

Evolution of Biological Diversity

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Explosive speciation of African cichlid fishes

George F. Turner

6.1 Introduction

Lakes can be considered as inverted islands, as far as freshwater organisms are concerned, and the great lakes of East Africa, clustered in and around the African Rift valley, can be considered an archipelago where a single family of fishes, the Cichlidae, has radiated to produce more than 1500 species. Even though they were only known from a small and unrepresentative collection of preserved material, the unusual diversity of these fishes came to the attention of major figures in the modern synthesis of evolutionary biology in the first half of the twentieth century (Huxley 1942; Mayr 1942). The cichlid fishes rapidly became established as a textbook example of 'adaptive radiation' or 'explosive speciation'. Recent studies are only now revealing that the number of species has been greatly underestimated, while the radiations in individual lakes may be much younger than has been suspected. The mechanisms underlying this extraordinary radiation are still unclear, but a combination of field studies, laboratory breeding experiments and application of molecular techniques has already overturned a number of theories.

6.2 Speciation rates

Species richness

Prior to the 1980s, most cichlid taxonomists operated with morphological species concepts, distinguishing species on the basis of anatomical differences among preserved material. In 1978, Holzberg demonstrated that a pair of sympatric 'colour morphs' of *Pseudotropheus zebra* at Nkhata Bay, Lake Malawi demonstrated subtle behavioural and ecological differences and courted assortatively in their natural habitat. Interpreting this finding in the light of Paterson's recently proposed Recognition Concept of species, Ribbink *et al.* (1983) granted specific status to any taxon exhibiting a clear difference in male breeding colours, providing preliminary identification features for 147 new putative species of

cichlid fishes of the 'mbuna' lineage from the rocky shores of the western and southern portions of Lake Malawi alone. To date, molecular studies have been consistent with Ribbink *et al.*'s hypothesis for all sympatric taxa examined. Allozyme studies have demonstrated significant differences in allele frequencies among three *Petrottilapia* species (McKaye *et al.* 1982) and two species of *Pseudotropheus* (*Maylandia*) (McKaye *et al.* 1984). More recently microsatellite DNA and behavioural observations have been used to demonstrate significant assortative mating among three putative species of *Px.* (*Maylandia*) and six of *Px.* (*Tropheus*) (van Oppen *et al.* 1998).

Most researchers now recognize African great lake cichlid species on the basis of differences in colours, in addition to morphology. Furthermore, recent field studies of previously neglected habitats have also led to increased estimates of species richness. Turner (1996) has listed 199 species, 79 undescribed, from the deep-water and offshore habitats of Lake Malawi, while Seehausen (1996) recorded 173 from the rocky habitats of Lake Victoria, 100 of which were discovered since 1986. Both of these studies were conducted over small areas of the respective lakes, and both reported that many taxa had restricted distributions even with the areas surveyed, suggesting that many more species await discovery in other localities. A recent survey of the eastern shore of Lake Tanganyika (Snoeks *et al.* 1994) has also led to an increase in the estimate of cichlid species in that lake from 173 to more than 200.

On present estimates, it is likely that Lake Victoria contains at least 500 species, Tanganyika 200 and Malawi 700–1000 species. Some caution must still be attached to these estimates, as they depend on the assumption that specific rank should be given to allopatrically distributed taxa which differ in coloration by roughly the same extent as sympatric taxa which are known to mate assortatively.

Age of radiations

Much of the early speculation about cichlid diversity was based on the assumption that the lakes were of great age. For example, in the 1940s Lakes Malawi and Tanganyika were thought to be of early Cenozoic origin, i.e. 40–65 Myrs old (Huxley 1942; Mayr 1942). Recent studies have indicated that the lakes are much younger.

Geological surveys suggest that Lake Tanganyika arose as a shallow depression linked to the Congo River system about 20 Myrs ago (Coulter 1994), and that it probably became largely isolated about 9–12 Myrs ago (Meyer *et al.* 1994). The cichlid fishes of Lake Tanganyika are morphologically, behaviourally and genetically much more differentiated than those of Lakes Malawi and Victoria. Molecular clock estimates derived from mitochondrial DNA sequences indicate that some Tanganyikan lineages diverged at least 5 Myrs ago (Meyer *et al.* 1994).

Geologists estimate that Lake Malawi is about 1–2 Myrs old at most (Ribbink 1994). MtDNA clock estimates put the origin of the radiation at about 700 000 years ago (Meyer 1993). Although incomplete lineage sorting leads to considerable problems in the use of mtDNA for phylogenetic reconstruction for

Malawi cichlids, coalescence theory suggests that the maximum age of divergence of known mtDNA genotypes is about 1.8 Myrs, although this may pre-date the radiation (Parker and Kornfield 1997).

Until recently, Lake Victoria was thought to be about 250 000–750 000 years old (Meyer 1993). Geologists have recently discovered that the deepest part of the lake was completely dry as recently as 12 400 years ago and hydrological modelling indicates that no peripheral refugia could have existed in the lake's vicinity during this time, suggesting that the entire cichlid radiation must have occurred since then (Johnson *et al.* 1996). The Victorian cichlids are undoubtedly the least differentiated of those of the three great lakes, both anatomically and genetically. In a study of 14 species from nine endemic genera, Meyer *et al.* (1990) found no variation at all in a 363 base pair (bp) sequence of the mitochondrial cytochrome-b gene and only two to three substitution differences in a 440-bp region which includes the normally hypervariable control region. This is consistent with a very recent radiation.

Monophyly of cichlid radiations

All three lakes contain cichlid lineages which have not radiated: *Tilapia* in all three lakes; *Astatoreochromis* in Lake Victoria; *Oreochromis* in Lakes Victoria and Tanganyika; *Tylochromis* in Lake Tanganyika; *Serranochromis* in Lake Malawi. *Oreochromis* in Lake Malawi is represented by two lineages, only one of which has radiated and that into a mere three species (Sodsuk *et al.* 1996). Mitochondrial DNA sequence analysis has provided strong evidence that the remainder of the cichlids in all three lakes have radiated within the catchments of the lakes they presently inhabit. All but six of the Lake Malawi cichlid species form a monophyletic group, with the riverine *Astatotilapia calliptera* as the probable sister taxon to all the lacustrine members of the clade (Meyer 1993). The cichlids endemic to Lake Victoria and its satellite lakes, such as Kyoga, Nabugabo and Edward, also form a monophyletic group, and also appear to be derived from (a different species of) *Astatotilapia* (Meyer 1993).

The molecular evidence is less easy to interpret in the case of Lake Tanganyika. Long thought to be polyphyletic (e.g. Nishida 1991), Meyer (1993) has made the intriguing suggestion that the Tanganyikan radiation is actually monophyletic, but that several taxa have escaped from the lake and colonized other water bodies. This theory seems plausible in the case of the Lamprologine tribe, since the riverine *Lamprologus* presently found in the Congo River seem to be a monophyletic group descended, relatively recently, from one of the Tanganyikan endemics (Sturmbauer *et al.* 1994). Sturmbauer and Meyer (1993) have also found that the endemic Tanganyikan tropheini is the sister group to the haplochromine tribe and that this split also occurred relatively recently, perhaps 2–3 Myrs ago. The haplochromines comprise more than 1500 species, including not only the entire Malawian and Victorian radiations, but also riverine species found as far apart as Algeria, Syria and South Africa (Daget *et al.* 1991). By contrast, only eight haplochromine species are found in Lake Tanganyika

(Coulter 1991), and six of these are mostly found in peripheral water bodies rather than the main lake itself. Genetic analyses have not yet been performed on haplochromines from outside of the East African region.

Relative rates of cichlid and other radiations

In the light of this recent work and similar studies on other island species flocks, how do the speciation rates of cichlid radiations compare with those of other textbook examples of explosive speciation? Three parameters must be considered: the age of the radiation, the number of species at present, and the number of founding lineages (Table 6.1). These can be combined to estimate the mean interval between speciation events, assuming zero extinction, and a speciation rate which is constant with time and invariant among all lineages within each radiation. The mean speciation interval is mathematically equivalent to the mean doubling time in an exponentially growing population, and is given by:

$$L = \frac{t \cdot \log_e(2)}{(\log_e N_t - \log_e N_0)}$$

where N_t = number of extant species, N_0 = number of founding species, and t = age of radiation.

This comparison (Table 6.1) shows that the Hawaiian *Drosophila* have a comparatively low speciation rate, as do the Lake Baikal amphipods, although in the latter molecular dating of the radiation has not yet been attempted. The speciation rate of the Tanganyikan cichlids is about average for an explosive speciation event, and comparable with or slower than those of the Baikal sculpins,

Table 6.1 Estimates for species richness and rates of speciation of some major 'island' radiations. (Mean speciation interval calculated from exponential growth model, see text)

Radiation interval	No. of species	Number of founder lineages	Age of radiation (Myrs)	Mean speciation interval (th. years)
Baikal sculpins ^a	27-29	1-2	2-2.5	400-600
Baikal amphipods ^b	254	1-5	25-30	3000-5000
Galapagos finches ^c	13	1	0.6-2.8	160-760
Hawaiian <i>Drosophila</i> ^d	800	1	23-40	2000-4000
Hawaiian crickets ^e	206-210	4	2.5	ca. 440
Tanganyikan cichlids ^f	170-200	1	5-12	650-1,600
Malawian cichlids ^g	600-1000	1	0.7-2	70-240
Victorian cichlids ^h	250-500	1	0.01-0.2	1-25

^a Molecular estimates of age of radiation from Kirilchik *et al.* (1995); other data from Martens *et al.* (1994).

^b Martens (1997); Martens *et al.* (1994); age of radiation estimated from age of lake.

^c Vinck *et al.* (1997); age of radiation estimate from allozymes.

^d Powell and Desalle (1995); age of radiation estimate molecular.

^e Orte (1989); age of radiation estimated from biogeography.

^f Age of radiation and number of founder lineages from Meyer (1993); number of species from Snoeks *et al.* (1994).

^g Age of radiation and number of founder lineages from Meyer (1993); number of species from Turner (1996).

^h Geological estimates of age of radiation from Meyer (1993) and Johnson *et al.* (1996); number of founder lineages from Meyer (1993); number of species from Sechausen *et al.* (1997a).

Hawaiian crickets or Galapagos finches. However, the cichlids of Lakes Malawi and Victoria demonstrate outstandingly rapid speciation rates which may be approached only by the far smaller radiation of the Galapagos finches, and are clearly the premier examples of large-scale rapid radiation of any extant lineages in a limited geographical area.

6.3 Adaptive radiation and competition

Cichlid radiation not due to lack of competitors

There is no evidence that lack of ecological competition has stimulated the radiation of cichlid fishes in African lakes. Indeed, all three of the largest lakes have a rich fauna of non-cichlid fishes. Lake Tanganyika is estimated to contain 145 species of non-cichlids, 61 of which are endemic, representing 21 families (De Vos and Snoeks 1994). Lake Malawi has 45 non-cichlid species in 10 families (Ribbink 1994), and Lake Victoria 40 species in 11 families (Greenwood 1994). In comparison, Lake Baikal, which is virtually the same size and shape as Lakes Malawi and Tanganyika, but is older than any of the African lakes, contains 56 fish species, 27 of which are endemic (Martin 1994). Other large ancient lakes, such as Titicaca, Biwa and Ohrid also have high levels of fish species richness and endemism (Martens *et al.* 1994). So, even forgetting about the cichlids, the African great lakes would be remarkable for the species-richness and endemism of their fish faunas. In Lake Malawi, the non-cichlid fishes include specialized algal scrapers, detritus feeders, pelagic plankton feeders, benthic invertebrate eaters including specialized crab and mollusc feeders and numerous fish-eaters occupying all habitats. Among the non-cichlids are the 18 largest fish species (Jackson 1961) and probably also the two most numerous species in the lake.

Supralimital evolution?

As is well-known, cichlids in African great lakes demonstrate a remarkable diversity of feeding behaviour and structures (e.g. Fryer and Iles 1972; Liem 1991), but it may be an exaggeration to say (e.g. Fryer 1996) that they demonstrate 'supralimital' characteristics which are more complex or extreme than shown by the family throughout the rest of its range. The South American cichlids are probably more diverse in body form than those of Lakes Malawi or Victoria, and perhaps almost as diverse in feeding strategies. Some of the feeding strategies of African lake cichlids do seem to be unique within the family, for example scale-eating, fin-biting or ramming mouthbrooding females to make them disgorge their young. All of these exotic strategies occur only in a few uncommon species.

That diversification has not really been supralimital, does not mean it is unimpressive. All three lakes contain algae rasps, zooplankton feeders, visually-hunting benthic invertebrate feeders, sediment sifters, ambush piscivores, pursuit hunters, mollusc crushers and quite a few other major trophic types. In

Lake Malawi, cichlids have colonized the deep benthic and open water pelagic zones to the limits of oxygenated waters at about 200 m (Turner 1996). Similar life-styles have led to similar morphologies among cichlids in the three lakes. Comparative morphologists have frequently suggested that these anatomical similarities may indicate phyletic relationships and that cichlid lineages have frequently moved between the different lakes (e.g. Greenwood 1983; Liem 1991). This has been convincingly disproved by molecular phylogenetic reconstructions which indicate that both the Malawian and Victorian cichlid radiations are monophyletic and suggest that both are derived from very similar small generalized invertebrate feeders (Meyer 1993).

Radiation of reproductive behaviour?

Cichlids are well-known for their protracted parental care, complex visual signalling courtship displays, and rapid colour changes. However, it is not correct to add these to the list of specializations of lake cichlids (e.g. Fryer 1996), as these are widespread and almost certainly plesiomorphic traits in the cichlids.

Is reproductive behaviour as evolutionarily labile as feeding adaptations? Irrespective of their ecology and the habitat they live in, all of the endemic cichlids of Lake Malawi and Lake Victoria are maternal mouthbrooders, as are their riverine sister taxa of the genus *Astatotilapia*. The sister taxon for this haplochromine clade appears to be the Tanganyikan tropheini, also maternal mouthbrooders (Sturmbauer and Meyer 1993). Within Lake Tanganyika, most mouthbrooders belong to a single clade which encompasses five to seven tribes (Nishida 1991; Sturmbauer *et al.* 1994), while the monophyletic lamprologine clade contains all but one endemic non-mouthbrooding species (Sturmbauer *et al.* 1994). Substrate brooders in Lake Tanganyika show many ecological and anatomical parallels with mouthbrooders in Lake Malawi. So, the broad division between mouthbrooding and substrate-brooding is relatively ancient and ecological circumstances within the lakes do not seem to lead to transitions between these states.

Within each of these broad categories, the role of ecology in shaping behaviour is less clear, largely because the phylogenies are less well resolved. Tanganyikan mouthbrooders range from sexually monomorphic monogamous biparental brooders to extremely sexually dimorphic polygynous maternal brooders. The latter include *Enantiopus melanogenys* which practices an extreme form of lekking behaviour, where male territories, delimited by tiny ridges of sand, are no more than two body lengths in radius and tightly clustered in virtually perfect hexagonal close packing. It is not yet known how often maternal mouthbrooding has evolved from biparental mouthbrooding, although the reverse transition seems unlikely given the stability of the strategy among the Malawian and Victorian endemics. Among cichlids, mouthbrooding is not confined to African lake species, and has evolved independently in several lineages in Africa and South America.

Most substrate brooders appear to be monogamous and practice biparental care, but there are a number of harem polygynists, ranging from *Lamprologus*

brichardi, a sexually monomorphic species where about 8% of males were observed to breed with two females (Limberger 1983), to *Lamprologus callipterus*, in which mature males weigh up to 80 times as much as females and may mate with as many as 56 females in a 4-month duration as harem-holder (Sato 1994). A mitochondrial DNA phylogeny of 25 lamprologine species, indicates polygyny has probably arisen independently as many as five times (Sturmbauer *et al.* 1994).

Pharyngeal jaws and the key innovation hypothesis

Cichlid fishes have two sets of jaws, the oral (external) set which is mainly used for prey capture and the pharyngeal (internal) set which does most of the crushing and chewing. This is not unusual in fishes, but the particular form and mode of operation of the cichlid pharyngeal apparatus is shared only with other families of the labroid assemblage, the wrasse, parrotfishes, damselfishes and surfperches. Since Liem's (1973) detailed anatomical studies of the cichlid pharyngeal apparatus, there have been numerous statements that this structure represents the 'key innovation' which has been responsible for the diversification of the cichlids (e.g. Nee and Harvey 1994). This is a difficult hypothesis to assess. Liem's study showed that the labroid pharyngeal apparatus was different from those of other fishes, so it is essentially a correlational study: labroids are diverse and species rich, and they have a particular type of pharyngeal jaws. More recently Galis and Drucker (1996) compared the cichlid pharyngeal apparatus with that of the less diverse (29 species, Moyle and Cech 1996), but phylogenetically not too distant centrarchids which are the dominant medium-sized percoid fishes in North American freshwaters. Galis and Drucker found that the upper and lower jaws of the cichlids were able to move independently, unlike those of the centrarchids, and that cichlids could transmit a greater force per unit area on to a prey item with an elliptical cross-section. However, it is not at all clear that either of these traits actually confer any great evolutionary advantage on the cichlids.

The surfperches (Embiotocidae) possess the labroid pharyngeal apparatus, but only comprise 23 rather similar species which have small mouths for picking up small benthic invertebrates (Moyle and Cech 1996). Damselfishes and anemone fishes (Pomacentridae) are species-rich (315 spp., Moyle and Cech 1996), but although numerous on coral reefs, are evolutionarily rather unadventurous feeders on plankton or algae growing on rocks. The wrasse (Labridae) are the only other family with the labroid pharyngeal apparatus to rival the cichlids in species richness (500+ spp., Moyle and Cech 1996) and in diversity of form and diet. The parrotfishes (Scaridae, 80 species) are probably best regarded as a specialized offshoot of the wrasse which use their massive dentition to feed from the surface layers of stony corals. A recent molecular phylogenetic study using single-copy nuclear DNA has demonstrated that the labroids are not a clade. Although wrasse might possibly be the sister group to the cichlids, the ecologically less varied damselfishes and surfperches seem to be closely related to each other, but not to the cichlids and wrasse (Streebman and Karl 1997).

Thus, it is clear that the cichlid-type pharyngeal apparatus is by no means a

guarantee of adaptive radiation. We can consider the question from another angle. How does the adaptive radiation of cichlids compare with those of other coexisting fish families in environments other than the African great lakes? Despite the presence of cichlids, South American freshwaters are dominated by characoids and catfishes. The adaptive radiation of the South American characoids is said to rival that of the African lake cichlids (Lowe-McConnell 1975), despite the fact that most species have rather unspecialized pharyngeal teeth (Moyle and Cech 1996). In terms of species richness, both the characoids and the catfishes greatly outnumber the cichlids, the former by about 10 to 1 (Lowe-McConnell 1975). Cichlids are not much more significant in the rivers of Africa, comprising only 10–20% of the fish species (Greenwood 1991) and most are algal/sediment feeders, or rather unspecialized small- to medium-sized predators.

The case for recognizing the cichlid pharyngeal apparatus as a key innovation and an explanation for adaptive radiation remains weak.

6.4 Speciation

Adaptive radiation and explosive speciation are not the same

It is important to distinguish clearly between the processes of adaptive radiation and speciation. Classical speciation theory views species as coadapted gene complexes occupying adaptive peaks in a fitness landscape, and considers the conditions necessary to shift between peaks. Reproductive isolation is modelled as arising from the accumulation of genetic incompatibilities between populations, either in terms of their effects on developmental processes or on fitness in relation to its environment. Adaptive change is seen as essential in permitting each species to occupy a different peak and so is inextricably linked to the speciation process.

However, in terms of the biological species concept, speciation is the establishment of reproductive isolation between two populations and not primarily the scaling of a new adaptive peak. Coexistence of species need not depend on niche separation (Silvertown and Law 1987) and indeed hybrids are not necessarily unfit relative to the parental species (Arnold and Hodges 1995). Among closely related species of *Drosophila*, prezygotic isolation tends to be stronger than postzygotic isolation (Coyne and Orr 1989). If sexual selection leads directly to reproductive isolation, newly-split species may not differ at all in characteristics of their niche, so both may lie on the same adaptive peak (Turner and Burrows 1995).

While many studies have claimed to demonstrate niche partitioning, no experimental studies have unambiguously demonstrated competition, let alone competitive exclusion, between sympatric African cichlid fishes. Unquestionably, many species have narrowly specialized diets and habitat preferences, but it also noteworthy that many species seem to occur syntopically and feed on the same things (Turner 1994; Rossiter 1995). Among lamprologines and biparental mouthbrooders in Lake Tanganyika, further niche partitioning may occur through segregation of breeding territories (Rossiter 1995), but this cannot be

true of most maternal mouthbrooders where territories are used only for spawning and the eggs are brooded in the mouths of the non-territorial females.

A striking feature of African lake cichlid communities is the frequent co-occurrence of several anatomically and ecologically very similar species which differ strikingly in male breeding colours (Ribbink *et al.* 1983; Turner 1994, 1996; Seehausen 1996). This suggests that speciation may occur through the establishment of reproductive isolation prior to the evolution of traits leading to niche differentiation. Under this scenario, adaptive radiation might well be important in permitting the coexistence of sibling species, but may not be important in the process of speciation *per se*.

Extralacustrine speciation

Has speciation occurred within lakes? The establishment of the monophyly of Malawian and Victorian haplochromine radiations (Meyer 1993) effectively rules out the idea that they arose from multiple colonization events. However, geological studies have demonstrated marked fluctuations in water levels of all three great lakes.

At low water levels, Lake Tanganyika was divided into two, or sometimes three, isolated lakes (Coulter 1991). The present-day distribution of mitochondrial DNA haplotypes closely follows the outline of these ancient lakes in *Tropheus* (Sturmbauer and Meyer 1992) and the tribe crenodontini (Verheyen *et al.* 1996), although not in *Simochromis* (Meyer *et al.* 1996). All are shallow water rocky-shore algal rasps, but Meyer *et al.* suggest that *Simochromis* are less strictly confined to rocky shores, permitting large-scale gene flow subsequent to the re-unification of the isolated palaeo-lakes. It is thus likely that these ancient basins must have persisted long enough to permit substantial genetic differentiation by mutation and drift, and there has clearly been the opportunity for allopatric speciation. However, there is no evidence that mitochondrial DNA variation associated with the outlines of these ancient lakes is a reflection of species status, rather than merely an indication of persistent low dispersal capabilities. Indeed, the gene trees produced by mtDNA conflict strikingly with current morphological taxonomy.

There is no evidence that either Lake Malawi (Owen *et al.* 1990) or Lake Victoria (Johnson *et al.* 1996) has even been subdivided into large basins. Proponents of extralacustrine speciation have thus proposed 'the Lake Nabugabo scenario' (Greenwood 1965). Nabugabo, with a surface area of ca. 30 km², is a swampy lagoon separated from Lake Victoria by a thin sand bar which formed about 3500 years ago. It contains five endemic haplochromine cichlids which differ in male colour from their relatives in Victoria. This is an exciting finding, suggesting extremely rapid evolution, perhaps by sexual selection, but it still remains to be shown that the Nabugabo forms are really biological species. Greenwood's hypothesis is that Lake Victoria's cichlid radiation is a result of many such events, but it would seem unlikely to be a general explanation for the diversification of Malawian and Victorian cichlids. Only a few species are

habitually found in shallow swampy areas likely to be cut off by such barriers. If the Nabugabo scenario were generally true, it would be expected that rocky shore, pelagic and deep-water assemblages would not contain many monophyletic groups, rather most species would have arisen independently from inshore swamp-living ancestors. The only published evidence is against the Nabugabo scenario: in a broad phylogenetic study of Malawian cichlids using mtDNA RFLP Moran *et al.* (1994) found a well-supported clade comprising only rocky shore and deep-water species.

In conclusion, the evidence for extralacustrine speciation is convincing for Lake Tanganyika, but for Lakes Malawi and Victoria, the only realistic possibility is isolation in small peripheral lagoons, which seems unlikely to explain diversification of most species.

Allopatric speciation within lakes

The shorelines of these large lakes are comprised of various habitats: rocks, sand, papyrus swamps, and river mouths. All three lakes also contain offshore islands. It has long been known that species or colour forms of littoral cichlids are often confined to small geographic areas within Lakes Malawi (Fryer 1959) and Tanganyika (Poll 1950), and it has recently been demonstrated also for those of Victoria (Seehausen 1996). Rocky shore cichlids are rarely observed over open sand, lack a dispersal phase in their life history and have poor depth equilibration abilities (cichlids have closed swimbladders), implying that populations isolated by habitat barriers, such as non-rocky beaches or deep channels, were free to speciate in allopatry within each lake (Fryer and Iles 1972; Ribbink *et al.* 1983).

McKaye and Gray (1984) tested the dispersal capabilities of rocky shore cichlids in Lake Malawi by constructing an artificial reef on a sandy beach about 1 km from the nearest rocky shore. Within 6 months the reef had been colonized by representatives of three of the four most diverse species complexes of rocky shore cichlids. After 30 months, a representative of the fourth complex was also established. The reef was not colonized by any of the four low diversity complexes present. These results suggest that taxa with higher dispersal capabilities are also those with greater species diversity and that sandy shores might not be as great a barrier to gene flow as had been suggested (Turner 1994). Hert (1992) found that territorial male *Pseudotropheus aurora* on Thumbi West Island, Lake Malawi, have a strongly developed homing ability and returned to their territories within a few days even when transplanted 2.5 km along continuous rocky shore. However, none returned when transplanted to the mainland shore only 1 km away, but on the other side of a deep mud-bottomed channel. When 18 individuals were released in open water over the channel at distances of 500–800 m, eight had returned within 4 days. This suggests that, although the fishes are capable of navigating back to their home territories across open water, they will not do so voluntarily, suggesting that deep channels do represent a significant barrier to these fishes. Significant genetic differences have been demonstrated between

isolated island populations using allozymes (McKaye *et al.* 1984) and mitochondrial DNA (Bowers *et al.* 1994; Moran and Kornfield 1995).

Recent investigations using microsatellite DNA has demonstrated that sandy beaches may after all be a barrier to gene flow among populations of rocky shore Malawi cichlids (van Oppen *et al.* 1997). When sampled from rocky headlands separated by sandy beaches of only 700–1,400 m width, all four species showed significant differences at all six loci investigated.

Founder events and genetic bottlenecking

The subdivision of the lakes into numerous isolated habitat patches and the fact that females carry broods of fertilized eggs in their mouths suggests that extreme genetic bottlenecking or founder effects could be involved in speciation in African cichlids, as has been suggested for other island radiations (Carson and Templeton 1984). Genetic studies have not supported this. Moran and Kornfield (1995) found that one Malawian rocky shore species endemic to a single island had reduced mtDNA haplotype diversity, but that four other species did not. Other studies have generally found high levels of within-population variation in microsatellite (van Oppen *et al.* 1998) and major histocompatibility complex loci (Klein *et al.* 1993). Intra-population variation in mtDNA is often very high, and even distantly related species have been found to share several mtDNA lineages, suggesting that polymorphisms have survived numerous speciation events (Moran and Kornfield 1993; Kornfield and Parker 1997). Recently, microsatellite DNA has been used to demonstrate that females of both rocky and sandy shore fishes in Lake Malawi generally mate with several males in the course of producing a single clutch, further reducing the feasibility of extreme founder effects (Kellogg *et al.* 1995; Parker and Kornfield 1996).

Sympatric speciation

Most studies of African cichlids have concentrated on the rocky shore fishes, perhaps because they live in shallow clear waters safe for scuba studies. Far less is known about deep water and pelagic areas of the lakes, but these too support large numbers of endemic species (Turner 1996), although admittedly probably not as many as the rocky shores. Sandy shores are also home to diverse cichlid communities, and although it is often stated that rocky shores represent as much of a barrier to these species as sandy shores do to rocky shore species (e.g. Fryer 1996), there is no real evidence for this and I have observed many supposedly sandy shore species on rocky habitats in Lake Malawi. Could these non-rocky shore species have evolved by sympatric speciation? There is now good evidence for sympatric origin of fish species, via disruptive ecological selection and divergent habitat use, in recently glaciated temperate lakes (Schluter 1996). This is difficult to demonstrate in large lakes where heterogeneous habitats provide possibilities for geographic isolation, but cichlids have also radiated in several tiny crater-lakes in Cameroon. These lakes have monotonous shorelines and no

possibility for habitat barriers. Previously thought to have been the result of multiple invasions, mtDNA studies have shown that the cichlid radiations of Lakes Barombi Mbo and Bermin are monophyletic, strongly suggesting sympatric speciation within each lake (Schliewen *et al.* 1994).

Sexual selection and speciation

All the endemic cichlids of Lakes Malawi and Victoria, and many of those of Lake Tanganyika are maternal mouthbrooders. Females provide all of the parental care and are generally small and drab. Males are larger, brighter, often have long fins. Sand-dwelling species often build relatively huge display structures or 'bowers' from sand. Males of some Malawian and Tanganyika cichlids aggregate on leks. These observations suggest the operation of strong sexual selection by female choice for male display traits.

Males of some sandy shore species from Lake Malawi experience strongly skewed mating success, which seems to be related to their position on the lek (McKaye 1991), the height of their sand bower (McKaye *et al.* 1990), and its symmetry which is in turn correlated with the male's level of parasite infestation (Taylor *et al.* 1998). Experiments with cichlid fishes from Lake George (Lake Victoria 'superflock') and the rocky shores of Lake Malawi have shown that females prefer males with larger numbers of yellow spots on their anal fins (Hert 1989, 1991) and that the preference was lost when these spots were eliminated by the application of dry ice (Hert 1989).

Sympatric members of the *Pseudotropheus zebra* complex from the rocky shores of Nkhata Bay, Lake Malawi, which are known to be reproductively isolated in their natural habitat (van Oppen *et al.* 1998), will mate assortatively in the laboratory where environmental cues, such as microhabitat preferences or seasonal spawning triggers, are absent (M. E. Knight *et al.*, unpubl.). Seehausen and van Alphen (1998) have shown that the red and blue forms of *Haplochromis nyererei* from Lake Victoria will court assortatively in the laboratory under white light, but females court at random under monochromatic light which eliminates the colour differences between males.

In a comparative study of Lake Malawi rock cichlids, Deutsch (1997) found no relationship between male coloration (hue or brightness) and environmental parameters, such as water depth or substrate type, suggesting that male colour was not influenced by habitat-related natural selection. There was also no indication that male colours were more divergent among sympatric species pairs than allopatric taxa, implying the absence of selection for reinforcement or reproductive character displacement. Seehausen *et al.* (1997b) found that males of Lake Victoria cichlids tend to be both brighter and more divergent in colour in areas of high water transparency, despite an increase in the abundance of visual-hunting predators. They also found that taxa which would not interbreed in clear water areas, hybridized in turbid areas, suggesting that sexual selection operates more strongly leading to reproductive isolation where permitted by environmental constraints.

6.5 Discussion

It is now clear that speciation rates in African lake cichlids have been extraordinarily fast. At the moment, it seems that the fastest diversification is occurring in lineages, such as the rocky shore species of Malawi and Victoria, where fine-scale population structuring resulting from habitat specificity and lack of dispersal is coupled with diversification in male courtship traits by sexual selection. However, this remains a working hypothesis and many questions remain unanswered.

Why have tilapias not produced large species flocks? Species of the genus *Oreochromis* are present in all three lakes. Like the haplochromines, they are strongly dimorphic maternal mouthbrooders, yet the only lacustrine radiation has been three species in Lake Malawi. Why are there fewer cichlid species in Lake Tanganyika than in Lakes Malawi and Victoria? Tanganyika is much older and has a greater diversity of cichlid lineages than the other lakes. Is it possible that ecological competition has become more severe and has thinned out the number of the species? Why have cichlids radiated so dramatically in lakes, but not in rivers?

Perhaps Seehausen *et al.*'s (1997b) work may indicate the answer. If divergent sexual selection for male coloration operates weakly in turbid areas in lakes, it may not operate at all in rivers where the water is often virtually opaque during the rainy season floods.

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