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

COLONY DYNAMICS

MONOGAMOUS QUEENS MEAN LAZY WORKERS

Social insects have long been a fascinating puzzle for evolutionary biologists. In these species, the majority of individuals are workers who shut off their ability to reproduce, instead serving the good of the colony. The reason for this selfless sacrifice is usually explained by the relatedness of all the insects in a colony – it can make sense to give up your shot at producing offspring if you have thousands of closely related nieces and nephews. But there's a paradox: reproductive colony queens are extremely promiscuous, a trait that increases colony productivity by increasing genetic diversity, but might also be expected to decrease worker's motivation to suppress their reproduction as it reduces relatedness. So, how is promiscuity in queens selected for? It could occur if workers increased their own reproductive ability in the presence of a monogamous queen, thereby sacrificing the good of the colony by becoming a less productive worker and producing a selection pressure on queens to choose polyandry.

To test this theory, Heather Mattila from Wellesley College, USA, and her colleagues from Cornell University, USA, decided to manipulate the mating of honey bee queens and measure the effects on the reproductive physiology and behaviour of their workers in a report published in *Current Biology*. They artificially inseminated queens with semen from either a single male bee or a pool generated from 15 bees, ensuring that the total volume of semen was kept constant as workers can detect the volume of semen in a queen's spermatheca. They also allowed some queens to mate naturally (which is always with multiple males). Following mating, they placed all the queens into new colonies.

Two months later, the researchers took a peek at the worker's ovaries by dissecting a sample of workers from each colony. They found that workers who lived in colonies with a queen that had been inseminated with sperm from a single male had ovaries with increased development – a sign that the workers were investing in their own reproductive ability. Meanwhile, workers in colonies where the queen had either received artificial insemination with sperm from multiple males or was naturally mated had a lower probability of having ovaries that had been activated.

As it appeared that workers increased their investment in their own reproduction when their queens had remained monogamous, the researchers decided to investigate what effect this had on how hard the workers worked. They installed a portion of each colony in an observation hive in a greenhouse, where they hung a feeder containing sugar water as a food source. They counted how many trips a day each worker made and how much time each worker spent 'waggle dancing' – communicating to the other workers where the food source was located. They found that colonies that had workers with more activated ovaries also had workers that spent far less time visiting the food source and dancing for their colony mates. Furthermore, when the researchers manipulated individual workers to activate their ovaries, they found that these workers were far lazier than untreated workers. So, in short, in colonies where the queen mated with only a single male, the workers increased ovary activation and were far less productive than those in colonies where the queen was inseminated by many males.

While the researchers can't tell from this experiment why workers might be increasing their ovary activation, workers will capitalize on shy queens who don't mate with multiple males by investing in their own reproduction at the cost of colony productivity. So, for the queen, promiscuity is a virtue.

10.1242/jeb.077792

Mattila, H. R., Reeve, H. H. and Smith, M. L. (2012). Promiscuous honey bee queens increase colony productivity by suppressing worker selfishness. *Curr. Biol.* **22**, 2027-2031.

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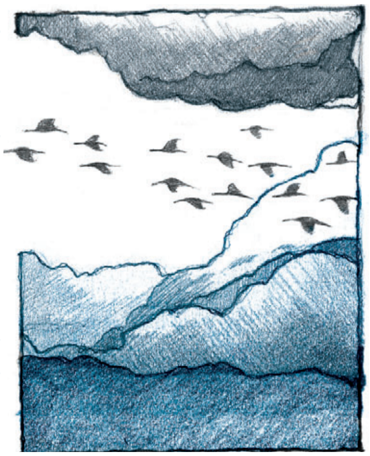
BROOD PARASITES



A MOTHER'S SECRET PASSWORD

Cuckoos are among nature's laziest parents. These birds are brood parasites that lay their eggs in the nests of other species. If undetected, the cuckoo chick will throw out the host's own chicks, obtaining exclusive care from its foster parent. Alternatively, if the host catches on, the cuckoo chick will be abandoned and left to die. While some birds endure high rates of cuckoo parasitism, others, such as Australia's superb fairy-wren, appear to have gained a leg up on their cuckoo parasites. How have they managed this feat? New research published in *Current Biology* by an international team of researchers led by Sonia Kleindorfer at Flinders University in Australia has identified the fairy-wrens' unexpected mechanism of cuckoo detection: egg whispering.

In contrast to most species, which reject cuckoos on the basis of visual cues, typically at the egg stage, superb fairy-wrens instead appear to reject cuckoo chicks using acoustic recognition. Until now, however, how a fairy-wren mother distinguishes its own chicks from that of a cuckoo has remained a mystery.

Using detailed audio-visual monitoring, Kleindorfer and her colleagues spied on fairy-wren females while they set up their nests. During egg incubation the researchers discovered a novel 'incubation call' that mother fairy-wrens produce at a high rate. And embedded within this call is a 'signature element', or password, that chicks repeat following hatching. Strikingly, each mother produces a different password, and the chicks of each nest learn only the appropriate message of that nest. That is, fairy-wrens are not born with a password hard-wired into their brains, but rather they have to learn it as an embryo from within the egg.

But how does this help fairy-wrens to thwart cuckoos? Simply, by only heeding the begging calls of chicks that repeat the correct signature element, parents can ensure that they are stuffing food into the mouth of their own fairy-wren chick instead of the gaping maw of a hungry cuckoo.

Less clear is why cuckoo chicks do not also learn the secret code *in ovo*. The answer to this question, the authors believe, lies in the timing. In a normal nest, fairy-wren eggs are exposed to their mother's lessons for around 5 days. And the more a mother teaches – that is, the more often she repeats the password – the more reliably the chick repeats it upon hatching. By contrast, cuckoo eggs are only exposed to the password for around 2 days, and this is apparently not long enough for a cuckoo embryo to get the hang of it. Thus, when the cuckoo hatches and fails to provide the secret 'handshake', the mother assumes that the chick is not her own and leaves it to die.

Cuckoos are remarkably plastic in their ability to mimic their hosts. This new escalation in the co-evolutionary arms race by superb fairy-wrens might, however, prove too tough an egg for the Australian Horsfield's bronze-cuckoos to crack. As with all evolutionary arms races, only time will tell.

10.1242/jeb.077784

Colombelli-Negrel, D., Hauber, M. E., Robertson, J., Sulloway, F. J., Hoi, H., Griggio, M. and Kleindorfer, S. (2012). Embryonic learning of vocal passwords in superb fairy-wrens reveals intruder cuckoo nestlings. *Curr. Biol.* **22**, 2155-2160.

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LEARNING ABILITY

BINGE DRINKING MAGGOTS GO COLD TURKEY

Chronic alcohol consumption triggers a host of physiological adaptations in the nervous system. These changes are thought to contribute to learning and memory defects seen in addicts undergoing withdrawal. Such cognitive ethanol dependence has been documented in humans and other vertebrates but never in invertebrates. In a recent edition of *Current Biology*, Brooks Robinson, Sukant Khurana, Anna Kuperman and Nigel Atkinson, from the University of Texas at Austin, USA, set out to test whether fruit fly larvae undergoing withdrawal from chronic alcohol consumption also have difficulties learning.

The team first tested how acute ethanol consumption affects a larva's ability to learn. Larvae fed ethanol-containing food for 1 h had internal ethanol concentrations equivalent to mildly intoxicating (~0.05 g 100 ml^{-1}) levels in humans. Despite their 'drunkenness', these acutely treated larvae were able to navigate away from a noxious stimulus (heat pulse) and towards an attractive odor equally well as animals fed non-alcoholic food. Next, the team paired the unpleasant heat pulse with the attractive odor in training trials, and then assayed whether or not animals would then find the odor repulsive. Animals that were not exposed to ethanol learned to navigate away from the odor after heat pulse training. However, ethanol-fed and heat pulse-trained animals were less likely to navigate away from the odor after training. These results show that acute alcohol consumption impairs a larva's ability to learn to associate noxious heat with odor, but does not affect the animal's ability to sense odor or heat.

Robinson and colleagues next tested associative learning in larvae chronically exposed to ethanol. Surprisingly, after a 6 day binge on food containing ethanol, larvae learned to associate heat pulses with odors just as well as animals that had never been exposed to ethanol. However, after experiencing a 6 h ethanol withdrawal, chronically exposed larvae showed impaired learning. Putting these animals back for 1 h on food spiked with ethanol restored their learning capabilities. These results suggest that larvae can indeed become physiologically adapted to, and cognitively dependent on ethanol.

Increased probability of firing action potentials (i.e. neuronal hyper-excitability) is common in vertebrates undergoing severe ethanol withdrawal. To test for this possibility, Robinson and colleagues fed larvae undergoing withdrawal and tee-total larvae picrotoxin, a drug that induces seizures and hyper-acitivity in excitatory circuits by blocking inhibitory synapses. After a brief picrotoxin treatment, ethanol-adapted larvae going cold turkey showed more seizure-like behavior than similarly treated tee-totallers. This experiment suggests that the central nervous systems of ethanol-adapted larvae are indeed hyper-excited and thus more easily prone to seizures. Furthermore, giving these withdrawing larvae a ‘fix’ (1 h of 5% ethanol in their food) partially reduced their sensitivity to picrotoxin. As ethanol reinstatement rescues both hyper-excitability and learning defects in animals undergoing withdrawal, it is likely that the two effects have related origins. This research therefore strongly suggests that neuronal hyper-excitability contributes in some way to the learning defects in larvae going though ethanol withdrawal.

Overall, the work of Robinson and Colleagues reinforces how eerily conserved ethanol’s physiological effects are across animal taxa. Alcohol addiction is truly the great leveller. It doesn’t matter whether you are man, mouse or maggot – over-consumption of alcohol will trigger very similar cellular and behavioral responses, with devastating consequences. But we should take heart at this, because it means that we can deploy a wide variety of animal models to effectively study and ultimately combat alcohol addiction.

10.1242/jeb.077818

Robinson, B. G., Khurana, S., Kuperman, A. and Atkinson, N. S. (2012). Neural adaptation leads to cognitive ethanol dependence. *Curr. Biol.* **22**, 2338-2341.

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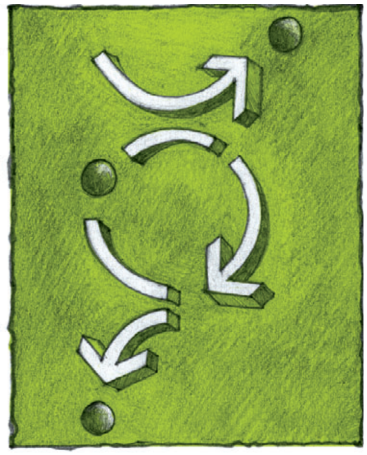
LILFE HISTORY



GROW FAST, DIE YOUNG

Anyone who has seen a middle-aged rock star understands that certain lifestyles take more of a toll than others. Live fast, die young! This rock star mantra is also the premise of life-history theory, one of the central tenants of ecological research. Life-history traits are all of those characteristics related to an individual’s lifestyle, such as growth rate, reproduction and lifespan. Life-history theory states that not all life-history traits can be maximized simultaneously, and individuals will need to make trade-offs among competing functions.

Theoretically, one of the key life-history trade-offs may be between growth rate and total lifespan. However, it is difficult to manipulate growth without manipulating other confounding factors, like nutrient availability. Who-Seung Lee, Pat Monaghan and Neil Metcalfe from the University of Glasgow addressed this long-standing question by taking advantage of the biology of juvenile three-spined sticklebacks (*Gasterosteus aculeatus*). Like all fish, sticklebacks are cold-blooded, and their metabolism and hence growth can be sped up or slowed down by changing water temperature. Furthermore, sticklebacks reproduce in the spring, and as reproductive success is related to body size, they are motivated to attain a large size prior to their first spring.

To examine the effect of growth rate on total lifespan, the scientists used water temperature and photoperiod to manipulate both how much the fish would need to grow and how fast they would have to grow prior to their first spring. The researchers predicted that higher growth rates would come at a cost to overall lifespan. Using juvenile fish captured in November, they experimentally manipulated the period available for growth; half the fish were kept under a normal photoperiod, while the other half were exposed to a delayed photoperiod, so that the fish perceived that they had an extra month before spring. Fish from both groups were then subjected to a ‘cold snap’ (6°C) or a ‘warm spell’ (14°C), or kept at a constant 10°C for 4 weeks. While all fish were fed the same diet, their metabolism, and therefore growth rate, was influenced by temperature. Thus, fish in the cold snap group grew more slowly than those in the other groups. After 4 weeks, all the fish were returned to 10°C for the rest of their lives.

When the fish were returned to 10°C, they faced a resource allocation decision. The fish stunted by the cold snap were much smaller than their counterparts, and to attain reproductive size they would need to grow quickly by directing all of their resources towards growth. Conversely, fish exposed to a warm spell were already larger and could afford to grow at a more leisurely pace. These warm spell fish could use some resources to fuel other processes that are important for overall lifespan, such as the immune system. There was even less pressure on fish that had been subjected to a delayed photoperiod – they had an extra month for growth. But did different growth rates influence overall lifespan?

Excitingly, the results matched the researchers’ predictions. All of the fish had similar final sizes, but fish exposed to the cold snap directed more resources towards growth and grew more quickly once returned to 10°C, and consequently had the shortest lives. By replicating the experiment with fish captured in January, with mere weeks before spring, the researchers found that lifespans were shortened still further by the shortened growth time frame. This paper elegantly provides the first experimental evidence that growth rates are directly linked to total lifespan, and this indeed represents a key life-history trade-off. There is now empirical evidence that if you grow fast, you die young.

10.1242/jeb.077800

Lee, W. S. Monaghan, P. and Metcalfe, N. B. (2012). Experimental demonstration of the growth rate–lifespan trade-off. *Proc. R. Soc. B* doi: 10.1098/rspb.2012.2370.

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