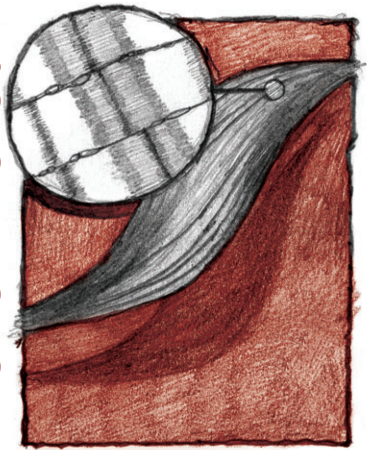
Keeping track of the literature isn't easy, so Outside JEB is a monthly feature that reports the most exciting developments in experimental biology. Short articles that have been selected and written by a team of active research scientists highlight the papers that JEB readers can't afford to miss.

Outside JEB

NEUROETHOLOGY



MUSCLE SPINDLES PREDICT THE FUTURE

When I'm typing, sometimes I hit in between two keys, or I hit the wrong key entirely, and before I know it, I'm already reaching for the delete key. I'm sure you do it too.

Hidden in this ordinary action is a rather impressive trick of the nervous system. When I hit between two keys, sensory cells in my skin and my finger muscles detect that something's gone awry. Then the signal travels up sensory nerves, into my spinal cord, and ultimately up into the motor cortex of my brain. The signal travels quickly, but it still takes 50 or 100 ms before my brain can receive the signal, process it and send out a corrective reaction.

As I type pretty quickly – I timed it at around 5–10 characters per second – the 100 ms it takes to process my typing error is actually an unacceptably long time. So, rather than typing (or correcting) slowly, my nervous system has learned to predict where my fingers are going to be. Based on the signals going out to my finger muscles and the sensory inputs coming in (which actually reflect the sensations from 50 ms or so earlier), cells in my brain can predict that I'm going to miss a key and start correcting early. By the time the cutaneous sensation of a missed key actually makes it up into my brain, it just serves to confirm what these cells had already predicted.

We've known that cells in the cerebellum seem to predict the future this way, but new research from Michael Dimitriou and Benoni Edin shows that the predictions may take place at a much lower level.

They examined the output of muscle spindles, which sense the contraction speed and acceleration of muscles, in healthy human subjects performing a typing task. The subjects typed a sequence like 5, 3, 5 on a numeric keypad, always beginning and ending with 5, which is in the dead center of the keypad. A subset of the muscle spindles, called type Ia afferents, fired at a rate that was proportional to the speed of their muscles, but at a time around 160 ms in the future.

Muscle spindles sense both speed and acceleration, and Dimitriou knew that speed and acceleration together can be used to make a fairly good prediction of future speed. So, he tested whether the predictions from the type Ia afferents were better than just extrapolating from current speed and acceleration. In fact, the Ia afferents performed substantially better, predicting about 80% of the variance in speed 160 ms in the future, whereas extrapolating speed and acceleration matched less than 50%.

Muscle spindles don't just send information up to the brain; they also receive descending inputs. The Ia afferents seemed to be incorporating some extra information coming from the brain – perhaps about the states of other muscles in the fingers – to make a better prediction. It seems, based on the researchers' findings, that those inputs must contain some information about what neighboring muscles are doing.

Interestingly, this means that when we're first learning to type – or perform any new motor behavior – our brains need to learn the task, but maybe our muscle spindles need to learn it too.

10.1242/jeb.049619

Dimitriou, M. and Edin, B. B. (2010). Human muscle spindles act as forward sensory models. *Curr. Biol.* **20**, 1763-1767.

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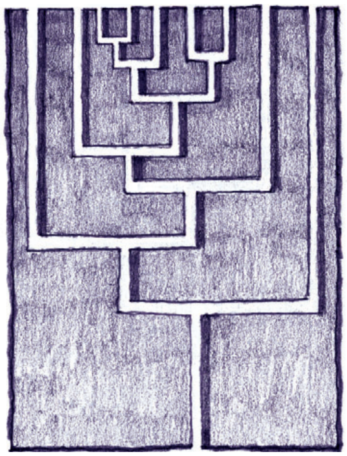
EVOLUTION



EVEN SOARING VAGRANTS ARE TRUE TO DARWIN'S GALAPAGOS

Darwin's early accounts of the distinctive species on the Galapagos Islands were central to the foundations of evolutionary theory. Since that time, data from numerous species have supported Darwin's hypotheses that native species of the Galapagos arose from their earlier inhabitants, remaining unique from other populations because of their geographical isolation. As an ultimate test of the effects of geographical isolation on residents of these islands, Frank Hailer and researchers at the Smithsonian Institution and the University of Missouri–St Louis sought an improbable candidate for isolation effects, the magnificent frigatebird (*Fregata magnificens*). This seabird is widely distributed and capable of easily travelling hundreds of kilometres, giving it great potential for mixing genes with other populations. As predicted by the capacity of frigatebirds to wander, Hailer and his colleagues document that this species does exhibit extensive gene flow amongst most populations; however, on the Galapagos Islands, even this highly adaptable vagrant is distinct from its mainland counterparts.

The authors obtained biological samples from fresh and museum specimens from eastern Pacific and Atlantic populations spanning the distribution range of this avian vagabond. Then they used mitochondrial DNA, microsatellite markers and nuclear introns to assess genealogical relationships. They revealed extensive gene flow across most of this species' range, including across the Isthmus of Panama, which is a major barrier to gene migration that has not been bridged by any other tropical seabird. Other researchers have also shown that magnificent frigatebirds banded in the Galapagos have been recovered over 1000 km away in Central America, demonstrating that island and continental populations may interact. However, the genetic data from this study show that the Galapagos population is unique. Measurements taken on magnificent frigatebirds in museums also revealed that the Galapagos birds are significantly larger than those from the mainland. Despite the birds' nomadic lifestyle and potential for mixing, these genetic and morphological results indicate long-term isolation on the Galapagos, probably for several hundred thousand years. So just what explains the uniqueness of magnificent frigatebirds on the Galapagos?

The authors speculate that the magnificent frigatebird may exhibit a tendency to breed at their birth location or a previous breeding site (philopatry), perhaps because of a movement barrier unique to the Galapagos or to a behavioural mechanism related to their intricate courtship routine. Indeed, Galapagos seabirds have been found to forage primarily in the nutrient-rich waters west of the archipelago while seabirds from the mainland of South America forage mainly on the continental shelf. These distinct foraging preferences could impart geographical isolation of the two populations. As the territory of the magnificent frigatebird on the Galapagos overlaps with that of the great frigatebird (*F. minor*), these birds may be especially picky in choosing their mates in order to avoid pairings with the other species. This type of finicky mate selection could also result in the rejection of mainland birds as potential mates, leading to reproductive isolation.

Future studies are necessary to determine the mechanism behind the evolutionary distinctiveness of the Galapagos magnificent frigatebird. In any case, the work by Hailer and his colleagues is an elegant modern day recapitulation of Darwin's early hypotheses on the unique species of the Galapagos Islands. These findings may also dictate a reconsideration of this bird's IUCN status (currently listed as Least Concern), given that this population consists of only about 1000 pairs.

10.1242/jeb.049627

Hailer, F., Schreiber, E. A., Miller, J. M., Levin, I. I., Parker, P. G., Chesser, R. T. and Fleischer, R. C. (2010). Long-term isolation of a highly mobile seabird on the Galapagos. *Proc. R. Soc. Lond. B*, doi:10.1098/rspb.2010.1342.

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IMMUNE RESPONSE

IMMUNE MEMORY FOUND IN MOSQUITOES

For people living in the Northern hemisphere, mosquitoes are more of an annoyance than a real threat. However, in many other areas of the world they pose serious health risks as they transmit devastating infectious diseases such as malaria caused by the *Plasmodium* parasite. Each year, more than two hundred million humans are infected, and almost one million die from malaria, mostly children under 5 years. To interrupt this dramatic cycle of infection and death, scientists around the world have analyzed the immune response against *Plasmodium* in the human host, but only a few have surveyed the mosquito's immune response. In a study published recently in *Science*, researchers from the National Institutes of Health led by Carolina Barillas-Mury have shown that mosquitoes are able to develop long-lived immunity to *Plasmodium*.

For someone suffering from malaria it is cold comfort to know that the mosquito may also suffer after being infected by the parasite. While the mosquito's immune system attacks the parasite to fight off infection, they lack an adaptive immune response, which remembers previous infections and bolsters a highly specific response after re-infection. Therefore they rely primarily on their innate immune system, which, according to current textbooks, has no memory. However, a few recent studies indicated that insects may have developed other strategies resulting in a specific immune priming that enhance phagocytic responses after renewed infection with the same pathogen.

To investigate whether mosquitoes develop antiplasmodial immunity in response to subsequent infections, the team fed two groups of mosquitoes with blood carrying the infectious stages of the parasite. One group was kept at a temperature that could allow the infection to develop (referred to as primed mosquitoes), while the other group was incubated at higher temperatures, which prevents development of the parasite and hence blocks the infection (referred to as naïve mosquitoes). After 7 days, they fed the mosquitoes again with blood containing the parasite, but this time they allowed the infection to become established in both groups and determined the number of parasites in the mosquitoes to obtain a measure of the strength of the antiplasmodial immune response. The scientists found that the number of parasites was significantly reduced in the group of primed mosquitoes. Hence, the mosquitoes had developed some kind of immune memory as they learned from the first infection and were much more effective in fighting off the second infection. But how do they fight the parasite?

As the innate immune system of insects is largely based on the activity of immune cells (called hemocytes in insects), the scientists went on to analyze these cells in both groups of mosquitoes. They focused on one subpopulation of hemocytes called granulocytes, which are known to be involved in killing invading microorganisms. Indeed, the number of granulocytes was permanently raised in the group of primed mosquitoes. Next they tested whether the hemolymph of the primed mosquitoes contained specific factors that could confer an enhanced immune response. Having injected cell-free hemolymph from naïve and primed mosquitoes into parasite-free recipient mosquitoes, the team then exposed these insects to malaria parasites to see whether any factor(s) in the cell-free hemolymph might bolster the mosquito's immune response. It did. The mosquitoes that had received hemolymph from the primed mosquitoes had an enhanced antiplasmodial immune response and an increased number of granulocytes.

So Carolina Barillas-Mury and her colleagues have shown that mosquitoes have an immune memory that helps them fight off *Plasmodium* infection, and once the soluble hemolymph factors involved in conferring antiplasmodial immunity in mosquitoes have been identified, they may open up new strategies that target the mosquitoes' immune response to fight malaria.

10.1242/jeb.049635

Rodrigues, J., Brayner, F. A., Alves, L. C., Dixit, R. and Barillas-Mury, C. (2010). Hemocyte differentiation mediates innate immune memory in *Anopheles gambiae* mosquitoes. *Science* **329**, 1353-1355.

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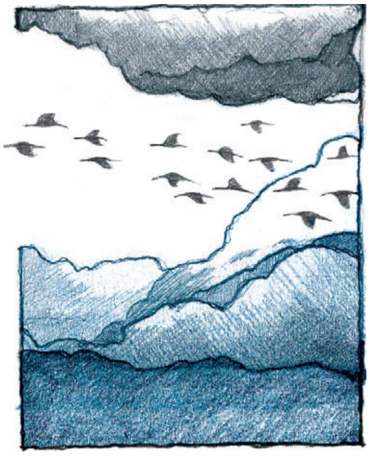
MATE SELECTION



FEMALE FINCHES BENEFIT FROM CHEATING

Gouldian Finches are beautiful colourful birds and, although commonly described as a monogamous species, female Gouldian Finches are anything but faithful. As Sarah Pryke and her colleagues at Macquarie University in Australia observed, female Gouldian finches will cheat on their mate at the slightest opportunity. Why would they do that? It's easy to explain why males cheat; increased progeny leads to increased fitness. However, breeding is more costly for females and an understanding of the benefits of promiscuity is more elusive. A recent paper in *Science* by Pryke and her colleagues proposes that infidelity, together with post-copulatory sperm selection, aids a female in choosing the best candidate as the father of her chicks.

Of the three morphs of Gouldian finches – red heads, black heads and yellow heads – the red and black head morphs are genetically incompatible, and – as Pryke and Simon Griffith noted in 2009 – interbreeding between the two morphs results in a 60% increase in offspring mortality. However, compatible males are not always around, and as some red head males are heterozygous and carry the black head allele, it's not always that easy for a female Gouldian finch to tell which prospective partner is the most compatible choice. Pryke and her colleagues performed a series of experiments to determine how often female Gouldian Finches engage in cheating, whether the propensity to cheat depends on the female's compatibility with her partner and the interloper, and whether post-copulatory mechanisms play a role in selecting the most compatible father for a female's offspring.

The researchers used 40 Gouldian finch females bonded to either a compatible or an incompatible male. During the experiments the females were visually separated from their social mate by an opaque plastic divider that split the cage in two. Pryke and her colleagues then presented the female with a compatible or an incompatible male, giving her the opportunity to copulate with the new male. The visiting males performed courtship displays in 95% of the cases and the females were quite promiscuous in response; 77.5% of the females solicited and copulated with the new males, irrespective of their compatibility status with their mate or the interloping male. However, fertilization of the eggs was not so indiscriminate; all of the offspring were fathered by her long-term mate when he was compatible and the interloping male was incompatible, but compatible interlopers fathered more offspring when the long-term mate was incompatible. This happened despite the fact that females had only one chance to indulge in an extra-marital affair, but multiple opportunities to copulate with their long-term partner.

For a long time, the adaptive reason for female promiscuity has been a mystery. This new study provides insight into the evolution of female infidelity in birds. When compatible males are unavailable, or when unable to determine whether their life partner is genetically compatible or not, Gouldian finch females are faced with a conundrum. And how do they circumvent these problems? Well…they cheat… and then, they select the most compatible sperm and fertilize their eggs with it to give their chicks the best father they can get.

10.1242/jeb.049643

Pryke, S. R., Rollins, L. A. and Griffith, S. C. (2010). Females use multiple mating and genetically loaded sperm competition to target compatible genes. *Science* **329**, 964-967.

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