

eukaryotic tissue to test whether tubulins can be specialized or not. The answer is a resounding yes.

It has been an amazing and satisfying surprise to discover the intricacy with which the sequence of the component tubulins can determine both microtubule structure and axoneme architecture and function. Using genetics to do our biochemistry, we made many exciting discoveries that could not have been predicted. Our first — key — test in this series of experiments was to ask whether another, slightly divergent fly  $\beta$ -tubulin could replace the normal testis  $\beta$ -tubulin. We discovered that the two tubulins were not functionally interchangeable. Even though the other isoform is a perfectly good tubulin in the tissues where it normally functions, it could not support axonemes or other testis-specific functions. We introduced a moth testis  $\beta$ -tubulin homolog into the fly testis and discovered that the moth tubulin brought with it the instructions for the moth's specialized 16 pf microtubules. We found that even an  $\alpha$ -tubulin 98% like the normal testis  $\alpha$ -tubulin was a dismal failure at making axonemes, although it could make spindles just fine. We discovered a carboxy-terminal sequence motif that specifies motile axoneme  $\beta$ -tubulins, conserved in all eukaryotes. We discovered that it matters how the 'parts' of the tubulins in a microtubule are put together: a heterologous  $\beta$ -tubulin can work in concert with the endogenous germ line  $\beta$ -tubulin, but if the tails and bodies of the molecules are swapped, the 'trans' configuration doesn't work — even though all the same tubulin sequences are present. We discovered that the identity of one internal amino acid in  $\beta$ -tubulin is crucial for the attachment of the outer dynein arms that power axoneme motility — this feature of axoneme  $\beta$ -tubulins is also conserved throughout phylogeny.

**Along with microtubule function, evolution of developmental mechanisms and the determination of body form has become half of your research efforts: how did that happen?** The I.U. Biology department is a broad, unified department, a fantastic place to do science, with one of the best evolution groups in the

country — making up for my life pre the E-word. I got into our now long-term evo-devo collaboration with my husband, Rudy Raff, through an experiment I urged him to do but ended up doing myself. In the 1980s, Rudy discovered an ideal system for experimentally accessing evolution of development, using two closely related species of Australian sea urchins that, although separated by only four million years, have completely different developmental pathways. One generates the typical long-lived planktonic pluteus larva and the other skips a feeding larval stage, going directly from a fertilized egg to a little sea urchin in just three to four days. Rudy, with his group, discovered the cellular and gene mechanisms involved in this reshaping of ontogeny.

I wanted to try making hybrids between the two species, so in 1998 I took a mini-sabbatical to the University of Sydney. Adding to the lure of the questions I could ask about developmental pathways was the alluring location. The only negative I can think of for fly genetics is that no field studies are required. Evolutionary biologists always seem to have exotic field sites. At last I found my own 'field', the world's best city.

I have always liked the fertilization literature, perhaps because of the featured role for sperm tail axonemes, and I figured out how to generate hybrids. As with tubulin genetics, I was hooked by spectacular and unexpected results. The cross in one direction generated viable hybrids — but with a novel ontogeny. Given this gift of biological revelation, we have pursued this system since then. Most recently, we discovered we can use the relatively giant (400  $\mu$ m) direct-developing embryos to experimentally model how soft tissues can be fossilized, seeking insight into ancient animals represented by rare fossils. Another new avenue to explore has thus suddenly opened up.

#### **What's next — retirement?**

No way. Both doing and teaching science are still much too exciting — and fun, the key word.

Department of Biology, Indiana University, Bloomington, IN 47405, USA.  
E-mail: [raff@indiana.edu](mailto:raff@indiana.edu)

## Quick guides

# Mosquito-specialist spiders

Fiona R. Cross  
and Robert R. Jackson

#### **What does 'mosquito specialist' mean?**

A mosquito specialist is a predator that actively prefers mosquitoes, by which we mean that it is differentially motivated to capture mosquitoes among possible prey. This would make it extraordinarily useful, as it would be targeting an insect that matters to people. At best, the mosquito is a nuisance and, at worst, it is a notorious disease vector. There may be many predators that eat a lot of mosquitoes, but experimental evidence is needed to show that a predator has the sensory capacity to distinguish mosquitoes from other prey and that it deploys a strategy of choosing this specific prey type. There is one predator for which the required evidence is actually available: its name is *Evarcha culicivora* (Figure 1), a jumping spider (family Salticidae) from the Lake Victoria region of East Africa.

All salticids are remarkable predators because, thanks to their unique, complex eyes, they can see with a level of spatial acuity unrivalled by other animals in their size range and they deploy intricate vision-guided stalking strategies. However, *E. culicivora* seems to have taken seeing detail to a level that is extreme even by salticid standards. The shoreline of Lake Victoria teems with insect life, especially chironomid and chaoborid midges, which vastly outnumber mosquitoes. These midges are known locally as 'lake flies', and they resemble mosquitoes. *E. culicivora* preys on lake flies and other insects, but it prefers mosquitoes — it can identify a mosquito in a crowd by sight alone, even when the insect is entirely motionless. However, *E. culicivora*'s target is actually even more specific and this specificity is part of a strategy of feeding indirectly on vertebrate, including human, blood.

#### **What does 'indirect feeding on vertebrate blood' mean?**

Mosquitoes take blood meals from

vertebrates directly and, unlike spiders, they have appropriate mouthparts for doing this. Nonetheless, *E. culicivora* feeds on vertebrate blood because it actively chooses blood-carrying mosquitoes. The mosquito is like a syringe with wings that involuntarily delivers blood to *E. culicivora*. By sight alone, *E. culicivora* will choose a female mosquito that has taken a recent blood meal when the alternative is a female mosquito that has not had a recent blood meal. Male mosquitoes never take blood meals and *E. culicivora* consistently chooses blood-carrying females when the alternative is a male.

**Is vision all that matters to this predator?** No — blood-carrying mosquitoes smell different from other prey and, besides being able to see extraordinarily well, *E. culicivora* is remarkably good at identifying blood-carrying mosquitoes even when restricted to using olfaction alone. Dual reliance on vision and olfaction also applies to the male–female interactions of *E. culicivora*. This predator has an exceptionally complex mating strategy, with both sexes actively engaging in display behaviour and both actively choosing their potential mates. Paralleling what was found in the context of predation, *E. culicivora* can identify potential mates either by sight alone or by smell alone.

**Why does *E. culicivora* feed on blood?** Part of the answer is that indirect blood meals give both sexes of *E. culicivora* an odour that makes them more attractive to the opposite sex. For *E. culicivora*, it is as though blood is perfume, and it seems to be a perfume that needs to be continually replenished. For a predator that singles out mosquitoes, this might have interesting implications. For *E. culicivora*, killing mosquitoes appears to be motivated by more than hunger in the context of nutrition. Even when satiated, this predator goes on killing mosquitoes for perfume.

Being a spider with blood on its mind, *E. culicivora* became more than just an arachnid curiosity; *E. culicivora*'s unusual behaviour appears to provide a handle on understanding selective attention.

**What is so interesting about selective attention?** 'Selective



Figure 1. An adult male of *Evarcha culicivora* feeding on a blood-carrying *Anopheles gambiae* female (photo by R. Jackson).

attention' is a term used mainly in cognitive psychology, whereas biologists tend to be more familiar with the term 'search images'. Both terms are relevant when an animal becomes prepared to detect and identify something specific. The word 'image' in 'search image' implies that animals are using vision and there is, indeed, a strong bias in the search-image literature toward examples of visual attention. However, one of the more interesting things about research on *E. culicivora* is that this species lends itself to experiments on olfactory as well as visual search images. *E. culicivora* deploys search images in the context of finding prey and in the context of finding mates, with seeing a mate or a preferred prey triggering selective attention to the visual characteristics of mate and prey, respectively, and with smelling a mate or a preferred prey triggering selective attention to the odour of mates and prey, respectively. There is also evidence of cross-modality priming, with the odour or sight of prey triggering selective visual or olfactory attention to prey, respectively.

With *E. culicivora*, there is another important departure from tradition. Most search-image experiments in the literature have been based on exposing the animal to a priming

stimulus repeatedly, with the formation of a search image being envisaged as coming about by perceptual learning. However, there is evidence of search-image formation by *E. culicivora* when it has only been exposed once to the sight or odour of prey or a mate. Rather than being based on perceptual learning, the examples of search-image use by *E. culicivora* appear to be instances in which priming calls up innate (pre-existing) search images.

**Are malaria vectors relevant to *E. culicivora*?** There is no reason to think that *E. culicivora* cares about a mosquito's status as a disease vector, and yet it does have a particular interest in *Anopheles*, the mosquito genus responsible for transmitting human malaria. This is especially evident for very young individuals. Newly-hatched juveniles of *E. culicivora*, for example, are only ~1.5 mm in body length and you might wonder whether such a small predator could bring down a blood-carrying mosquito. They do indeed have problems with some mosquitoes. When attacked head on, a mosquito may take flight and shake the tiny spider loose, but things happen differently when the encounter is with *Anopheles*. Small

*E. culicivora* juveniles adopt *Anopheles*-specific prey-capture behaviour that takes advantage of how *Anopheles*, unlike other mosquitoes, rests with its abdomen tilted up. The tiny *E. culicivora* juvenile sees well enough to discern the mosquito's posture and then plots a path to the mosquito that takes it in from behind. Once beneath the mosquito's upward-tilted abdomen, the juvenile grabs hold from underneath. Though the mosquito may take flight, the *E. culicivora* juvenile usually manages to hold on and, before long, when its venom takes effect, the mosquito falls to the ground, with the *E. culicivora* onboard.

Perhaps this is not surprising, but the small juveniles of *E. culicivora* also actively choose *Anopheles* in preference to other mosquitoes. Something that is more surprising, however, is that this preference is also expressed by larger juveniles and adults of *E. culicivora*, especially when they are well fed. These larger individuals have no apparent difficulty overpowering any mosquito, but whether they gain some specific adaptive advantage for preferring *Anopheles* is unknown. However, by targeting vectors of human malaria, *E. culicivora* is a potentially important predator.

#### Where can I find out more?

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School of Biological Sciences, University of Canterbury, Private Bag 4800, Christchurch, New Zealand, and International Centre of Insect Physiology and Ecology (ICIPE), Thomas Odhiambo Campus, P.O. Box 30, Mbita Point, Kenya.  
E-mail: [fiona.r.cross@gmail.com](mailto:fiona.r.cross@gmail.com);  
[robert.jackson@canterbury.ac.nz](mailto:robert.jackson@canterbury.ac.nz)

## Spider monkeys

Filippo Aureli<sup>1</sup>  
and Colleen M. Schaffner<sup>2</sup>

**What are spider monkeys?** Spider monkeys are one of the largest New World monkey species. Males and females are essentially monomorphic, reaching approximately 50–60 cm in height, not including their tail, and weighing between 8 and 10 kg. They are almost exclusively arboreal, and have some specialized adaptations to cope with treetop life. They have the most developed prehensile tail of any primate, and have such a dramatically reduced thumb that it is essentially non-existent. These adaptations enhance the spider monkeys' acrobatic and agile primary mode of travel (Figure 1). They move through the forest canopy using tail-assisted brachiation, which involves hanging from the arms and tail and swinging from point-to-point.

Spider monkeys live as far north as Southern Mexico, throughout Central America and in several countries in South America. They prefer pristine forest and spend the vast majority of their time in the upper canopy. There has been considerable debate about the number of different spider monkey species and confusion about how many different subspecies exist. Nonetheless, using DNA information there appears to be four distinct species: *Ateles belzebuth*, *A. geoffroyi*, *A. hybridus* and *A. paniscus*.

Spider monkeys have a slow developmental rate and a relatively long lifespan for their size. Although spider monkeys are likely reproductively capable at about five years of age, it takes as long as eight years for them to reach full adult size. There are reports of two captive spider monkeys reaching 44 and 52 years of age. Although wild individuals possibly do not live as long, it is probable that they live into their late 20s or early 30s.

**What is their social system?** The social system of spider monkeys is rare among group-living animals: they live in multi-male, multi-female communities with a high degree of fission–fusion dynamics. The community members are rarely

all together, even at night, but are typically found in subgroups. These subgroups fuse with each other to form temporally larger subgroups, which then undergo fission into smaller subgroups with different composition; this can happen several times in the course of a single day. Their subgroup size can vary from one solitary individual to the entire community (15–100 individuals). The subgroup composition is also highly variable with mixed-sex, mixed-age subgroups, all-male subgroups or subgroups with only females and their offspring.

Males are believed to remain in their natal community for their entire lives, although future long-term studies of these long-lived animals may reveal different patterns. Most female spider monkeys leave the community where they were born before conceiving the first infant. Integration into a new community is not easy for immigrating females, who are usually attacked by resident females for months. Full integration is usually achieved when the immigrating female has her first infant. Females are very interested in other females' infants and frequently approach and embrace new mothers to signal their benign intention in interacting with the infant.

As it is typical in other species, individuals belonging to the sex that remains in the natal group form stronger bonds with one another. Thus, in spider monkeys it is males that have the opportunity to develop the strongest bonds. They cooperate with one another to defend the community territory. They also compete with one another to access females. Thus, their relationships are relatively unstable and may change opportunistically. Young males are highly attracted to adult males, but they risk attacks, sometimes lethal, as they can be viewed as either additional allies or competitors, depending on the community composition. Females have weak relationships with one another, and most of their interactions are concentrated around immigrations and infants. Relationships between males and females are usually friendly, but males seem to attack females for reproductive purposes. This aggression has been interpreted as coercion, but it is usually mild and may function as a form of courtship.