## VISION

Fisheye views

Archerfish eyes must cope with the light spectrum of two very different media. These fish live among mangroves and in rivers, and are renowned for their ability to bring down an insect target from overhanging foliage by spitting a stream of water at their prey, as pictured here. Shelby Temple and colleagues have investigated the visual pigments and spatial resolving power of archerfish eyes, and present the results in the context of the requirements for vision at the water–air interface (S. Temple *et al. Proc. R. Soc. Lond. B* doi:10.1098/rspb.2010.0345; 2010).

Using microspectrophotometry, the authors find that — as is known

in other species — the pigments and spectral tuning vary between different parts of the retina (in this case, subdivided into dorsal, ventro-nasal and ventro-temporal regions). They interpret these variations in terms of the tasks the eye has to perform when operating along three visual axes; that is, three directions in which the eye might look.

A simplified description of their conclusions is that the dorsal retina has maximum spectral sensitivity at 454 and 570 nanometres, a combination that Temple *et al.* consider is well suited for discriminating between shades of brown, and for identifying objects
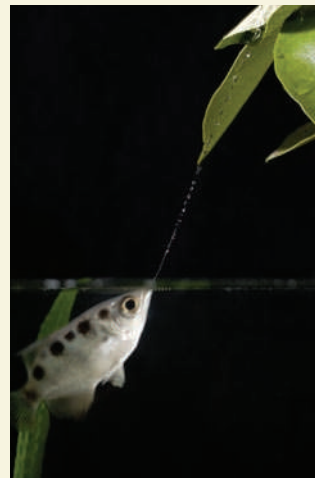
beneath them. The values for the ventro-nasal retina (visual axis up and behind) are 502 nm and 620 nm. The 502-nm peak is tuned, the authors suggest, for detecting

dark images against a background of bright sky, such as the silhouette of an aerial predator.

The ventro-temporal retina presents peak sensitivities at 453 nm, 535 nm and 565 nm. This combination is possibly used for colour vision along the visual axis appropriate for sighting prey against a background of foliage. From video recordings, Temple *et al.* conclude that this part of the retina aligns with spitting angles, and they estimate that the visual resolution allows an archerfish to tell the difference between two objects 2 mm apart at a range of 550 mm.

Archerfish can be trained to spit at coloured targets. That, say Temple *et al.*, makes them excellent subjects for investigating further aspects of the function of intra-retinal differences.
Tim Lincoln

20 of the mutations was comparable for all three tumours, that 26 showed increased prevalence in the xenograft and/or the metastatic tissue, and that the prevalence of 2 was significantly decreased relative to the primary tumour. This suggests that at least three cell clones from the primary tumour carried over into the metastatic and xenograft tumours: one carried mutations that decreased in prevalence, one had mutations that increased in prevalence, and one carried mutations whose prevalence did not change compared with the primary tumour. This metastasis therefore does not seem to have formed from a single cell, but rather from a cell population that, in this case, contained at least these three clones.

Another remarkable result was that 16 of the 20 mutations present at increased prevalence in the metastatic tumour were also present with higher prevalence in the xenograft. This pattern of concordant selection of one or more clones carrying common mutations during progression to metastasis and establishment of a xenograft suggests that similar evolutionary pressures are at work on these cells in both environments. This may provide some indication of the aspects of the metastatic process that are influenced by the aberrations carried in the selected clone, because some processes needed for metastasis, such as invasion and barrier penetration, may not be important selective forces in the xenograft environment. These aspects of metastasis therefore may not be influenced by aberrations that are selected in both xenograft and metastasis.

Of course, Ding *et al.*[4] assessed the evolution of only one tumour. But if their results can be reproduced in larger studies, comparative investigations of primary-tumour/xenograft/metastasis triplets might facilitate identification of genomic aberrations that play a significant

part in the pathophysiology of the tumour and metastasis, and provide clues about the biological roles of these genomic regions. They could also provide information about clonal diversity in metastatic lesions, which may help to identify subpopulations of cellular molecules, and thus influence cancer therapy.

Ding and colleagues' data therefore hint that future sequencing of some metastatic-cancer genomes should be considerably deeper than contemplated at present to allow statistically robust estimates of mutation prevalences to be obtained. Moreover, functional assessments of the affected genomic regions will be needed to determine which genes in the selected clones are drivers and which mere passengers. Concordant selection of mutations in the metastatic and xenograft tumours could provide

initial clues to the most useful candidates for functional assessment.
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BEHAVIOURAL ECOLOGY

Ways to raise tadpoles

Hanna Kokko and Michael Jennions

To reduce parental care, just add water — that's the conclusion of an intriguing investigation into the extent of the motherly and fatherly devotion that different species of frog extend to their offspring.

Nature documentaries frequently invite their viewers to contemplate that only a tiny minority of the perfectly formed larvae floating in the sea, or crawling on land, can ever hope to make it to the adult stage. Parents of many species seem surprisingly unconcerned, leaving their progeny to fend for themselves. In some species, however, parents provide their offspring with costly, time-consuming services,

ranging from protecting them against predators and environmental stresses to giving them shelter or food.

Why does this diversity of solutions exist? Theoreticians state that parents may reduce care to increase the number of young produced and/or to improve the parents' own survival. Both trade-offs reduce the lifetime fecundity of parents, so parents are likely to provide care

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only if it substantially improves the survival of the offspring they do produce[1]. A study of frogs by Brown *et al.*[2], just published in *The American Naturalist*, shows that a species' breeding habitat can influence offspring survival in a surprisingly deterministic way: tadpoles have a chance of surviving on their own only if they live in relatively large pools of water.

It has proved difficult to identify specific ecological factors that affect whether parental care will evolve, yet the answer provided by Brown and colleagues[2] is simple and elegant. To start with, they built a phylogeny depicting the evolutionary relationships among 404 frog species that are distributed across the order Anura and that have been investigated for whether and how they provide parental care.

Frog species differ enormously in whether they care for their young and in the type of care given: parents may protect eggs by laying them in terrestrial burrows, or brood the young in pockets of tissue on their back or in the mother's stomach[3]. Although Brown *et al.* did not consider all frog species (of which there are more than 5,300), their phylogeny uncovered compelling ecological generalities. Species that deposit eggs and tadpoles into phytotelmata (small pools of water found in hollows in plants) are more likely to provide parental care than those breeding in terrestrial waters such as streams, ponds and rivers. The estimated rate of evolutionary transitions from providing no care to providing care was nine times higher in species that breed in these tiny pools than in those that use terrestrial waters.

Why does a limited water source turn frogs into devoted parents? One possible answer is that the food supply that a small body of water offers is so meagre that parents using these as breeding grounds have been strongly selected to improve the survival of their offspring. To test this idea, Brown *et al.* investigated one of the evolutionary contrasts in their data set in detail, reporting fascinating differences between two species of poison frog that live in the same habitat in Peru.

Individuals of the variable poison frog species (*Ranitomeya variabilis*) have large home ranges, and both sexes frequently switch mating partners. Eggs are laid above a suitable phytotelma, and either the tadpoles fall into the water or, more commonly, the male parent returns and helps the tadpoles to rupture the egg membrane. He then transports the tadpoles on his back (Fig. 1) to another hollow. In this species, males place tadpoles in water volumes averaging about half a cup (112 millilitres). In the closely related, similarly sized mimic poison frog (*Ranitomeya imitator*), mating pairs are often monogamous. Their home ranges are small, and males carry the tadpoles to a tiny phytotelma which is, on average, the volume of half a shot glass (24 ml). The male parent thereafter returns periodically to monitor whether it is time to feed the tadpoles. If he calls incessantly, the female makes her way to the pool and lays a specialized 'trophic' egg,

Figure 1 | Tadpole transport. After tadpoles have emerged from eggs, males of both the variable poison frog (*Ranitomeya variabilis*; top) and the mimic poison frog (*Ranitomeya imitator*; bottom) carry these offspring on their back from the place of birth in a phytotelma (a water-filled hollow in a plant) to another phytotelma. Brown *et al.*[2] find that these frogs otherwise differ considerably in the amount of care provided by the parents. The smaller phytotelmata favoured by *R. imitator* are associated with a greater degree of parental attention being paid to the tadpoles.

which is promptly eaten by the tadpoles.

Tadpoles of both species are thus cared for, but tadpoles of the variable poison frog develop without being fed and receive care from only one sex (males). Is it a coincidence that variable poison frogs use larger breeding pools than mimic poison frogs, or did feeding evolve in mimic poison frogs specifically to combat a low food supply in tiny pools?

To shed light on this question, Brown *et al.*[2] carried out a translocation experiment. They show that tadpoles of both species grow and survive poorly in small pools when they are denied parental attention, whereas such problems do not arise in larger pools. The fact that tadpoles of both species suffered similar fates is crucial to the interpretation of the experiment. It allowed Brown *et al.* to circumvent the chicken-and-egg problem that species in which care is routinely given might have evolved tadpoles that obligately rely on parental care, which could have led to an overestimation of the value of parental care in small pools.

The phylogeny constructed by Brown *et al.* also reveals that the production of trophic eggs is generally associated with breeding in phytotelmata. However, trophic egg production by

frogs is rare, so factors other than the need to feed offspring are probably required to explain the patterns of parental care in frogs more fully. For example, breeding in a small body of water could decrease the likelihood of brood parasitism (in cases in which more than one pair are using a breeding pool), because later-hatching tadpoles are often cannibalized by those that hatched earlier[4]. In addition, the use of a small breeding ground increases the certainty of genetic parentage, making it more likely that parental care will evolve. It also influences which sex provides care — males, females or both parents[5] — but evolutionary transitions do not occur as easily in all directions[6]. It might not be a coincidence that the poison frog species that engages in biparental care is also the one that is genetically more monogamous.

Even so, caution should be exercised in using the argument that monogamy is conducive to biparental care and therefore concluding that circumstances that make offspring needy also favour monogamy. The co-evolution of traits tends to occur with a delay. Thus, the first monogamous parents of a hypothetical species might not reap any benefits from their behaviour as they will not yet have responded to the novel conditions of reliable parentage by switching to a more intensive form of care. It may be, however, that home-range size or other ecological factors make monogamy more likely in some species and that this later selects for care by both parents.

Regardless of the details of the final story, there is little doubt that frogs, with the diverse ways in which they care for their offspring and an increasingly well-resolved phylogeny, are becoming an important group in helping to explain why there is so much variation in parental care among animals[7]. Unfortunately though, this diversity continues to be lost. For instance, the details of the ecology of the only two species of gastric-brooding frog will never be known, as both became extinct in the mid-1980s. ∎

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