

INVITED REVIEW

Speciation in rapidly diverging systems: lessons from Lake Malawi

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Abstract

Rapid evolutionary radiations provide insight into the fundamental processes involved in species formation. Here we examine the diversification of one such group, the cichlid fishes of Lake Malawi, which have radiated from a single ancestor into more than 400 species over the past 700 000 years. The phylogenetic history of this group suggests: (i) that their divergence has proceeded in three major bursts of cladogenesis; and (ii) that different selective forces have dominated each cladogenic event. The first episode resulted in the divergence of two major lineages, the sand- and rock-dwellers, each adapted to a major benthic macrohabitat. Among the rock-dwellers, competition for trophic resources then drove a second burst of cladogenesis, which resulted in the differentiation of trophic morphology. The third episode of cladogenesis is associated with differentiation of male nuptial colouration, most likely in response to divergent sexual selection. We discuss models of speciation in relation to this observed pattern. We advocate a model, divergence with gene flow, which reconciles the disparate selective forces responsible for the diversification of this group and suggest that the nonadaptive nature of the tertiary episode has significantly contributed to the extraordinary species richness of this group.

Keywords: adaptive evolution, cichlid, Lake Malawi, mbuna, multiple radiation, speciation

Received 9 August 2000; revision received 4 January 2001; accepted 4 January 2001

Introduction

Explosive taxonomic radiations are useful systems in which to study the process of species formation. The extraordinary biological diversity of these systems evolves through multiple cladogenic events. By comparing such events among closely related taxa, one can begin to identify common factors that influence the speciation process. Identification of these factors is further simplified because these radiations often occur in insular habitats (such as isolated lakes) in which the spectrum of factors affecting diversification is reduced. The young age of most rapid radiations may also simplify the identification of factors involved in the speciation process. Because speciation has occurred relatively recently in these systems, a greater proportion of the phenotypic differences between two lineages are likely to be directly attributable to the forces which cause speciation. For these reasons, an examination

of the largest extant vertebrate radiation known, the cichlid fishes of East Africa, should prove informative. In this review we examine the patterns of diversification in a subset of this group, the fishes of Lake Malawi's rock-dwelling assemblage, in an attempt to identify common processes in their radiation. We advocate a model of multiple diversification that may account for the extraordinary biological diversity in this and other explosive radiations.

The East African cichlid radiation is concentrated in the three Great Lakes of Tanganyika, Malawi and Victoria. Lake Tanganyika, the oldest of the three lakes (basin age estimated to be between 9 and 12 million years old) (Cohen *et al.* 1993) supports at least 197 endemic cichlids in 49 endemic genera (Poll 1986). These genera can be grouped into 12 separate tribes that are thought to have diverged from seven distinct ancestral lineages (reviewed by Meyer 1993). These tribes are relatively old compared to other East African cichlid lineages; phylogenetic evidence suggests that some of the tribes originated at least five million years ago (Nishida 1991; Sturmbauer & Meyer 1993) making them older than either the Victoria or Malawi lake

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basins (Fryer & Iles 1972). Lake Tanganyika's cichlids are morphologically and behaviourally more diverse than the cichlids of Lakes Victoria and Malawi (Fryer & Iles 1972), however, the latter two lakes each possess a greater number of cichlid species than Lake Tanganyika.

Lake Victoria was formed 250 000–750 000 years ago (Johnson *et al.* 1996) when the tilting of the Tanzanian shield back-ponded west flowing rivers. It is thus more shallow than Lakes Tanganyika and Malawi which are situated in the cleft of the East African Rift. More than 300 endemic species of cichlids occur in Lake Victoria (Seehausen 1996), all of which were thought to be derived from a single common ancestor (Meyer *et al.* 1990). However, recent molecular data suggest that Lake Victoria was colonized by at least two separate lineages. These two lineages, one representing Lake Victoria's rock-dwelling cichlids (*mbipi*) and the other representing all other endemic cichlids from Lake Victoria, each invaded the lake and rapidly diverged within the last 12 500 years (Nagl *et al.* 2000).

The cichlid flock of Lake Malawi is intermediate to those in Lakes Tanganyika and Victoria in almost every respect. Cichlids are thought to have invaded Lake Malawi approximately 700 000 years ago, and their morphological diversity is considerably greater than the much younger species flock of Lake Victoria. In addition, the Malawian radiation has produced the greatest number of endemic species of the three species flocks (well over 400 endemic species distributed among 49 endemic genera; Moran *et al.* 1994) and appears to be monophyletic in origin (Meyer *et al.* 1990; Kocher *et al.* 1993; Moran *et al.* 1994). For these reasons, the cichlid fishes of Lake Malawi appear ideally suited for the study of rapid radiations.

Early models stressed the importance of vicariant events in generating the species diversity in East African lakes. The multiple invasion model suggested that each lake had been colonized by multiple lineages which had evolved independently in either space (Mayr 1942) or time (Fryer 1977). Molecular phylogenetic studies provide little support for these models. A study of the Tanganyikan tribes had suggested that their diversification might predate the formation of the lake basin (Nishida 1991) but this notion was later rejected (Meyer 1993) after a reevaluation of the lake basin's age (Cohen *et al.* 1993). Although it is possible that the 12 Tanganyikan tribes were derived from multiple riverine ancestors, it is clear that most of the subsequent radiation occurred within the lake basin. Likewise, Victorian cichlids appear to have diverged prior to their invasion of the current lake basin. However, the vast majority of the species within this lake (some 300 species) arose *in situ* within the past 13 000 years (Nagl *et al.* 2000). In contrast, molecular phylogenies suggest the separate, monophyletic origin of the haplochromine cichlids within Lake Malawi (Meyer *et al.* 1990; Moran *et al.* 1994). The multiple invasion model is not adequate

to explain the extraordinary diversity of East African cichlids.

Vicariance resulting from changes in lake level may have played an important role. East Africa is prone to dramatic changes in climate and precipitation. As a result, lakes in this region experience frequent fluctuations in lake water levels (Owen *et al.* 1990) and may fragment during dry periods. This is particularly apparent in Lake Tanganyika. Seismic data indicate that approximately 25 000 years ago water levels in Lake Tanganyika were 600 m below the current level. During this period, three separate sublakes existed within Lake Tanganyika's current shoreline (Scholz & Rosendahl 1988). This fragmentation is reflected in the phylogeographic patterns of Lake Tanganyika's rock-dwelling cichlids (Sturmbauer & Meyer 1992; Verheyen *et al.* 1996; Rüber *et al.* 1998, 1999). Mitochondrial phylogenies indicate that many haplotype lineages are restricted to particular subbasins. Furthermore, several cross-lake haplotype affinities were identified which correspond to currently inaccessible subbasin shores. Given the stenotopy of the taxa involved, a previous connection across a palaeo-shoreline is the most parsimonious explanation for the observed haplotype affinities.

While the effect of this vicariant event is widespread, it is not universal. Not all taxa in Lake Tanganyika show these phylogeographic patterns (Meyer *et al.* 1996) and basin morphologies of other lakes do not generate multiple basins during low water stands (Scholz & Rosendahl 1988). The effect of fluctuating lake levels may have been more subtle in these systems (van Oppen *et al.* 1997; Arnegard *et al.* 1999; Markert *et al.* 1999; Danley *et al.* 2000).

Ecological and behavioural factors appear to have had the largest effect on the diversification of cichlids in all three lakes. It has been difficult, however, to partition and rank the effects of these forces. Below we examine the patterns of diversification in one of these species flocks, the rock-dwelling cichlids of Lake Malawi. Through an examination of the phylogenetic history of this group, we attempt to identify forces that have influenced their diversification and to partition the effect of these forces to particular periods in the radiation. We conclude by suggesting a model that unifies the disparate forces that have acted during each stage of this radiation.

The pattern of diversification

Lake Malawi cichlids have experienced sequential episodes of diversification (Fig. 1). Lake Malawi was colonized by a generalized cichlid that first diverged into two major clades (the rock-dwelling *mbuna* and a sand-dwelling clade) plus several oligotypic lineages (Moran *et al.* 1994; Seehausen *et al.* 1999). Adaptation to the rock and sand macro-habitats resulted in the divergence of many morphological and behavioural characteristics including body shape, trophic

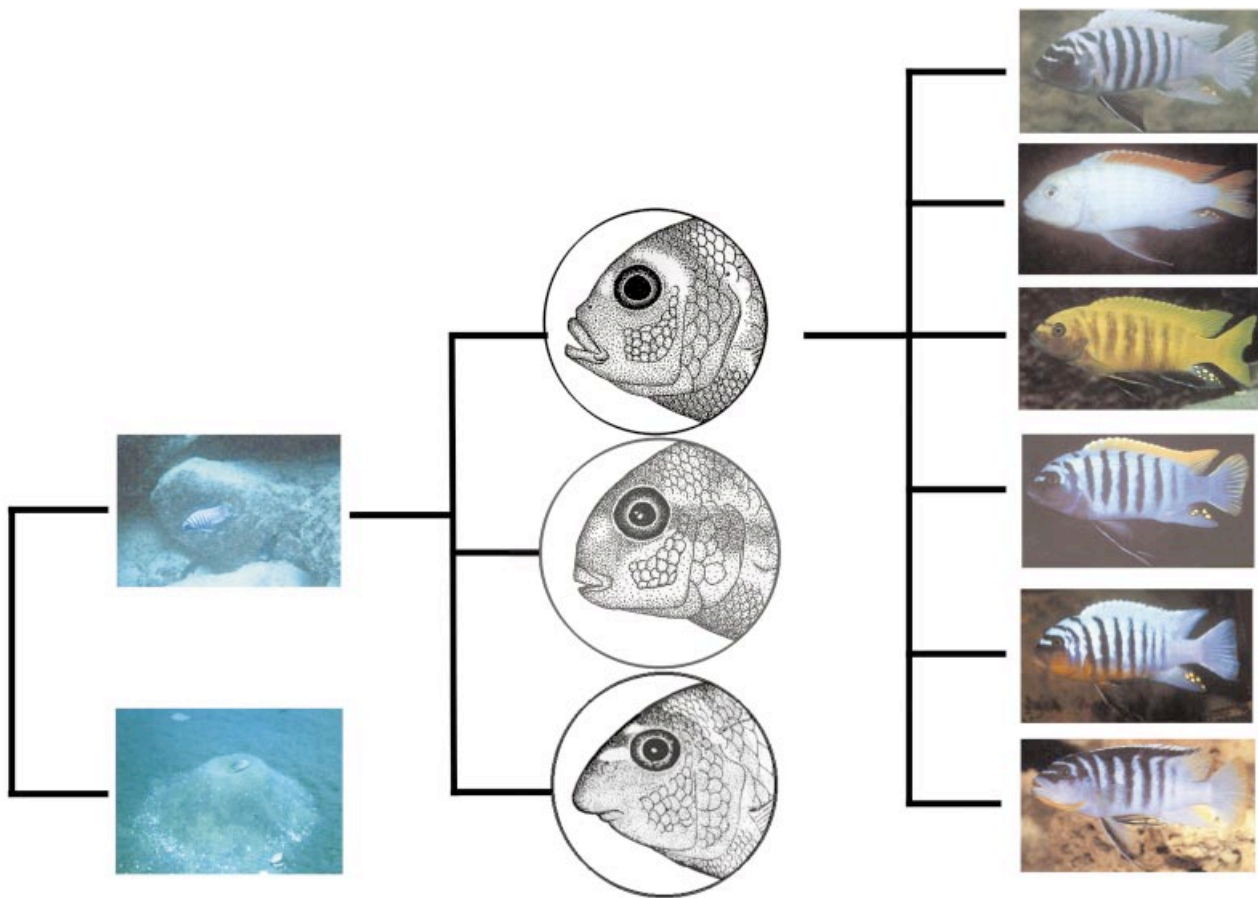


Fig. 1 A proposed phylogenetic history of Lake Malawi's rock-dwelling cichlids based on several molecular phylogenies of Lake Malawi cichlids (Meyer *et al.* 1990; Kocher *et al.* 1993; Meyer 1993; Moran *et al.* 1994; Moran & Kornfield 1995; Albertson *et al.* 1999). Lake Malawi is presumed to have been invaded by a riverine generalist closely allied with Lake Tanganyika's haplochromine tribe approximately 700 000 years ago. This common ancestor subsequently diverged during the primary radiation into the sand-dwelling and rock-dwelling lineages. The rock-dwelling lineage diverged during the secondary radiation into the 10–12 currently recognized mbuna genera. These genera are distinguished primarily on the basis of trophic morphology suggesting the importance of trophic competition during this period of the radiation. The spectacular species richness of the mbuna principally arose during the tertiary radiation. During this period, as many as 25 species per genus diverged presumably in response to sexual selection via female choice for male secondary sexual characteristics such as colour pattern. Line drawings courtesy of R. C. Albertson, colour images courtesy of Konings (1990).

morphology, melanin patterning, reproductive behaviours, and habitat preference (Fryer 1959; Ribbink *et al.* 1983).

The mbuna and non-mbuna clades each contain more than 200 species and are thought to be reciprocally monophyletic (Moran *et al.* 1994). However, determining the relationships of species within these two large clades has been problematic. Morphological characters frequently converge among distantly related lineages within Lake Malawi (Meyer *et al.* 1990) as well as among the species flocks of different East African lakes (Kocher *et al.* 1993). Molecular studies have also failed to resolve the phylogenetic relationships within these clades. The paucity of DNA sequence variation (Meyer *et al.* 1990; Moran *et al.* 1994), and the retention of ancestral polymorphisms, has

stymied attempts to develop fully resolved phylogenies (Moran *et al.* 1994; Kornfield & Parker 1997).

A recent genome wide survey of several thousand loci has begun to overcome these obstacles. Albertson *et al.* (1999) reconstructed the inter- and intrageneric phylogenetic relationships of several mbuna genera after surveying 2247 amplified fragment length polymorphism (AFLP) loci. The resulting phylogeny, while limited in scope, confirmed the current β level taxonomy of the mbuna and the previous hypotheses concerning the phylogenetic relationships between the mbuna and other Lake Malawi cichlids.

The evolutionary relationships among Lake Malawi's cichlid fishes suggest that this group has experienced at

least three sequential episodes of diversification (Fig. 1). The primary radiation resulted in the divergence of the rock-dwelling species from the sand-dwelling species. The secondary radiation, responsible for the diversification of mbuna genera, is closely associated with the refinement of the mbuna trophic apparatus. Although the mbuna are generally similar in body shape, melanistic body markings and habitat preferences, there are striking differences in their trophic morphology (Reinthal 1990b). The diversification of species during the tertiary radiations is commonly attributed to the divergence of reproductive characters (Fig. 1). Species within genera are nearly identical with respect to most morphological characters and are primarily identified on the basis of male secondary sexual characteristics such as colouration (Stauffer *et al.* 1997).

This type of phylogenetic history, which is punctuated by multiple diversification events, is a common pattern in rapidly radiating systems (Schluter & McPhail 1993; Sturmbauer 1998). In the sections below we attempt to identify the forces that may explain this evolutionary pattern in Lake Malawi's mbuna. Other rapidly radiating systems are also examined to determine the generality of these processes.

The primary radiation and the creation of macrohabitat clades

The diversification of the mbuna has been episodic and each episode appears to have been dominated by the refinement of phenotypes related to a particular adaptive axis. In the earliest split, adaptation to the two major macrohabitats resulted in two large benthic clades: the sand-dwellers and the rock-dwellers. During this period, strong selection on multiple characters resulted in the divergence of many morphological and behavioural characters related to ecological specialization.

An early ecological split appears to be common in cichlid radiations. Lake Victoria's cichlids diverged early in their radiation into rock- and sand-dwelling clades (Nagl *et al.* 2000), as have Lake Tanganyika's cichlids (Sturmbauer 1998). West African cichlids have experienced sympatric divergence of benthic and pelagic forms in multiple crater lakes (Schliewen *et al.* 1994). This pattern also occurs in a great number of other lacustrine fish groups. Three-spine sticklebacks have diverged into limnetic and benthic forms in multiple North American lakes (Schluter & McPhail 1993). Ecological divergence has also occurred in variety of other fish lineages including lake whitefish, brown trout, arctic char, and rainbow smelts (reviewed by Schluter 1998).

A similar pattern of diversification can be seen in rapidly radiating terrestrial systems. Anoline lizards of the Greater Antilles repeatedly evolved multiple ecomorphs associated with separate habitats (Losos *et al.* 1998). Darwin's finches diverged into ground finches and tree finches early

in their radiation (Lack 1947; Stern & Grant 1996). These studies suggests that ecological divergence in the early stages of a radiation may be a common phenomenon.

The secondary radiation and the refinement of mbuna trophic apparatus

The secondary radiation leading to the diversification of the mbuna genera represents a refinement of the trophic apparatus. The narrow scope of the morphological and behavioural changes associated with this episode suggest that selection, while strong and divergent, was focused on the trophic morphology and had little impact on other characters.

Two major adaptive innovations common among all cichlid lineages are primarily responsible for the diversification of the mbuna trophic structures; the restructuring of the pharyngeal jaw apparatus (Liem 1974), and the decoupling of certain oral jaw elements (Liem 1980). In their ancestral state, the pharyngeal jaws aid the transportation of food from the buccal cavity to the stomach. Through minor changes in the musculature, skeletal, and nervous systems, the cichlid pharyngeal jaws have adopted a food processing role; a task previously performed by the oral jaws (Liem 1974). The decoupling of upper oral jaw elements allows the independent manipulation of the premaxilla and maxilla thereby increasing the diversity of kinematic pathways associated with jaw movement (Liem 1980).

The combination of these two adaptive innovations increased the diversity of trophic resources available to cichlids and permitted the diversification of trophic structures in the mbuna and other cichlid lineages (Liem 1974). In various mbuna species the pharyngeal jaw apparatus acquired diverse new functions including: shearing prey, stacking scales scraped from other fish, and compacting filamentous algae (Liem 1991). The adoption of food processing functions by the pharyngeal jaw apparatus freed the oral jaws from the dual function of food collection and processing. The oral jaws subsequently diversified and became specialized solely for food collection. These specializations led to a variety of foraging strategies including plucking macroinvertebrates from the algal mat covering the rocks, combing loose algae and diatoms from attached algae, grazing on epiphytic algae, and plucking scales from the sides of fish. Although the trophic apparatus became more specialized morphologically, trophic versatility persisted through the maintenance of multiple kinematic pathways associated with the manipulation of the oral elements. As a result, cichlids exploit a range of trophic niches usually occupied by several families, if not orders, of fishes (Greenwood 1964).

Trophic versatility, however, is not necessarily expected to promote divergence. On the contrary, morphological

and behavioural plasticity might be expected to retard the speciation rate (Meyer 1987; Ribbink 1994). However, many species with extremely versatile jaws subsist on a very limited diet. For instance, *Metriaclima zebra*, which has the greatest number of kinematic pathways associated with jaw movement of all the mbuna (Liem 1980), also has an extremely limited diet (Reinthal 1990a). Furthermore, mbuna trophic resources appear to be narrowly partitioned (Reinthal 1990a; Genner *et al.* 1999). The estimated dietary overlap of most mbuna species appears to be extremely limited and, in those cases in which dietary overlap is considerable, species could be distinguished based on other aspects of their feeding ecology (Reinthal 1990a; Genner *et al.* 1999). Such strong trophic partitioning is expected to generate the rapid divergence of new species (Robinson & Wilson 1998). The persistence of kinematic pathways associated with trophic versatility, however, may retard the extinction rate during periods of reduced resource availability (McKaye & Marsh 1983).

The resulting picture, generated from morphological, dietary, behavioural, and phylogenetic studies, suggests that the mbuna genera diversified in response to competition for trophic resources, with only minor changes in structures unrelated to trophic morphology. This progression, from ecological diversification to the refinement of trophic structures during a secondary radiation, is well known among other East African cichlid radiations (Seehausen 1996; Sturmbauer 1998). It is also observed in other lacustrine fish groups. For example, arctic charr are known to have diverged into benthic and limnetic forms following their invasion of Icelandic lakes. The limnetic form then diversified into piscivorous and planktivorous morphs (Snorrason *et al.* 1989). The differentiation of beak morphologies in Darwin's finches after their adaptation to the major ecological habitats on the Galapagos Islands are probably the best known example of this process in terrestrial vertebrates (Grant 1981).

The tertiary radiation and the divergence of reproductive characters

The tertiary radiations, those resulting in the diversification of extant species, appear to have been strongly influenced by sexual selection (Holzberg 1978; Ribbink *et al.* 1983; Dominey 1984; Hert 1991; McKaye 1991). The selective pressures operating during this episode resulted in the diversification of male secondary sexual characteristics (primarily colour patterns) (Ribbink *et al.* 1983; McKaye *et al.* 1984; Deutsch 1997) while the majority of other morphological characters are highly conserved. A similar process appears to have occurred in the sand-dwelling cichlids of Lake Malawi (McKaye *et al.* 1993; Taylor *et al.* 1998) and in the diversification Lake Victoria haplochromine species flock (Seehausen & van Alphen 1998).

The reproductive biology of the mbuna suggests that sexual selection may be a particularly potent force. In their lek-like mating system (Barlow 1991), parental investment is highly skewed. Males defend permanent territories (Ribbink *et al.* 1983), experience a large variance in reproductive success (Hert 1991), and provide the females with no resources other than a place to mate (Holzberg 1978). In contrast, females are free to choose among many males (Parker & Kornfield 1996; Kellogg *et al.* 1998) but are required to mouthbrood the large yolk-rich eggs for several weeks after fertilization. Adult size and reproductive colour patterns are sexually dimorphic. Males are larger and are brightly coloured, whereas females are generally smaller and cryptically coloured (Ribbink *et al.* 1983). The reproductive biology of the sand-dwellers can be characterized in a similar manner (McKaye 1983; McKaye *et al.* 1990, 1993; Taylor *et al.* 1998).

Several studies suggest that male colouration is a target of sexual selection. A comparison of the within to between genera variation in colour pattern suggests that male reproductive colouration has diversified more rapidly than other characters such as depth preference, preferred substrate size and aggression (Deutsch 1997). Deutsch (1997) used this finding to argue that the diversity of male colour patterns is the result of sexual selection. Field studies indicate that male colour pattern can influence the variance in male reproductive success. Spots on the male's anal fin are similar in shape and colour to mbuna eggs and are thought to attract females and increase fertilization rates (Wickler 1962). Hert (1991) noted that male reproductive success varied according to the number of egg spots. Males with more egg spots were generally more successful and males with no egg spots failed to mate.

Laboratory studies of mate recognition indicate that adult colour pattern is an important aspect of the mbuna mate recognition system. Males can apparently distinguish con- and hetero-specific females based on visual cues alone. Among these, melanistic colour patterns appeared to have the largest effect (Knight & Turner 1999). A similar result was found when examining female mating preferences based on male colour patterns (Danley and Kocher, unpublished data).

Male reproductive colouration appears to play a significant role in the reproductive biology of most haplochromine cichlids. Among the rock-dwelling cichlids of Lake Victoria, Seehausen & van Alphen (1998) observed the maintenance of female mating preferences for conspecific males based on visual cues under natural lighting conditions. Their mate recognition broke down, however, when a similar test was performed under monochromatic light that eliminated the differences in male body hue. Under monochromatic light, females of both species preferred the larger and more active species. These results suggest that male body hue is the primary discriminatory

factor among a hierarchy of visual cues used by females (Seehausen & van Alphen 1998). Clearly the divergence of male colour patterns has significantly contributed to the rapid diversification of the haplochromine cichlids in East Africa's two most species rich lakes.

The dramatic influence of sexual selection is apparent in other rapidly diversifying systems including labrid fishes (JT Strelman *et al.*, in preparation), anoline lizards (Fitch & Henderson 1987; but see Losos & Chu 1998), Hawaiian *Drosophila* (Carson 1997) and a large number of bird species (Barraclough *et al.* 1995; Mitra *et al.* 1996; Prum 1997; Møller & Cuervo 1998; Uy & Borgia 2000). These observations suggest that sexual selection may predominate in the later stages of many radiations.

Remarkably, most members of the mbuna clade appear to have experienced the evolutionary pattern described above. However, this pattern is not without exception. At each cladogenic stage, at least one lineage does not conform to the described pattern. For instance, several oligotypic lineages have been identified that appear to have originated prior to the split between the rock- and sand-dwelling clades (Moran *et al.* 1994; Seehausen *et al.* 1999). Likewise, a single rock-dwelling genus (*Melanochromis*) appears to have diverged early from the lineage that gave rise to the remaining mbuna (Albertson *et al.* 1999). Members of this lineage can be distinguished from the other mbuna on the basis of many morphological characteristics including body shape and melanistic body markings (most notably the occurrence of horizontal stripes rather than the typical vertical barring) (Bowers & Stauffer 1997). The sister relationship between *Melanochromis* and the remaining mbuna was highly supported in Albertson *et al.*'s (1999) study, but a more complete sampling of the mbuna genera is needed to test this hypothesis.

An exception to the pattern of diversification during the tertiary radiation can be identified as well. Only two species within the genus *Labeotropheus* have been identified based on a number of morphological and behavioural characteristics. Notably, these species are distinguished based on aspects of body shape and habitat preference (Ribbink *et al.* 1983) rather than the differences in male colour pattern, which typically distinguish mbuna congeners. Interestingly, these deviant lineages are remarkably species poor compared to those lineages that follow the typical pattern of diversification.

While a particular divergent selective pressure may predominate during each selective episode, it is unlikely that a single force operates to the exclusion of others (Fig. 2). Variation in gut contents of closely related species suggests that competition for trophic resources is pervasive throughout the diversification of the mbuna (Reinthal 1990a,b). Variation in microhabitat preference among and within genera suggests that competition for space has also continually influenced their diversification (Ribbink

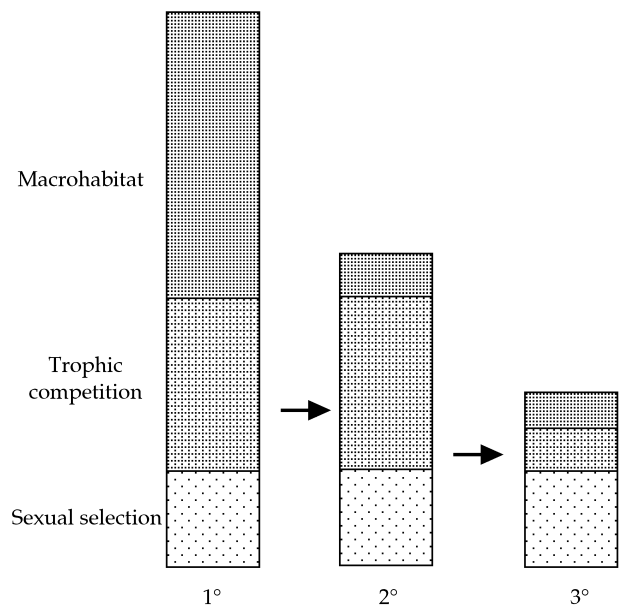


Fig. 2 The strength and composition of divergent selection operating during each of the three radiations. During the primary radiation, ecological pressures resulted in strong selection on macrohabitat preference (dark grey) and resulted in the divergence of the sand- and rock-dwelling clades. Selection on the mbuna trophic apparatus (stippled) dominated during the second radiation. The tertiary radiation appears to have been driven by divergent selection on reproductive characters. Note, however, that while the relative proportion of each selective factor may change during each cladogenic event, none are completely eliminated.

et al. 1983; Hert 1990). Likewise, sexual selection has most likely operated throughout all stages of the radiation; its historical effects are more difficult to identify however. The emerging pattern suggests that while many forces influence the process of diversification at each cladogenic stage, a single divergent selective force predominates during each episode.

Speciation models

While most early models of the speciation of Lake Malawi cichlids focused on extrinsic factors, more recent hypotheses are concerned with intrinsic aspects of their biology. The 'key innovation' hypothesis (Liem 1974) argues that certain trophic structures are responsible for the remarkable ability of cichlids to rapidly radiate in novel lacustrine environments. Liem suggests that the cichlid pharyngeal jaw apparatus represents a 'crucial ... morphological innovation' (Liem 1974; p. 439), which has granted members of this family a significant competitive advantage and has allowed them to rapidly colonize African lacustrine environments. This key innovation, however, occurs in all labroid fishes, the majority of which (including most other cichlid lineages) do not approach the exceptional species diversity observed

in the Great Lake cichlids. This key innovation is clearly not the sole factor influencing the rapid divergence of East African cichlids.

Other hypotheses have focused on the role that the cichlid mating system has played in their rapid radiation (Holzberg 1978). Dominey (1984) was the first to discuss Fisher's process of runaway sexual selection with respect to the diversification of East African cichlids. Several additional authors have extended the discussion with specific respect to Lake Malawi cichlids (Holzberg 1978; McElroy & Kornfield 1990; McElroy *et al.* 1991; McKaye 1991; Ribbink 1994; Moran & Kornfield 1995; Turner & Burrows 1995; Parker & Kornfield 1996; Deutsch 1997; Knight & Turner 1999). Recently Higashi *et al.* (1999) proposed a model in which male secondary sexual characteristics and female mating preferences diverge simultaneously. Three outcomes were observed in their simulations: (i) no change in either trait; (ii) fixation of a particular male character and the corresponding female preference; and (iii) the sympatric fixation of alternative states of the male and female characters (a result that leads to prezygotic isolation). The authors argue that the clear waters of the East African rift lakes and the reduced levels of natural selection on male characters increase the likelihood of sympatric speciation in these cichlid flocks. Divergent sexual selection, however, is not limited to clear water habitats. Lake Victoria is considerably more turbid than Lakes Malawi and Tanganyika, and yet sexual selection on male colour patterns has played an important role in this system (Seehausen *et al.* 1997; Seehausen & van Alphen 1998). The recent eutrophication and resulting dramatic increase in turbidity of Lake Victoria, however, threatens the diversity of these cichlids which rely heavily on visual cues for their mate recognition system (Seehausen *et al.* 1997).

Good genes models of sexual selection have also been discussed with reference to Lake Malawi cichlids. Taylor *et al.* (1998) argue that female mating preferences are influenced by the male's resistance to parasites. In field studies, male mating success was negatively correlated with the number of liver parasites. Given the absence of male parental care, this observation was taken as evidence of a good genes mechanism of female mate choice. Hert (1991) has made similar arguments relating to male foraging efficiency. Male mating success was correlated with the occurrence and frequency of yellow egg spots on the male's anal fin. The production of such carotenoid based colour has been linked with foraging efficiency in other fish groups (Endler 1983). Hert (1991) suggests that female mate choice may be dependent on the male's ability to acquire carotenoids, a trait that if heritable may have fitness effects in a female's offspring.

The combined effect of competition and assortative mating in driving the diversification process has recently gained attention. Kondrashov & Kondrashov (1999) exam-

ined the sympatric divergence of a population whose members compete for a bimodally distributed resource. Their simulations suggest that populations will diverge when linkage disequilibrium develops between a mating character and characters influencing the ability to compete for a limiting resource. Other models predict that a similar outcome can occur even if the resource is unimodally distributed (Dieckmann & Doebeli 1999).

An integrative model

Each of the models discussed above fails to adequately address the diversification of Lake Malawi cichlids *in toto*. Most models are applicable to a narrow range of phylogenetic history but do not address the entire process. Models which integrate the various selective forces known to influence the diversification of East African cichlids are needed (Galis & Metz 1998; Sturmbauer 1998). Below we adapt the divergence with a gene flow model developed by Rice & Hostert (1993) in which selection and gene flow interact to produce a cyclical process characterized by the reduction of both the strength of divergent selection and rates of gene flow. This model differs from previous dynamic models of cichlid diversification in its reliance on intrinsic (rather than abiotic) triggers of cladogenic events and its recognition of the important role that nonadaptive evolution has played in the diversification of haplochromine cichlids in East Africa.

The diversification of Lake Malawi cichlids, with particular reference to the mbuna, can best be considered in terms of the antagonistic forces of selection and gene flow. Several models have been developed which discuss the divergence of populations with varying rates of ongoing gene flow (Endler 1973; Lande 1982; Rice & Hostert 1993). The model developed by Rice & Hostert (1993) is particularly appealing given the patterns of diversification observed in Lake Malawi. This model predicts that populations will diverge so long as selection is strong (relative to gene flow), divergent, and acting on multiple characters (Fig. 3). Prezygotic isolation is expected to develop under these conditions without direct selection on the mate recognition system. Isolation develops as a correlated response (via pleiotropy or genetic hitchhiking) to selection on other characters. The model also predicts that a positive feedback loop might develop (Fig. 4). In such a situation, competition for a limiting resource generates divergent selection. Populations respond to this selection by acquiring adaptations that reduce competition for the contested resource. Consequently, both the strength of divergent selection and the level of interpopulational gene flow decrease, and the strength of stabilizing selection increases. As gene flow is reduced, selective pressures that previously had been too weak to overcome the ongoing levels of gene flow now cause additional divergence. The process is a self-priming

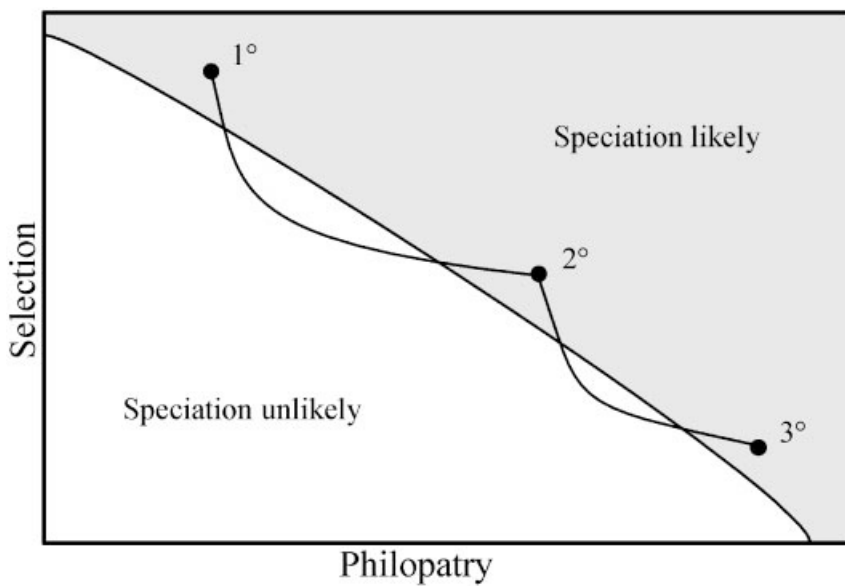


Fig. 3 Speciation with limited gene flow with reference to Lake Malawi's rock-dwelling cichlids. Populations are expected to diverge so long as divergent selection is strong relative to the levels of ongoing gene flow. Thus, if a population's position is plotted on a coordinate grid consisting of selection and philopatry, one can predict the likelihood of a speciation event. Lake Malawi's rock-dwelling cichlids have crossed the curve and entered the speciation domain of the plot at least three times during their evolution. During each radiation, adaptation reduces both the strength of divergent selection and the level of gene flow, thereby allowing subsequent radiations to occur. The size of the arc connecting adjacent cladogenic periods is expected to be roughly proportional to the size of the largest genetic factor fixed during the adaptive episode.

Speciation engine

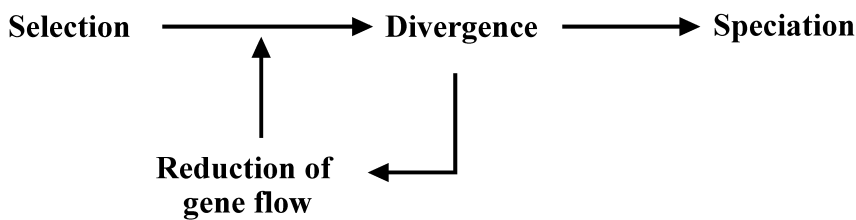


Fig. 4 The speciation model advocated here predicts the formation of a positive feedback loop in which each cladogenic event can potentially lead to subsequent episodes. See text for complete details.

Adapted from Rice and Hostert (1993)

engine in which each iteration of the cycle primes subsequent divergence episodes.

Several aspects of this model are relevant to the diversification of Lake Malawi cichlids. The positive feedback nature of the process predicts that multiple episodes of diversification, each related to a separate selection pressure, could occur. This expectation is matched by the proposed phylogenetic history of Lake Malawi's rock-dwelling cichlids as supported by their current taxonomy and recent molecular studies (Meyer *et al.* 1990; Moran *et al.* 1994; Albertson *et al.* 1999). As discussed above, the mbuna diversified in three major episodes; an initial split between sand- and rock-dwelling clades, the divergence in trophic morphology, and the diversification of sexually selected characters.

The model also predicts that levels of gene flow will decrease with time. The selection-adaptation process is expected to cause a reduction in gene flow with each cladogenic event. Indirect evidence supports this prediction. The ancestor to Lake Malawi's haplochromine cichlids is thought to have been a generalized riverine cichlid. This

precursor to Malawi's extant cichlids was most likely well equipped to disperse great distances through a variety of habitats. Recent estimates of ongoing levels of gene flow indicate, however, that mbuna migration is extremely restricted over limited geographical scales (van Oppen *et al.* 1997; Arnegard *et al.* 1999; Markert *et al.* 1999; Danley *et al.* 2000). These results clearly indicate that gene flow has decreased from its initially high levels. It is difficult to infer the levels of gene flow that occurred during the secondary radiation; however, the lakewide distribution of mbuna genera suggests it may have been significant. In contrast, many species have very narrow distributions, occurring only at a single island or headland. While inferring historical levels of gene flow can be problematic, the evidence suggests that gene flow has declined since the colonization of the lake.

The model also predicts that the overall divergent selection pressure will decrease with each cladogenic event. Adaptation reduces competition for a particular resource and thereby reduces the overall selective pressure. The

residual competition for other limiting resources then drives additional cladogenic events once gene flow is sufficiently lowered (again by adaptation). While the strength of selection at previous cladogenic stages cannot be measured directly, it is possible to infer the relative strength of selective pressures at various stages by the number of the characters involved in the diversification. The diversification of the rock/sand-dwelling forms resulted in changes in multiple characters including; body shape, reproductive behaviour and morphology, habitat preference, preferred diet, and jaw morphology (Fryer 1959). The divergence of genera resulted primarily in the diversification of trophic structures, while overall morphology, behaviour, and colour patterns are conserved (Ribbink *et al.* 1983). Divergence of species within genera is primarily reflected in the diversification of male colour patterns; most other morphological characters are conserved (Bowers & Stauffer 1997; Stauffer *et al.* 1997). The decreasing complexity of the divergent characters at each of the cladogenic episodes suggests that overall selection is declining, in agreement with the predictions of this model.

The proliferation of taxa during the tertiary radiation

The diversification that occurred during the tertiary radiation largely accounts for the extraordinary biological richness of the mbuna clade. Ten to 13 mbuna genera are currently recognized, and many mbuna genera contain over 15 species (likely an underestimate as many species remain undescribed). Species diversity generated during the tertiary radiation exceeds the diversity originating in the two previous episodes.

The potentially nonadaptive nature of sexual selection may be responsible for the extraordinary proliferation of taxa during this radiation. During the initial two cladogenic periods, the Rice & Hostert (1993) model predicts that populations responded to natural selection in a manner that reduces the level of competition for the limiting resource, thereby reducing the strength of divergent selection acting on them. This adaptive response, i.e. a phenotypic change which reduces the impact of divergent selective pressures, is not necessarily expected to develop in response to sexual selection. In fact, the strength of sexual selection may increase as a correlated response to changes in the preferred male trait (Lande 1981). In this regard, evolution during the tertiary period may not have been adaptive; phenotypic changes in male secondary sexual characteristics may not reduce the strength of divergent sexual selection acting on them.

Gene flow, however, is expected to dwindle among populations experiencing sexual selection. Female mating preferences and male secondary sexual characters may diverge among isolated populations. As a result, the likeli-

hood that a migrating male will successfully reproduce decreases. The combination of the continuing selective pressure and the reduction in gene flow means that populations are likely to remain stuck in the 'speciation' domain of the selection vs. gene flow relationship.

Nonadaptive evolution may also permit the evolution of genetic architectures that accelerate phenotypic divergence. Mutations with large phenotypic effects are expected to increase the rate of phenotypic fixation in a population (Templeton 1982; Coyne 1992; Voss & Shaffer 1997). While little is known concerning the size of allelic effects fixed during adaptive episodes, recent modelling suggests that the size of the largest fixed factor is correlated to the complexity of the phenotypic change (Orr 1998). Complex characters, such as habitat preference (which involves a number of morphological, physiological, and behavioural traits) have a greater dimension in Orr's model. Such characters are expected to evolve through the fixation of alleles with larger effects relative to simpler characters.

The extension of Orr's model into the cichlid system suggests that the size of the largest factor fixed by natural selection during each of these cladogenic events will decrease with time (just as the complexity of the phenotypic changes associated with each episode decreased). However, this model assumes that diverging populations each approach separate fixed optimal phenotypes. If no fixed optimum exists, such as when female preferences are open-ended and natural selection on the preferred male character is weak, the size of allelic effects fixed by sexual selection may exceed those that are fixed under natural selection. Such a genetic architecture may permit the rapid divergence of phenotypic characters and ultimately increase the speciation rate during nonadaptive evolutionary episodes.

Conclusions

Malawian rock-dwelling cichlids have experienced a minimum of three separate radiations in their phylogenetic history. The first radiation resulted in the differentiation of the sand- and rock-dwelling forms and is a classic example of ecological differentiation common in many other rapid radiations. The trophic morphology of the rock-dwelling cichlids differentiated dramatically during the second radiation, while most other morphological and behavioural characters were conserved. These observations suggest that strong divergent selection on the ability to acquire trophic resources dominated during the second radiation. Divergence during the third radiation is largely restricted to male nuptial colour patterns that have likely diverged in response to sexual selection via female choice. This type of nonadaptive evolution may explain the high rate of species proliferation during the tertiary radiation. All together

these radiations have generated over 200 species classified into 12 genera of rock-dwelling cichlids in Lake Malawi.

Future research efforts should focus on a number of areas. First, more detailed phylogenetic analysis is needed to describe the supergeneric, generic, and superspecific groupings of the rock-dwelling cichlids. The phylogenetic model of the mbuna diversification proposed here relies heavily on the currently recognized taxonomic relationships of the mbuna. It is possible, however, that mbuna taxonomy does not accurately reflect their phylogenetic history (see Rüber *et al.* 1999). More complete taxon sampling is needed to verify the phylogenetic model advocated here and to identify any additional structuring in the radiation. Second, the strength of competition for both trophic and reproductive resources need to be evaluated. Fieldwork that documents the strength of ongoing selection and manipulative laboratory studies, possibly involving hybrids, may be used to quantify the strength of divergent selection on intermediate phenotypes. Third, female preference functions need to be evaluated within the rock-dwelling cichlids. Such information could be used to evaluate the model proposed here to explain the proliferation of species during the third radiation. Fourth, the genetic basis of convergent characters deserves future attention. Convergence in morphological characters between lakes has been documented (Kocher *et al.* 1993). Likewise within isolated lake basins, phenotypic convergence in characters such as male colouration (Deutsch 1997; Seehausen *et al.* 1999) can be considerable. Given the likelihood that gene flow is maintained at low rates between incipient species within Lake Malawi, it is possible that introgressive hybridization may have played a significant role in the diversification of this group (*sensu* Wang *et al.* 1997). It would be interesting to know whether the convergence of phenotypic characters within Lake Malawi is due to the sharing of ancestral polymorphisms, the result of newly arisen mutations, or introgressive hybridization.

Acknowledgements

We would like to thank Julie Baldizar, members of the Kocher laboratory, particularly R. Craig Albertson and J. Todd Strelman, and Lukas Rüber for their insightful comments on previous versions of this paper. Thanks to R. Craig Albertson for providing the line drawings, and Ad Konings for providing the colour images for Fig. 1.

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