Animal Behavior: The Family that Works Together Stays Together

A new study shows that biparental care in frogs is more likely to evolve when tadpoles are reared under environmentally harsh conditions. Biparental care facilitates both social monogamy and genetic monogamy; frogs that work together to raise their offspring have higher mating fidelity to one another.

Michael J. Ryan

Natural selection often conjures up images of conflict, survival of the fittest being the most striking description of the idea. Conflict is also apparent in natural selection's kissing cousin, sexual selection. Conflict between the sexes has been known since Bateman [1] showed that male fruit flies increase their fitness by mating more often, while such promiscuous tendencies had little influence on female fitness, and as we now know can even increase the prospects of early female mortality [2]. There are exceptions to Batemen's Principle [3], but there are also legions of examples attesting to its ubiquity [4]. Not all of nature, however, is red in tooth and claw. Conflict's more optimistic antithesis, cooperation, guides many social interactions, especially in the context of parental care. It can warm our hearts to see father and mother laboring together to raise their offspring, while at the same time sharing in the bliss of social and sexual fidelity. But these situations also tweak our more cynical evolutionary interests, because they are the exception rather than the rule. In a recent study, Kyle Summers and his colleagues [5] show that parental care is more likely to evolve in frogs when tadpoles are raised under environmentally harsh conditions, with biparental care occurring when conditions are harshest. Furthermore, in one focal species the mother and father are truly monogamous as there is little evidence that mating fidelity is violated (Figure 1).

Most anurans have a dual life cyle, befitting animals from the Class of vertebrates that first ventured out of the water to invade Earth's terra firma. Eggs have little protection from desiccation and usually are deposited in the water. They hatch out into tadpoles, which are aquatic and are ideal food sources for scores of marauding predators. Tadpoles are not defenseless: some are unpalatable [6]; others school with kin to benefit from a selfish herd effect, while aiding in the survival of common genes [7]; while yet others evolve conspicuous bright targets on their tails as decoys to deflect the strikes of predators from more vulnerable body parts [8]. Nevertheless, these ponds are dangerous places where mortality can be quite severe [9]. But a lucky few survive, hatch, develop into froglets and recapitulate history as they break their ties with their aquatic past and move onto a firmer footing.

One strategy for enhancing offspring survival is to keep the developing young out of these treacherous waters. There are a number of anuran reproductive modes that do so: eggs are deposited in foam nests that float on top of the water, on leaves overhanging the water, or in the wet leaf litter to later be transported to water upon hatching [9]. One very large group of frogs (~240 species), the spectacularly colored poison frogs of the family Dendrobatidae, has adopted this latter strategy. Eggs are deposited terrestrially and are attended usually by the male, but in some species females either assist in egg attendance or take on the job by themselves. The parents periodically moisten the eggs, and once the eggs hatch the tadpoles are transported to small pools of water (Figure 2). In many species the tadpoles are deposited in the axes of leaves, and especially in bromeliads; this is referred to as phytotelm breeding.

Comparative analyses across all frogs show that, once phytotelm breeding is established, parental care is more likely to follow (Figure 1). The reason is that although the tadpoles now develop in a safe, predator-poor habitat, they are also in a harsh, food-poor habitat. The smaller the pool of water, the less the food that is available. Without sufficient food the tadpoles might turn to cannibalism or starve. This sets the stage for an extreme form of parental care — trophic egg feeding. As male parental care is the primitive condition in frogs, this necessitates the recruitment of females. A female deposits fertilized and unfertilized eggs in the phytotelm which are then devoured by the tadpoles.

Brown *et al.* [5] do not rest their conclusions about parental care on the correlational data provided by the comparative analysis. Instead they conducted transplant experiments between two closely related species *Ranitomeya variabilis* and *R. imitator*. The former has male-only care, and prefers to put its tadpoles into larger bodies of water (~100 ml). The latter has biparental care where the mother and father cooperate in caring for the young that are deposited in smaller pools of water (~25 ml) where the mother nurtures the tads with trophic eggs. The hypothesis is that the small pools of *R. imitator* will not support tadpoles without trophic egg feeding. The transplant experiments, in which the tadpoles of each of these species is switched between smaller and larger pools, support the hypothesis.

The cooperation of the *R. imitator* parents results in social monogamy, as each member of the pair is forced to associate with the other during the extended period of parental care. The advent of molecular markers has shown us, however, that the apparent bliss of social monogamy is often a mere façade for deceit and promiscuity [10]. Not in this case, however. Microsatellite analysis shows that *R. imitator* is also genetically

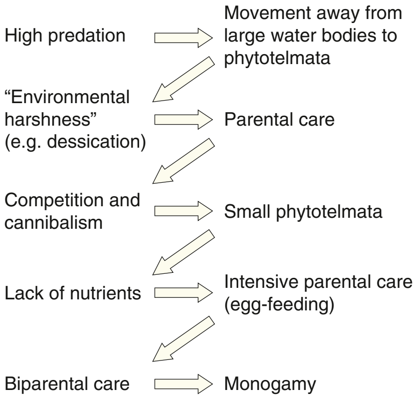

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Figure 1. Evolution of parental care.

A flow chart outlining the major events in the evolution of parental care and genetic monogamy in poison frogs.

Figure 2. Tadpole transport. A male *Ranitomeya imitator* transporting one of its tadpoles. Photo courtesy of Jason Brown.

monogamous — the only such species of frogs known to science.

This is an exciting research program that has shown how a single ecological variable, pool size, can drive the evolution of parental care, biparental care, trophic feeding, and social and genetic monogamy. Equally impressive is how this study recruits methods from a variety of disciplines, including correlational data derived from comparative studies, well-controlled experimental manipulations, and descriptive analyses using molecular markers, to provide powerful insights in addressing a very general question — does the family that works together stay together?

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Section of Integrative Biology, 1 University Station C0930, University of Texas, Austin, TX 78712, USA.
E-mail: mryan@mail.utexas.edu

DOI: 10.1016/j.cub.2010.03.014

Nucleosome Positioning: An Essential Component of the Enhancer Regulatory Code?

The organization of transcription factor binding sites within enhancers plays a key role in the function of these elements. A recent study suggests that the intrinsic propensity to bind to nucleosomes can also play a decisive part in determining enhancer function.

Ahmet Ay and David N. Arnosti

It is chastening to realize that a single cultured cell ‘knows’ more about transcriptional regulatory grammar than we, despite our knowledge of cell biology, biophysics, and bioinformatics. A nucleus programmed with its complement of transcription factors will correctly interpret the potential of a regulatory sequence in DNA to deliver stereotypical gene expression responses. Diverse efforts from genetics to biochemistry, and more recently systems biology, have worked to bridge this knowledge gap. Much of our understanding has come from simple identification of relevant proteins and *cis* regulatory elements that interact to drive transcription. A more formidable undertaking is understanding the design of transcriptional enhancers, and how sequence translates to function. Comparative genomic studies have emphasized the malleability of *cis* regulatory elements, which makes them difficult to identify or classify using only bioinformatic approaches. More recently, genome-wide surveys of *in vivo* transcription factor occupancy have presented snapshots of ‘who is bound where, when’ [1,2]. In addition, several groups have employed ‘fractional occupancy’ mathematical models to capture the properties of transcription regulators jostling for positions on enhancers [3,4]. Neither of these latter approaches is entirely satisfactory, because many sites bound *in vivo* are not functional, and mathematical representations of protein–DNA interactions are often too simple to capture the true environment that