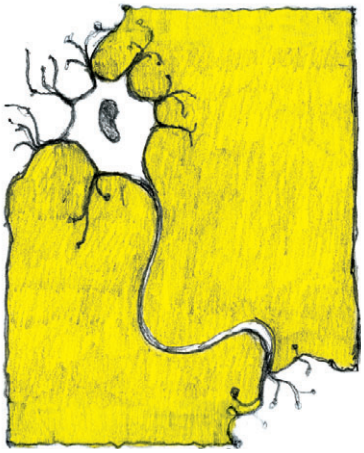
LOCOMOTION



## NEURONAL CONTROL OF ACCURATE LOCOMOTION

We may associate Olympic gymnasts with extreme precision and coordination, but in nature, precise movements are performed without much notice every day. Complex environments pose as an obstacle to steady locomotion, and yet animals appear to cope with these obstacles effortlessly. This accurate locomotion requires serious neural coordination. How the brain coordinates accuracy during movement is still unclear, but new research suggests the different neurons of the pyramidal tract may be involved.

The pyramidal tract consists of nerve fibers connecting the primary motor cortex of the brain with motor neurons in the brain stem and anterior spinal cord. These connections are extremely important, as pyramidal tract neurons control all voluntary motions and damage to the region results in severe motor disability.

Scientists have long known two different types of neuron exist in the pyramidal tract: large, fast-conducting neurons and smaller, slow-conducting neurons. Erik Stout and Irina Beloozerova of St Joseph's Hospital and Medical Center, AZ, USA, looked how these two types of neuron might control accurate locomotion. The two researchers trained cats to run on a flat track and on a horizontal ladder track, where the cats had to step precisely on the rungs of a horizontal ladder, and never in the gaps between rungs. Stout and Beloozerova then recorded the activity from slow-conducting and fast-conducting pyramidal tract neurons, to see whether there were differences in their activity patterns between different motions.

Both slow and fast pyramidal tract neurons had different activity patterns during flat *versus* ladder running. Slow-conducting neurons, however, changed their activity in a much more concerted way than fast-conducting neurons. During the late stance and early swing phase of each stride on the ladder, slow-conducting neurons increased their average rate of discharge and decreased their discharge variability. Slow-conducting neurons also increased the magnitude of stride-related frequency modulation during ladder running. While fast-conducting neurons displayed some similar trends in their modulation between different locomotor tasks, the differences were small in magnitude and often insignificant.

Because there were very few kinematic differences between flat and ladder running, the changes in slow-conducting neuron activity are probably related to the high accuracy demands of ladder running. This suggests that slow-conducting neurons are more important than fast-conducting neurons for the control of precise movement. The proximate mechanisms by which slow-conducting neurons control precise limb placement are still elusive. Stout and Beloozerova note that while fast-conducting neurons chiefly influence distal musculature, slow-conducting neurons can influence both proximal and distal musculature. They propose that maybe proximal limb musculature plays a greater role in accurate paw placement than previously thought.

As technology for instrumenting small slow-conducting neurons improves, perhaps neuroscientists can narrow in on the fine controls of accurate locomotion. Eventually, we may know exactly how slow neurons help us tread carefully.

10.1242/jeb.081612

**Stout, E. E. and Beloozerova, I. N.** (2013)? Differential responses of fast- and slow-conducting pyramidal tract neurons to changing accuracy demands during locomotion. *J. Physiol.* **591**, 2647-2666.

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## CORRECTION: FLIGHT CONTROL, THIS IS THE ANTENNAE

In the Outside JEB article written by Kara Feilich (doi: 10.1242/ jeb.077826) the first author's last name in the article text and reference was incorrectly spelled as Hinterwith. The first author's name is Armin Hinterwirth and the reference should read:

**Hinterwirth, A. J., Medina, B., Lockey, J., Otten, D., Voldman, J., Lang, J. H., Hildebrand, J. G. and Daniel, T. L.** (2012). Wireless stimulation of antennal muscles in freely flying hawkmoths leads to flight path changes. *PLoS ONE* **7**, e52725.

10.1242/jeb.092254