

a continuous path? Whatever the nature of this understanding, there seem to be large individual variations, because only three of seven rooks in Tebbich *et al.* [5] solved the training task, and none passed the transfer task.

There has been a tendency to try to fit animals' cognitive abilities into one of two categories: either they exhibit abilities equivalent (or nearly so) to those of humans, or their abilities are based on associative learning, and are therefore somewhat inflexibly tied to the specific stimuli used during training. The real situation is likely to be much more complicated than this, and the details of what is and what is not understood, and how those differ between species and between tasks are fascinating. The striking inter-individual differences [4,5] also suggest that genetic or developmental conditions might also play an important role in determining the details of adult cognitive abilities.

But how is information about physical causality acquired? The causal structure of the world cannot be perceived directly — you cannot 'see' gravity — and must be inferred from the spatio-temporal relationships between objects. One suggestion is that natural selection has equipped some species with a theory-generating mechanism which uses the conditional probabilities between causes and outcomes to assign causality [6]. For example, if X and Y together are always followed by event Z, but Y alone is not followed by Z, X must be the cause of Z. Non-human animals can make some of these inferences through associative learning [7], and there is evidence that even very young children are capable of quite complex and subtle forms of reasoning [8]. Furthermore, work by Schultz and Gopnik [9] has suggested that young children perform interventions or experiments when investigating the cause of an event, in order to falsify hypotheses about causes.

There is, however, another possibility; not all causes are equally plausible as explanations of outcomes, because of the

constraints of the physical world. Animals with certain expectations about the way that the world works would be able to narrow the field of candidate causes substantially, because some causes are simply 'impossible'. We know, for example, that very young children understand that solid objects will not pass through solid barriers [10]. Knowledge about rigid objects would allow an organism to predict that, if it moved the nearest side of an object, the far side would move away an equal distance. By violating these putative expectations, and observing what animals anticipate happening, we can explore what those expectations might be.

The experiments reported by Seed *et al.* [4] also point out the importance of designing ethologically valid tasks when investigating cognitive capabilities. In this case, the fact that the animal is able to pull the food towards itself seems to enable it to perform at a much higher level, perhaps because each stage of the action brings the food closer rather than pushing it further away. Also, details of exactly what animals can and cannot do are more illuminating than the presence or absence of a particular response. The world is a bewilderingly complex place for young organisms, and we need to think much more about the ways in which information about the

physical world is structured and acquired.

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## Polyloid Hybrids: Multiple Origins of a Treefrog Species

*Hyla versicolor*, a tetraploid treefrog, is reported to have originated via multiple hybridization events involving three diploid ancestors. Its complex reticulate history provides insights into the roles that polyploidy and hybridization can play in the origin of species.

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The roles that polyploidy and hybridization play in the origin of plant and animal species have been discussed for many years. The two processes often occur together in the form of allopolyploids — hybrids with two

or more copies of each parental genome — but each process can be viewed separately, because many polyploids are not hybrids and vice versa. The appearance of polyploids, a form of instantaneous speciation, is common in seed plants and ferns [1]. Nevertheless, Stebbins [2] argued that polyploidy

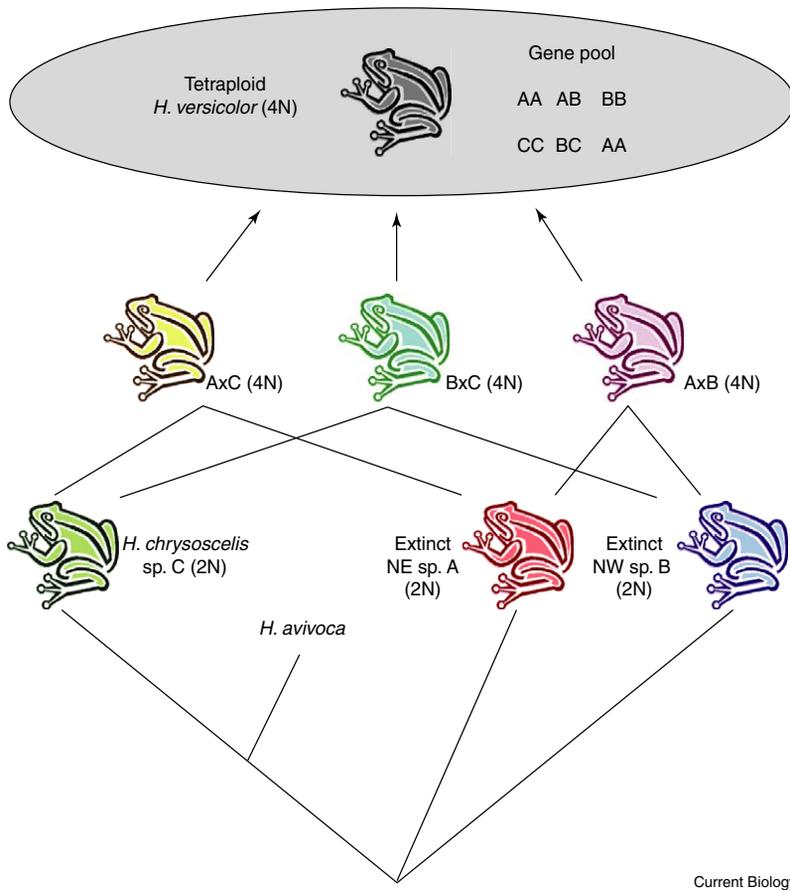


Figure 1. Evolutionary scenario for multiple hybrid origins of the tetraploid gray treefrog. DNA evidence suggests that ancestry of *Hyla versicolor* involved genetic contributions from *H. chrysoscelis* and two diploid progenitors, extinct species A and species B. Tetraploid hybrids involving these species (A X B, A X C and B X C) are hypothesized to have merged reproductively into modern *H. versicolor*. (Modified from Holloway *et al.* [6].)

does not play a significant creative role in macroevolution, because duplicated genes would dilute the phenotypic effects of potentially beneficial new mutations and slow rates of ‘progressive’ evolution. In contrast, polyploid speciation is rare in animals [3], but its significance in animal macroevolution was eloquently stated by Ohno [4], who argued that polyploidy provides the raw materials for evolutionary innovation. Duplicated gene copies were freed from the tyranny of indispensable functions, allowing them to acquire mutations that might confer novel functions.

The genetic earmarks of paleopolyploidy are hard to trace, because the vast majority of duplicated genes deteriorate or are lost, but the modern genomic era has provided strong support for Ohno’s thesis that two rounds of whole genome duplication created

the vertebrate genome [5]. As more genomes are sequenced, it will be interesting to see if paleopolyploidy was also associated with macroevolutionary changes in invertebrates and plants. Recently evolved polyploid species, on the other hand, often exhibit genetic earmarks that expose their origins [1], and Holloway *et al.* [6] provide an excellent example in their recent study of the gray treefrog, *Hyla versicolor*, an allotetraploid that arose via multiple hybrid events involving three diploid ancestors.

The creative role of hybridization in evolution has been debated for many years [7]. Mayr [8] viewed hybridization as a destructive process which counteracts speciation and retards evolution. The view that hybridization is maladaptive and evolutionarily inconsequential changed during the era of convenient genetic markers

which exposed its earmarks [9]. Armed with new information, biologists have resurrected Anderson’s [10] view that hybridization plays a creative role in adaptive evolution by expanding variation and increasing the scope for selection [11]. Though the paleohybridization events that might have contributed to macroevolutionary changes are unlikely to leave visible earmarks, the record of ancient genomic fusions (symbiosis) during the evolution of eukaryotic cells remains clear in the nuclear and cytoplasmic genes of plants and animals [12].

Hybridization and polyploidy converge during the evolution of allopolyploid organisms. A large proportion of polyploid angiosperms retain earmarks of hybrid or reticulate origins [13]. Common bread wheat is an allohexaploid composed of three evolutionarily divergent genomes (AABBDD). During meiosis, the two homeologous A chromosomes pair with each other, as do the B and D chromosomes, resulting in reduced gametes with balanced chromosome sets, but additional genome restructuring may be needed to stabilize meiosis and restore fertility [14]. Perhaps the abundance of polyploids and hybrids in plants is associated with vegetative reproduction, which allows such variants time to persist while stabilizing mechanisms evolve.

Except for some marine and aquatic invertebrates, asexual reproduction is uncommon in animals, so it is not surprising that allopolyploidy also is uncommon. Schultz [15] noted that polyploidy and hybridization are intimately associated in asexual animals, leading him to postulate that these processes may provide steps that facilitate polyploid evolution. Though asexuality may help to stabilize new polyploid lineages, it is not necessary for polyploid evolution, however.

A curious feature of sexual and asexual allopolyploids is that phenotypically well-defined biotypes, such as AABB or AACC, may have arisen multiple times. Thus, an array of allopolyploids —  $A^1A^1B^1B^1$ ,  $A^2A^2B^1B^1$ ,  $A^1A^1B^2B^2$ , and so on — that formed via

recurrent hybridization events may be recognized as a single well-defined morphospecies [1,16]. This finding challenges commonly held beliefs that new species evolve from a single common ancestor — that they are monophyletic. Nevertheless, allopolyploid ‘species’ with polyphyletic origins often exhibit coherent phenotypes and occupy distinct ecological niches [7].

A remarkable example of recurrent hybrid origins of an allotetraploid ‘species’ was recently reported for the gray treefrog, *H. versicolor* [6]. Earlier studies revealed that this tetraploid species is related to the diploid gray treefrog, *H. chrysoscelis*, and may be a hybrid that had multiple origins, but other putative parental forms could not be identified with the available genetic markers [17]. The new phylogeographic study [6], examining one mitochondrial and three nuclear gene sequences, revealed that *H. versicolor* has a complex reticulate makeup consisting of DNA sequences from *H. chrysoscelis* (species C) and two hypothetical ancestors, extinct species A and B (Figure 1). Regional populations of *H. versicolor* possess unique alleles that reveal traces of ‘missing’ progenitors that once occupied the northeastern and northwestern part of the tetraploid’s present range. Recurrent hybridization events involving progenitors A, B and C are believed to have generated an array of allotetraploid biotypes — *AACC*, *BBCC* and *AABB* — that might be expected to behave as separate biological species, as is often the case in allopolyploid plants [1,16]. But apparently in the treefrogs, these biotypes merged into a single interbreeding sexual species.

Why should divergent allotetraploid biotypes merge reproductively, given the prominent mating calls that typify treefrog species? The merger may be a direct consequence of tetraploidy. *Hyla versicolor* has a slow-pulse mating call and the diploid, *H. chrysoscelis*, has a fast-pulse trill [18]. If all the putative allotetraploid biotypes — *AACC*, *BBCC* and *AABB* — shared the slow-pulse recognition system, they could have

recognized one another as mates and merged to form the interbreeding complex recognized as *H. versicolor*. Each component of this complex scenario — polyploidy, recurrent hybrid origins, and merger of parallel evolutionary lineages — has been seen before in sexual or asexual taxa, but to my knowledge this is the first report of these elements converging during the origin of a single species.

Traditional species concepts do not readily embrace reticulate entities like this frog, but evolution is not necessarily straightforward or parsimonious. Discerning the bifurcating and reticulating paths that accompany recent evolutionary events is not easy. This study of allotetraploid treefrog evolution is a testament to the value of examining multiple genetic markers for reconstructing evolutionary histories. Furthermore, it shows us another way in which polyploidy and hybridization might converge as creative forces in evolution. Perhaps scenarios like this can provide additional insight into steps that might have occurred during the major genomic transitions that occurred during evolution of the vertebrate genome.

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## Memory: Obstacle Avoidance without Visual Cues

Avoiding obstacles is essential when we move about the world, yet little is known about how we do this when visual cues are not present to guide us. Recent evidence from behavioural studies in cats suggests that working memory may be crucial.

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Although we usually depend on visual input to avoid obstacles in our path, there are some situations where visual information is either

not available, or is unreliable. For example, when moving through a familiar environment in the dark, we rely heavily on memory for the location of objects in the room to guide us. Similarly, when driving, objects in the mirror are closer than