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<http://dx.doi.org/10.1016/j.cub.2012.10.003>

Evolution: Cichlid Models on the Runaway to Speciation

Rapid speciation has fascinated biologists for a long time. A recent study shows that ecological opportunity and sex-biased color differences increase the likelihood of speciation in African cichlid fishes.

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Speciation, the origin of novel species, is a complex and multilayered process that has remained hard to understand for empiricists and theoreticians alike. Researchers have dedicated much effort to pinpointing the factors and conditions that are responsible for some taxa diversifying rapidly while others linger in a speciation stasis. Only now are we realizing that it is the coupling of different intrinsic (e.g. natural history, genetics) and extrinsic (e.g. climate, habitat, behavioral interference) factors that produces the speciation momentum of adaptive radiations [1,2]. During adaptive radiations, a typically generalist ancestor diversifies in a short period of time into multiple specialized species that then occupy novel ecological niches. Famous examples include Darwin's finches in the Galápagos archipelago and the Caribbean *Anolis* lizards. But arguably the most spectacular radiations among vertebrates are those of African cichlid fishes inhabiting the three African Great Lakes — Malawi, Victoria and Tanganyika (Figure 1). The independent adaptive radiations of cichlid fishes in these lakes have produced a great number of

species — estimates point to over 1500 — the vast majority of which are endemic to each lake and differ in their pigmentation patterns, body shapes, and reproductive and social behaviors [1]. Interestingly, several extant cichlid lineages did not diversify explosively. Radiating and non-radiating lineages can be found not only in the East African Great Lakes, but also in dozens of other smaller African lakes inhabited by distinct cichlid assemblages. This naturally widespread system of closely related species provides the perfect setting for evaluating which intrinsic and extrinsic attributes account for some lineages, but not others, having undergone adaptive radiations [1].

This was exactly what Wagner *et al.* [2] set out to do in a recent paper: in an elegant continent-wide study, the authors compiled data on colonization and diversification of African cichlids in 46 lakes. Physical and environmental data for each lake (e.g. age, depth, net solar radiation) and lineage-specific traits (e.g. mating systems, brooding of eggs and fry in the mouth, sexual differences in pigmentation) that could potentially explain diversification were contrasted using phylogenetic logistic and hurdle Poisson regressions. These comparative methods assess the association between predictor extrinsic

and intrinsic variables, and whether or not a lineage diversified in a lake.

Wagner *et al.* [2] found that environmental conditions increasing ecological opportunity in deeper lakes with higher solar energy input, together with high levels of sexual dichromatism (sex-biased differences in pigmentation), predict an increased likelihood of cichlid diversification. Importantly, cichlid diversification is best explained by the combined effects of extrinsic environmental variables and intrinsic lineage-specific traits. This explains differences in diversification rates between lakes and why only some lineages diversify in a subset of the lakes inhabited by cichlids. Deeper lakes with higher energy input are probably more stable over evolutionary times. They also have a greater number of ecological niches, which are more productive and more diverse, and are overall able to sustain larger numbers of individuals (higher carrying capacity). Together, these environmental factors increase the ecological opportunity for cichlids and allow them to radiate.

In addition, radiations are more likely to occur in sexually dichromatic lineages, which also explains differences in speciation rates among lineages within lakes. High sexual dichromatism is commonly interpreted as evidence for strong sexual selection. In cichlids, sexual dichromatism has evolved only in species with polygamous mating systems, in which females are choosy and select among males based on their eye-catching pigmentation, while males mate with as many females as possible. Therefore,

sexual selection has the potential to promote speciation if male display traits and associated female preferences vary within and among populations.

The study by Wagner *et al.* [2] is a perfect example of how data on cichlid radiations meet predictions from speciation theory, as sexual selection has been found to be a likely candidate for driving speciation in several mathematical modeling studies [3,4]. Additionally, sexual selection has been identified as an important factor in promoting the long-term coexistence of ecologically similar species [5]. Such coexistence is possible if there is spatial variation in local carrying capacity and mate-search costs in females [5]. Alternatively, sex-reversal genes and sex-linked color polymorphisms might mediate speciation and coexistence, all driven by sexual selection [6]. For example, if a new sex-linked color variant arises by mutation within a population, but only increases fitness in the sex opposite to which it arose in, sex-reversal genes can become established by changing the sex of the carrier. In this way, sexual selection can drive a change of the sex determination system and allows the coexistence of new and ancestral species with different pigmentation, even without ecological differentiation or geographical isolation. These conditions are likely to be met in at least some cichlid lineages with varying sex determination systems, in which disruptive sexual selection despite ecological similarity seems to be the rule [6–9]. Therefore, as predicted by speciation theory, strong sexual selection and premating isolation are responsible for creating new species and/or maintaining species coexistence, provided that species live in a complex and productive habitat [2]. This process has the potential for positive feedback: more complex and more productive habitats allow higher population densities and more species to coexist. These conditions then favor more intense sexual selection, which in turn promotes species emergence and coexistence by stronger female preference for male display traits.

One aspect not discussed by Wagner *et al.* [2], which is important to understand the process of radiation, is the geography of speciation in cichlids. Do the very successful cichlid lineages radiate when species occupy separate

ranges (in allopatry) or when they co-occur (in sympatry)? Speciation by sexual selection can theoretically occur in any geographical context. It is thought to be easier in allopatry, where mutation and random genetic drift might suffice. By contrast, divergence in female preference for male traits in sympatry is more difficult and has to be stronger than the homogenizing effects of gene flow, for instance by Fisher's runaway processes — whereby certain traits are preferred by females making their possession advantageous for males and, in turn, advantageous for the females to have these preferences, creating a positive feedback loop that further exaggerates male traits and female preferences for them. Between these two extremes, parapatric speciation along ecological gradients is more likely to occur than fully sympatric speciation [10]. In contrast to speciation likelihood in different geographic settings, tempo of speciation is slowest in allopatry (often a by-product of mutation and drift) and fastest in sympatry (actively driven by selection). Divergence of female mating preferences in populations with abutting ranges (parapatry) can produce rapid speciation without geographic discontinuities as a result of divergent selection along environmental clines (ecological speciation) [4,8]. Because the phylogenies of the most diverse cichlid lineage (Haplochromini) indicate a burst in speciation, fuelled by sexual selection [2], we hypothesize that the bulk of the radiations took place in parapatry, a scale that combines both effects of high likelihood and fast tempo of speciation.

Is our understanding of cichlid speciation complete? The above generalizations drawn by Wagner *et al.* [2] and their work are important tools for understanding cichlid adaptive radiations. Nevertheless, several cases do not fit these generalizations. What can we learn from these exceptions? Wagner *et al.*'s [2] analyses predict the radiation of sexually dichromatic lineages in large lakes, yet Lake Tanganyika falls out as an outlier for both environmental and biological variables [2]. Lake Tanganyika is thought to have seeded rivers and lakes in surrounding African regions [11]. It is the oldest and deepest of the African Great Lakes and its cichlid fauna is the most diverse in ecology,



Figure 1. African cichlids of the Lake Tanganyika catchment.

Top: Male of the sexually dichromatic species *Astatotilapia burtoni* (Haplochromini), with visible egg dumplings on the anal fin. Also known as egg-spots, they are ovoid markings found in the anal fins of some cichlids, presumably important in male breeding success. Bottom: Male and female *Neolamprologus brichardi* (Lamprologini) look alike. In spite of being sexual monochromatic, Lamprologini is the most species-rich Tanganyikan clade, with around 100 out of 250 species found in the lake. Both species' genomes and transcriptomes have been sequenced. Photos: Hugo F. Gante.

morphology and behavior, consisting of 14 or so lineages, but not in number of species [1].

Only six lineages present in Lake Tanganyika show some level of sexual dichromatism, and not all have radiated (Figure 1). Most challenging to our understanding of intrinsic factors responsible for cichlid diversification is that several lineages that radiated are indeed sexually monochromatic (Figure 1). Despite being sexually monochromatic, they can be very colorful, with different species showing distinct combinations of stripes, bars and blotches in diverse background colors in body and fins. Sexually monochromatic lineages very often prefer different habitats and have different breeding modes, ranging from mud-sand dwelling mouthbrooders to spawning adhesive eggs on rocky substrates [12]. How can we explain the high levels of diversity in these sexually monochromatic lineages? Recent mathematical models indicate that rapid phenotypic and ecological diversification is possible under spatially heterogeneous ecological selection, low migration and genetically based habitat choice, with no need for sexual selection [13]. It could be that

these monochromatic lineages in Tanganyika diversified primarily by natural selection, while Haplochromini in lakes Malawi and Victoria and dichromatic Tanganyikan lineages diversified primarily by sexual selection.

Several other open questions are relevant for understanding cichlid adaptive radiations. For instance, why do only certain lineages show sexual dichromatism? Two conditions need to be simultaneously met for the evolution of sexual dimorphism: a net selection differential and an imperfect genetic correlation between the sexes [14]. Which of these two conditions differ among cichlid lineages is still unknown. Thus, more data on the genetic architecture and rates of evolution of female and male traits are necessary to understand what makes sexual dichromatism such a powerful speciation driver in cichlids; or has hybridization shaped the radiation of diverse monochromatic lineages as it did in dichromatic ones [15,16]? Many of the above questions are tightly linked and can be addressed using the high-quality genome and transcriptome data now starting to become available [17].

The cichlid model system exemplifies the progress that has been achieved in our understanding of speciation and adaptation [2]. It also makes visible the knowledge we are still lacking in speciation research. We

anticipate these and other questions will prompt the writing of new tomes on cichlid adaptive radiations and their mechanisms of speciation, and further advance our understanding of biodiversity in general. To that end we need more empirical data on intrinsic species traits, and their extrinsic environments to feed and contrast the myriad of existing mathematical models of speciation [10]. In particular, with the arrival of the much-anticipated cichlid genomes, we will open an unprecedented window into the evolution of this charismatic model system.

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<http://dx.doi.org/10.1016/j.cub.2012.09.045>

Cell Biology: Cohesin Ring Exit Gate Revealed

A multiprotein complex called cohesin mediates sister chromatid cohesion by entrapping sister DNAs into a tripartite ring. Recent studies show that Wapl opens the newly identified DNA exit gate of the cohesin ring, only when Smc3 is deacetylated, and that mutations in human Smc3 deacetylase cause a developmental disorder.

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The interconnection of sister chromatids, established during their synthesis at S phase and maintained until their disjunction at anaphase, is essential for faithful chromosome partition in mitosis. This connection is

mediated by a multiprotein complex called cohesin, which consists of two rod-shaped proteins, Smc1 and Smc3, the kleisin family protein Scc1 (also called Mcd1/Rad21), and Scc3 (SA1/SA2) [1]. Within this complex, Smc1 and Smc3 bind to each other to form a V-shaped heterodimer, whose opposite ends are linked by the kleisin

subunit Scc1, thus creating a tripartite ring structure that can entrap sister chromatids [2] (Figure 1). The cohesin ring can be loaded onto chromosomes throughout the cell cycle, and this is dependent on the loader complex Scc2–Scc4. However, sister chromatid cohesion is usually established only during S phase, when Smc3 is acetylated by replication-fork-associated Eco1 [3–5]. Conversely, the dissociation of cohesin from chromosomes occurs potentially via two distinct pathways. When chromosomes separate at the onset of anaphase, an activated endopeptidase called separase cleaves the Scc1 subunit to open the cohesin ring, thus releasing sister DNAs [6]. In an alternative pathway, the Wapl protein,