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

DEFENCE

ATTACK OF THE EXPLODING TERMITES

Aging is not always the most graceful of processes in animals. Hair greys, eyesight dims and teeth lose their edge. But perhaps no animal has it as tough as termites. A paper recently published in *Science* by J. Šobotník and an international team of colleagues shows that as *Neocapritermes taracua* workers age they develop a backpack stuffed with toxic chemicals that explodes when they are attacked.

The researchers had noticed that workers of *N. taracua* come in two varieties: a regular-looking 'white' worker, and one that has two long dark blue markings at the space where the thorax and abdomen join ('blue' workers). And when either blue or white workers were attacked by other termite species, they burst, emitting a small amount of fluid. Upon closer inspection, the researchers found that the blue markings appeared to be caused by small groups of dark blue crystals held in pouches between the abdomen and an outgrowth of the thorax.

To figure out what was going on, the researchers went to French Guiana and collected several colonies of *N. taracua*. Based on previous studies, they hypothesized that, as older workers were less useful to the colony – because their mandibles were worn and not as effective at chewing – they would be more likely to have blue crystals, more likely to burst when attacked and, when they burst, produce more toxic fluid. They first compared the mass of blue crystals to the sharpness of the mandibles in *N. taracua* workers and found that older workers (with duller mandibles) had greater amounts of blue crystal. Then they set up fighting matches where they paired *N. taracua* workers with other termite species to see how long blue and white workers held out before bursting. They found that blue workers were more aggressive to other species, and burst more quickly than white workers.

Šobotník and the other researchers then applied fluid from burst white and blue workers to termites of other species to compare the toxicity of the fluids. In addition, they gently removed the crystals from the blue workers, to see whether they were solely responsible for any differences in toxicity. They found that the fluid emitted by blue workers (complete with blue crystals) was extremely effective at killing other termites, whereas the fluid emitted by white workers was much less potent. However, without their blue crystals the blue workers' fluid was far less toxic. Similarly, if the team added blue crystals to the fluid from a white worker, the toxicity of the mixture was increased (although it was never as toxic as the unaltered mixture from a blue worker).

This pointed to the blue crystals being an important component of the toxicity. Using several chemical techniques, the researchers found that the blue crystals contained a 76 kDa protein, likely an oxygen-binding copper protein from the hemocyanin/phenoloxidase family, containing a large amount of copper (which gave the crystals their blue colour). The also found that salivary gland extract (which mixes with the blue crystals during the explosion) from the blue and white workers appeared to differ in composition. This led the researchers to conclude that blue *N. taracua* workers have a two-component toxin: the crystal protein and salivary gland components mix to produce the toxin.

Aging is not exactly a peaceful process in this termite species. Rather than settling down and picking up a hobby as they age, workers of *N. taracua* develop a hash of toxic chemicals that they carry around in a backpack on their cuticle, ready to burst at any moment in a Kamikaze mission against their enemies.

10.1242/jeb.077594

Šobotník, J., Bourguignon, T., Hanus, R., Demianová, Z., Pytelková, J., Mareš, M., Foltynová, P., Preisler, J., Cvačka, J., Krasulová, J. and Roisin, Y. (2012). Explosive backpacks in old termite workers. *Science* **337**, 436.

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POST-REPRODUCTION

BENEFITS OF BEING A MUMMY'S BOY

As humans, we often take grandmothers for granted. Dispensing baked goods and well-intentioned advice, grandmothers are an integral part of our human societies. However, human grandmothers represent an incredibly rare phenomenon among all living things: they are post-reproductive. The vast majority of plants and animals do not live past their reproductive years. Dramatic examples of a single reproductive bout followed by death within days, such as occurs in Pacific salmon, are far more common in the animal kingdom than the curious case of post-reproductive individuals. The rarity of post-reproductive individuals has led many researchers to ponder, what is the purpose of life after reproduction?

Human females have the longest post-reproductive period in the animal kingdom, but female killer whales are close runners-up. Female killer whales cease reproducing at approximately 30 or 40 years of age, and yet can live for approximately 90 years, with a post-reproductive period that rivals humans. In a 36-year long-term study of over 500 resident killer whales off the coast of Washington, USA, and British Columbia, Canada, a group of researchers have uncovered convincing evidence that there is an evolutionary benefit to this extended post-reproductive period.

Led by Emma Foster from the University of Exeter, UK, the group of scientists from Exeter, the University of York, UK, the Center for Whale Research, USA, and the Pacific Biological Station, Canada, tracked family groups of whales for multiple generations. The scientists identified mother–offspring pairs by recording small calves with their mothers. As there is no dispersal in killer whale family groups, the disappearance of an individual from a family group indicates that the individual has died. From this long-term data set of family trees and family member survival, the researchers were able to assess the consequences of a mother's death on the survival of her sons and daughters.

The group of scientists found that for an adult female killer whale, there is no benefit of having her mother around. Once grown, female survival is independent of whether her mother is still alive. However, having a surviving post-reproductive mother significantly increased survival for sons, even for 35-year-old, fully grown male killer whales. Killer whale mothers help their grown sons forage, and they also form alliances with their sons, defending them during fights with other whales. It seems that with mum around to help feed and defend her sons, these males have a better chance of long-term survival even as adults.

From an evolutionary perspective, this favouritism may have arisen because resident killer whales live in permanent matrilineal family groups, where grandmothers, mothers, sons and daughters live and hunt together. However, males will mate with females from other family groups. Thus, although a grandmother must incur the costs of raising her daughter's offspring within the family group, other killer whale families raise the offspring of her sons. For a mother, the fewest costs and greatest benefits occur when she ensures that her sons survive and reproduce, rather than by producing more offspring of her own or by favouring her daughters. For these adult males, it seems that there are distinct benefits of having a post-reproductive mother around and being a mummy's boy.

10.1242/jeb.077602

Foster, E. A., Franks, D. W., Mazzi, S., Darden, S. K., Balcomb, K. C., Ford, J. K. B. and Croft, D. P. (2012). Adaptive prolonged postreproductive life span in killer whales. *Science* **337**, 1313.

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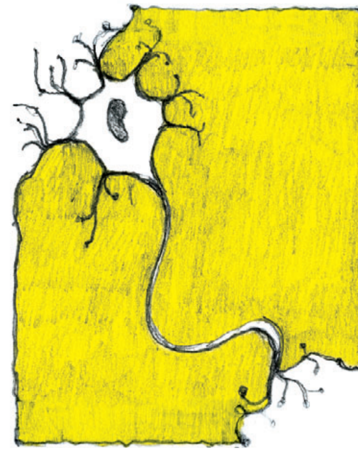
SENSORIMOTOR CONTROL



HORSE-HEAD GRASSHOPPERS LOOK BEFORE THEY REACH

Looking at an object and then reaching out and grabbing it is something humans do without thinking. To do this, a brain must encode an object's position in two-dimensional visual space, and then transform the information into activation of motor neurons, which finally move a limb through three dimensions. This sensorimotor transformation has been thought to be too complex for smaller-brained invertebrates to pull off. In a recent issue of *Proceedings of the Royal Society B*, Jeremy Niven, Swidbert Ott and Stephen Rogers tested this assumption by studying how horse-head grasshoppers walk across gaps.

Horse-head grasshoppers (Orthoptera: Proscopidae) have evolved to look like sticks and spend their lives climbing and hiding among twigs and branches. Niven and colleagues wanted to know whether horse-heads use their visual systems to target forelimb movements as the creatures navigate through environments with the kind of complex substrates that they usually encounter in the wild. The team set up two horizontal rods at right angles to each other with a gap in between. They filmed individuals walking along one rod and reaching across the gap to the other rod. During a reach, animals moved their forelimbs directly to the rod on the other side and made no rhythmic searching movements with their forelimbs. Furthermore, proscopid antennae are too short to be effective as long-range mechanoreceptors. These results suggest that horse-heads do not 'feel their way' across gaps in a substrate with either legs or antennae.

However, the team's initial results did not preclude the possibility that gap detection triggers a stereotyped leg movement that simply sweeps through a large space until contact is made with a substrate. To test this hypothesis, Niven and colleagues varied the separation between rods in both horizontal and vertical dimensions, and then measured trajectories of limb movements during reaches. They found that horse-heads do adjust limb trajectories depending on the position of the target rod. The team also found that limb placement was very accurate (less than 10% of all reaches within range missed their mark) and no attempts were made to reach out to targets beyond the range of the forelimbs. These results suggest that proscopids have specific targets in mind when reaching for footholds and can judge reaching distances accurately.

Next, the team next wanted to determine the role that vision plays in judging target distances. They observed that when confronted with large (but not small) gaps, horse-heads would make side-to-side ‘peering’ movements with their heads. When Niven and co-workers deprived individuals of binocular vision (by painting over one of their two eyes), the amount of peering at small gaps increased and individuals almost always initiated reaches with the limb on the same side as the unobstructed eye. They were still able to make accurate reaches with the forelimb on their sighted side; however, the manipulation did prevent accurate reaching by the limb on the sightless side and supressed its use. Taken together, these results suggest that horse-head grasshoppers do rely on visual cues to target limb movements and that they are able to switch flexibly between two different strategies for targeting limbs to points in space (peering *versus* binocular cues).

The work of Niven and co-workers reminds us not to underestimate the capabilities of invertebrate nervous systems. The work also demonstrates the value of taking a comparative approach to studying the neural basis of animal behavior. If we take the time to study unusual animals, we can up-end long-held assumptions in biology.

10.1242/jeb.077610

Niven, J. E., Swidbert, R. O. and Rogers, S. M. (2012). Visually targeted reaching in horse-head grasshoppers. *Proc. R. Soc. Lond. B* **279**, 3697-3705.

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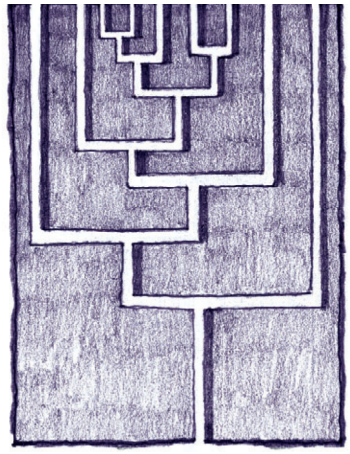
EVOLUTION



PARASITES AND THE GREAT DIVIDE

Animals and their parasites coevolve in an endless game of cat and mouse. As one escapes, the other finds new ways of attack. Of what long-term evolutionary consequence is all of this dodging and weaving? New research published in *The American Naturalist* by Camillo Berenos and colleagues at the University of Zurich in Switzerland provides evidence that it might cause the formation of new species.

How new species form remains an evolutionary puzzle. The classical view holds that new species emerge passively following geographic separation. Adaptation can play a similar role in speciation. Here, speciation occurs when some part of a population evolves along one adaptive path while another takes a different route. But what causes these adaptive splits to begin with? Berenos and colleagues tested the idea that parasites send hosts scattering down different paths of resistance. As a consequence, because these separate paths are mutually incompatible, the host populations become less able to interbreed.

Using an experimental approach where evolution is followed in real time, the researchers forced the flour beetle, *Tribolium castaneum*, to coevolve with its parasite, the microsporidian *Nosema whitei*, for 17 generations in the laboratory. Although only a brief evolutionary period, it was sufficient to drive extensive changes in the beetle host. And crucially, these changes were specific to the presence of the parasite. In each of the six coevolved lineages, the rate of parasite-induced mortality dropped by nearly twofold, while resistance in parasite-free populations remained unchanged.

Because these parasites are killers, it is unsurprising that beetles evolved increased resistance. More interesting is how these changes influenced mating success. When the researchers crossed coevolved resistant beetle lineages they found that they were happy enough to mate; there were no barriers to reproduction. However, fecundity in crosses between beetles from different coevolved populations declined by 16% compared with fecundity in crosses of beetles from the same population. This suggested that different modes of resistance had become fixed in the six coevolved lineages and that these separate solutions were genetically incompatible. Supporting this, the researchers found a significant positive relationship between the reduction in fecundity in between-population crosses and their level of evolved resistance. That is, lines that had evolved greater parasite resistance were more reproductively isolated from the others.

Populations separated by time or space will slowly drift apart genetically, and this can eventually lead to reproductive isolation – a precondition for speciation. What this study elegantly shows is that biotic factors can serve as a proxy for time and space. Like an arsonist’s accelerant, parasites stoke the flames of genetic change, rapidly pushing hosts to different slopes of the genetic landscape. Pushed far enough, hosts become less able to interbreed. How often this scenario unfolds in nature is unknown. However, although mountains emerge to split populations only rarely, parasites are ubiquitous. This study shows that parasites not only kill and maim, but, through their actions, they may also be the wind in the sails of speciation.

10.1242/jeb.077586

Bérénos, C., Schmid-Hempel, P. and Wegner, K. M. (2012). Antagonistic coevolution accelerates the evolution of reproductive isolation in *Tribolium castaneum*. *Am. Nat.* **180**, 520-528.

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