Phenotypic plasticity: its role in trophic radiation and explosive speciation in cichlids (Teleostei: Cichlidae)

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Abstract—Phenotypic plasticity is the capacity of an organism's phenotype to vary in different environments. Although diet-induced phenotypic plasticity has been documented in New World cichlids, it has been hypothesised that this type of plasticity would be limited in certain Old World cichlids, because of the morphological constraints on the jaw imposed by mouth-brooding. This hypothesis was experimentally tested by determining the effect of different diets on the head and jaw morphology of split broods of several species of haplochromine cichlids from Lake Malaŵi, Africa, and two substrate-spawning cichlids, one from the Old World, *Tilapia mariae* (Boulenger), and one from the New World, *Herichthys cyanoguttatum* (Baird and Girard). Different feeding regimes resulted in differences in head morphologies in both New and Old World cichlid species. Although Old World mouth-brooding haplochromine cichlids exhibited phenotypic plasticity, the magnitude of head-shape plasticity observed was greater in the New World substrate-spawning cichlid, *H. cyanoguttatum*. The Old World tilapiine cichlid, *T. mariae*, did not exhibit phenotypic plasticity of head morphology. Experiments with modified foods demonstrated that the observed changes were unrelated to dietary nutrition, but were a result of differing feeding modes. Phenotypic plasticity might have contributed to the extensive trophic radiation and subsequent explosive speciation observed in Old World haplochromine cichlids. The existence of phenotypic plasticity has implications for morphology-based species descriptions as well.

Keywords: cichlids; phenotypic plasticity; speciation; trophic polymorphism.

INTRODUCTION

Phenotypic plasticity is defined as environmental modification of the phenotype (Bradshaw, 1965), and has been documented in a wide range of organisms, including fishes (Barlow, 1961; Behnke, 1972; Chernoff, 1982; Meyer, 1987, Chapman et al., 2000), amphibians (Calhoon and Jameson, 1970; Newman, 1988),

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reptiles (Legler, 1981), birds (James, 1983), mammals (Williams and Moore, 1989), insects (Atchley, 1971), and plants (Bradshaw, 1965; Schlichting, 1986). Two types of phenotypic plasticity, developmental conversion and phenotypic modulation, can be characterised by direction and magnitude, respectively (Smith-Gill, 1983). Developmental conversion results in discrete morphs in response to an environmental cue (Stearns 1989; West-Eberhard, 1989). Levins (1968) postulated that such conversions can be controlled by developmental switches, or controllers that determine attributes. For example, gender in turtles is determined by incubation temperature. Such switches can be non-plastic and under strict allelic control (Mayr, 1963). In contrast, phenotypic modulations or reaction norms result in continuous variation of a particular trait in response to an environmental stimulus (Woltereck, 1909; Stearns, 1989). The direction and magnitude of phenotypic modulation may be similar or different for related species (Schlichting, 1986). The plasticity of the trait itself is affected by natural selection, and as such, is under genetic control (Bradshaw, 1965; West-Eberhard, 1989); thus, a given reaction norm may have a distinct evolutionary trajectory different from the plasticity with which it is associated (Schlichting and Levin, 1986).

The Great Lakes of Africa, including lakes Malaŵi, Tanganyika, and Victoria, harbour the most speciose ichthyofauna of any of the world's lakes (Fryer and Iles, 1972; Kocher et al., 1993). The endemic haplochromine cichlid fishes provide one of the best examples of explosive vertebrate speciation. Despite the morphological plasticity, which has been observed in other fishes due to such environmental factors as diet (Meyer, 1987), temperature (Stearns, 1989; Page and Burr, 1991), light (Witte et al., 1990), and predation pressure (Witte et al., 1990), some authors have assumed the morphology of African cichlid fishes to be developmentally canalised (van Oijen, 1982).

Observed morphological variability observed in the Cichlidae may be due, in part, to phenotypic plasticity (Hoogerhoud, 1984; Meyer, 1987, 1990a, 1990b; Witte et al. 1990; Wimberger, 1991, 1992). Witte (1984) hypothesised that differences in pre-maxilla development in wild-caught vs. aquarium-raised *Haplochromis squamipin-nis* Regan from Lake George were due to differences in diet. Hoogerhoud (1984) noted diet-dependent differences in the pharyngeal jaw apparatus of *Gaurochromis* and *Labrochromis* to be of the same magnitude as differences between these two genera. Furthermore, the phenotypic divergence of the pharyngeal apparatus of the New World *Herichthys minckleyi* (Kornfield and Taylor, 1983) exceeds that observed among species of molluscivorous cichlids inhabiting Lake Victoria (Hoogerhoud, 1984). Differences in bone structure of the lower pharyngeal jaw associated with *Astateroeochromis alluadi* Pellegrin that were fed different diets were noted (Huysseune et al., 1994; Smits et al., 1996a, b).

Meyer (1987) and Winberger 1991, 1992) have directly tested the effects of diet on phenotypic plasticity in New World cichlids. In general, cichlid species that feed by biting tend to have a short, blunt (obtusorostral) snout, whereas species that rely heavily on suction have a long, pointed (acutorostral) snout (Barel,

1983). Meyer (1987) examined the effect of diet on the head morphology of *Herichthys managuense* (Günther). Meyer (1987) fed full siblings two different diets for 8.5 months and then quantified head shape. Those individuals fed flake food and oligochaetes developed a short, blunt (obtusorostral) snout, whereas those individuals fed brine shrimp naupli developed a long, pointed (acutorostral) snout. The feeding regimes were then reversed for 8.5 months. Those individuals that had a short, blunt snout converged to the long, pointed snout form (Meyer, 1987); however, the acutorostral form did not converge to the obtusorostral form. Meyer (1987) concluded that a diet of flake food and oligochaetes at early ages delayed ontogenetic transformation to the adult phenotype. Meyer (1987), however, hypothesised that the plasticity of mouth-brooding Old World cichlids may not be as pronounced due to constraints on the jaw morphology for mouth brooding; thus, surrounding morphological structures may prevent a plastic structure from responding to its environment (Witte et al., 1990). Furthermore, free-swimming substrate-spawning fry, which feed at a younger age, are smaller than mouth-brooding fry. Because bone remodels less with age (Hinton and McNamara, 1984), substrate-spawning fry were predicted to be more plastic than mouth-brooding fry (Wimberger, 1991); thus, any changes in head morphology of mouth-brooding juveniles that occur before feeding commenced could be maladaptive (Wimberger, 1991).

Two species of *Geophagus* were selected by Wimberger (1991, 1992) to examine the magnitude of plasticity in mouth-brooding vs. substrate-spawning New World cichlids. Both species of *Geophagus* followed the expected trend, with those fish raised on flake food having a short, blunt snout and those fish raised on live brine shrimp having long, pointed snouts (Wimberger, 1991). In a preliminary study, F_1 siblings derived from wild-caught *Metriaclima pyrosontos* Stauffer, Bowers, Kellogg and McKaye from Lake Malaŵi, were randomly divided into two groups. Stauffer et al. (1995) fed one group flake food and the other brine shrimp naupli. The two groups developed different head shapes after 18 weeks (Stauffer et al., 1995). Based on these studies, it appeared that mouth brooding may not suppress the phenotypic plasticity induced by diet in either New World or Old World cichlids. Witte (1984) reported that wild-caught and laboratory-reared *Haplochromis squamipinnis* Regan had differently shaped premaxillaries. Laboratory-reared individuals of this Lake Victoria species frequently dug in the sand for food, increasing the power of their bite. Wild *H. squamipinnis* do not exhibit this digging behaviour, but are piscivores, feeding by sucking fish from the water column. Furthermore, the change in premaxillary shape was not restricted to juveniles, indicating that the plasticity was not limited by some ontogenetic factor (Witte, 1984). Greenwood (1965) reported that the pharyngeal jaw apparatus of the Old World cichlid, *A. alluadi*, is plastic. Individuals feeding on thick-shelled snails had stronger pharyngeal bones with larger molariform teeth than those feeding on thinner-shelled snails. Twenty weeks of living in the absence of light resulted in

changes in the ocular structures of the Old World cichlid *Oreochromis mossambicus* (Peters) (Witte et al., 1990).

Only one study has documented phenotypic plasticity in situ for Old World cichlids. A significant decrease in the body depth and size of the Lake Victoria cichlid *Haplochromis piceatus* Greenwood and Gee was documented in the 1980s (Witte et al., 1990). Dwarfed specimens (smaller individuals caught in the 1980s), when raised in the laboratory, grew to the size of normal individuals (larger individuals caught before 1980). The observed difference was attributed to a decreased growth rate due to the trawl fishery begun in the 1970s, and the appearance of a new predator, the Nile perch (Witte et al., 1990). The decreased body depth of the dwarfed fish was hypothesised to be a result of increased swimming activity because of predation pressure.

The underlying hypothesis of this study, based on the work of Meyer (1987) and Wimberger (1991, 1992) on New World cichlids, was that feeding modes required for ingestion of two diets would result in a morphological difference between the two groups through dynamic bone remodeling. The purposes of this study were to: (1) investigate feeding mode induced phenotypic plasticity of three species of mouth brooders from Lake Malaŵi, *Labeotropheus fulleborni* Ahl, *Melanochromis auratus* (Boulenger), and *M. pyrsonotos*; (2) compare these results with the plasticity observed in Old World substrate spawning *Tilapia mariae* Boulenger (spotted tilapia) and the New World substrate spawning cichlid, *Herichthys cyanoguttatum* (Baird and Girard) (Rio Grande cichlid); and, (3) test the hypothesis that observed morphological trends were due to mode of feeding rather than dietary nutrition.

MATERIALS AND METHODS

Wild-caught adults were bred in the laboratory, and broods were collected and randomly split in two feeding groups to block for genetic effects. One group of each brood was fed brine shrimp naupli of *Artemia* species, which requires a suction mode of feeding, whereas the second group was fed commercial flake food, which requires a biting mode of feeding (Meyer, 1987). Three broods of *M. pyrsonotos* (69 individuals), three broods of *M. auratus* (73 individuals), three broods of *L. fuelleborni* (64 individuals), one brood of *H. cyanoguttatum* (66 individuals), and two broods of *T. mariae* (50 individuals) were raised on these diets. Temperature, photoperiod, substrate, and aeration were kept constant among aquaria. Aquaria were cleaned frequently to prevent grazing of algal growth.

Following 5 months to 1 year of feeding (all young were raised until approximately 50 mm; however substrate spawning young, which require a longer period of time to reach a given size, were usually raised for 9-12 months, whereas mouth brooding young were typically raised for 5-8 months), the broods were anaesthetised and subsequently preserved in a 10% formalin solution. After a week of formalin fixation, the fish were placed in permanent storage in 70% ethanol. A se-

ries of head and body truss measurements (Barel et al., 1977) were made on each individual using dial calipers and JAVA image analysis software.

Significant ($P < 0.05$) differences of standard lengths between feeding modes of each brood were compared using ANOVA. To investigate feeding mode-induced phenotypic plasticity of three species of mouth brooders from Lake Malaŵi, the following head measurements were recorded for each brood: head length, lower jaw length, snout length, postorbital head length, horizontal eye diameter, vertical eye diameter, pre-orbital depth, cheek depth, and head depth. Data were analysed using sheared principal components analysis (SPCA), developed by Humphries et al. (1981). Sheared principal components analysis restricts variation due to size to the first principal component, so that the sheared second and third principal components are strictly shape related. Such an analysis, which ordinates factors independently of a main linear ordination (Reyment et al., 1984), permitted the delineation of shape irrespective of size, without having to rely on the use of ratios (Atchley, 1978; Mosimann and James, 1979; Humphries et al., 1981; Reyment et al., 1984; Bookstein et al., 1985). The covariance matrix was factored in the calculation of all sheared principal components.

Each brood was analysed separately. Differences among feeding groups for each brood of each species were illustrated by plotting the sheared second principal component (SPCII) against the sheared third principal component (SPCIII). If these clusters overlapped, a MANOVA was used to determine if the clusters formed by the minimum polygons of the sheared PCA scores for each treatment of each brood were significantly different ($P < 0.05$).

To compare the results observed in the Lake Malaŵi cichlids with substrate spawning cichlids, we collected and analysed data, as described above, using an Old World substrate-spawning cichlid, *T. mariae* Boulenger (spotted tilapia), and the New World substrate-spawning cichlid, *H. cyanoguttatum* (Baird and Girard) (Rio Grande cichlid). In order to determine whether mouth-brooding restricts head-shape plasticity in cichlids, we compared the average deviation (mm) among feeding groups with significantly loaded head-shape characters.

The hypothesis that head morphology changes were due to mode of feeding rather than nutrition was analysed in *Metriaclima prysonotos* using a flake food designed specifically for this project by O.S.I., Marine Lab., Inc., Burlingame, CA, USA. It was comprised of brine shrimp with a small amount of starch to hold the flake together, without any added vitamins. This flake, therefore, required a biting mode of feeding, but was nutritionally comparable to brine shrimp, which requires a suction mode of feeding. The flakes did not differ in consistency or integrity. One brood of *M. pyrsonotos* was randomly divided among two dietary treatments: (1) commercial flake food or (2) O.S.I. brine shrimp flake food, and a second *M. pyrsonotos* brood was raised on: (1) brine shrimp or (2) O.S.I. brine shrimp flake food. Fish were maintained on their respective diets for a period of 6 months, and shape analyses were conducted as above.

RESULTS

Head morphology of Lake Malaŵi cichlids differed between feeding groups. When the SPCII was plotted against the SPCIII of the head morphometrics, the minimum polygon clusters that were formed for each of the two treatments (brine shrimp vs. commercial flake food) in each of the three broods of each of the Lake Malaŵi cichlids were significantly ($P < 0.05$) different from each other (figs. 1-3, broods with the highest number for each species are pictured). The most heavily loaded characters were pre-orbital depth, snout length, lower-jaw length, post-orbital head length, and cheek depth (tables 1-3). In eight of these nine broods, lower jaw length was one of the three variables that had the highest loadings in either SPCII or SPCIII. When these variables were each plotted against standard length, there was no indication that any of the variables were impacted by allometric growth (e.g., fig. 4).

   The minimum polygon clusters formed by plotting SPCAII versus SPCAIII for head morphometrics of the two treatments of *T. mariae*, the Old World substrate-spawning species, were not significantly different ($P > 0.05$) for either of the two broods (table 4; fig. 5a, b).

   The minimum polygon clusters formed by plotting SPCAII versus SPCAIII of the two treatments for the head morphometrics of *H. cyanoguttatum*, the New World substrate-spawning species, were significantly different ($P < 0.05$; table 5; fig. 6).

   Four head-shape characters, lower jaw length, preorbital depth, snout length, and post-orbital head length, were highly loaded in *H. cyanoguttatum* and Lake Malaŵi mouth-brooding species. A plot of the average deviation (mm) between feeding groups for these four characters in *L. fulleborni, M. auratus*, and *M. pyrsonotos*, the
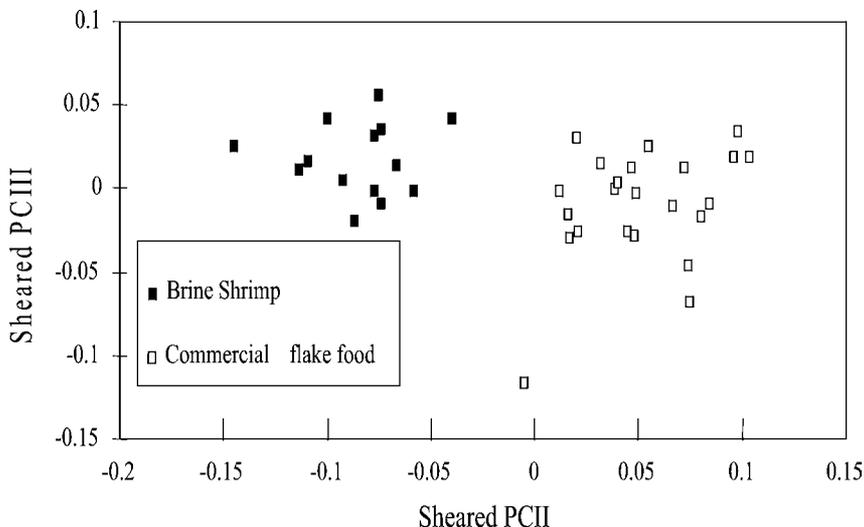

Figure 1. Plot of sheared PCII versus PCIII of the head morphometric data of *Labeotropheus fulleborni* brood 1 fed brine shrimp and flake food.
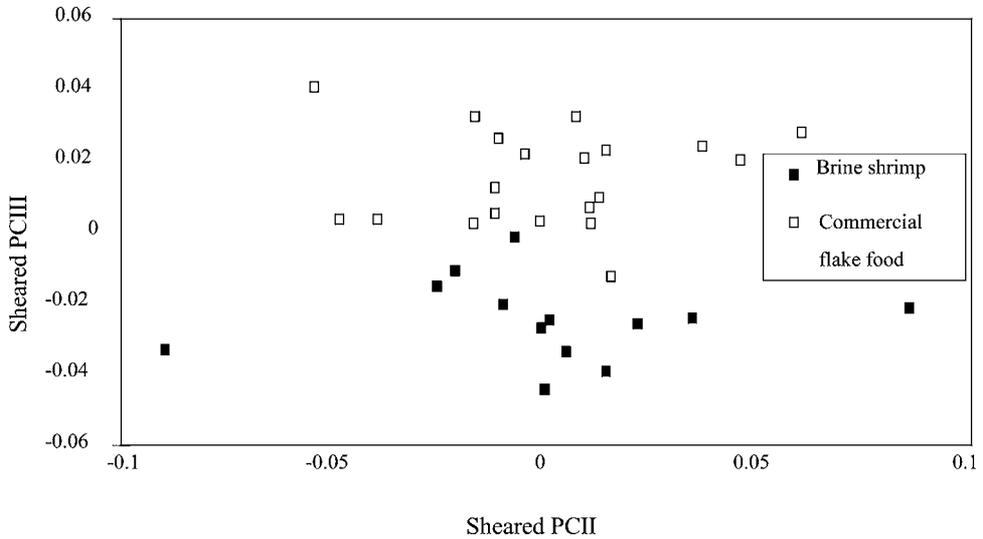
Figure 2. Plot of sheared PCII versus PCIII of the head morphometric data of *Melanochromis auratus* brood 2 fed brine shrimp and flake food.
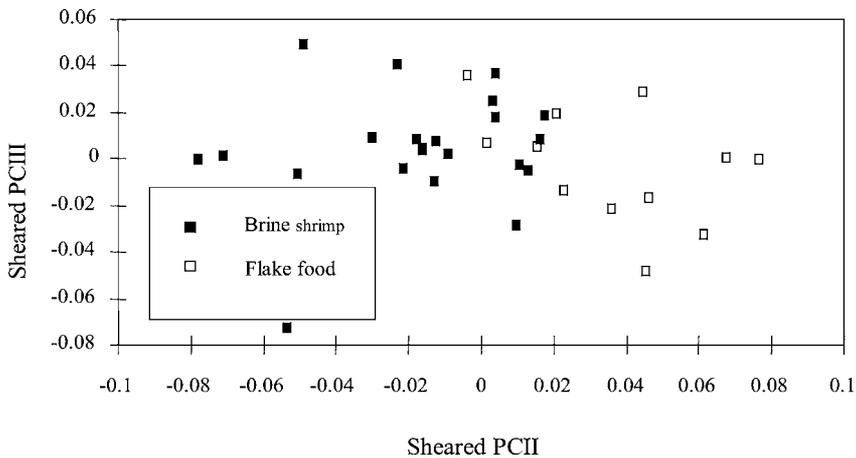

Figure 3. Plot of sheared PCII versus PCIII of the head morphometric data of *Metriaclima pyrsonotos* brood 2 fed brine shrimp and flake food.

Old World mouth-brooding cichlids, as compared to *H. cyanoguttatum*, indicated that mouth-brooding may inhibit phenotypic plasticity of head shape in Old World haplochromine cichlids (fig. 7). Although there were no observed differences in plasticity of lower jaw length, deviation between dietary groups in preorbital depth, snout length, and post-orbital head length was substantially less among mouth-brooding cichlids than in the *H. cyanoguttatum* brood.

For the *M. pyrsonotos* brood in which one-half of the brood was fed commercial flake food and the other half brine shrimp flake food, the minimum polygon clusters

Table 1.
Head morphometric measures and highest variable loadings of *Labeotropheus fuelleborni* broods. Means and standard deviations for individuals fed brine shrimp are listed on the first line, and those fed flake food are on the second line. Asterisks indicate significant differences ($P < 0.05$) between feeding groups, and sample sizes are given in parentheses.

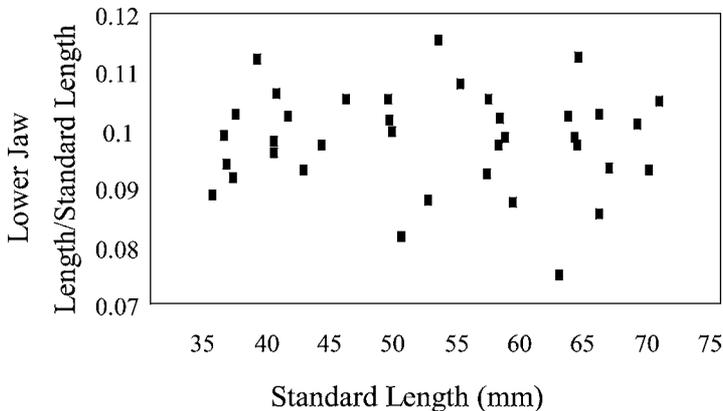| Sheared PCII Character	Mean	Std. Dev.	Loading	Sheared PCIII Character	Mean	Std. Dev.	Loading
Percent head length				**Percent head length**			
*Brood 1 (14, 23)							
Lower jaw length	28.8	1.93	−0.742	Cheek depth	31.2	2.12	−0.794
	29.8	*3.16*			*32.9*	*3.75*	
Preorbital depth	20.2	1.68	0.473	Preorbital depth	20.2	1.68	0.405
	22.4	*1.42*			*22.4*	*1.42*	
Cheek depth	31.2	2.12	0.395	Vertical eye diam.	28.9	2.43	−0.313
	32.9	*3.75*			*26.5*	*1.68*	
*Brood 2 (2, 3)							
Cheek depth	30.7	0.30	0.870	Lower jaw length	29.4	0.88	−0.671
	37.2	*2.26*			*32.7*	*3.19*	
Preorbital depth	21.0	3.11	−0.286	Horizontal eye diam.	28.1	2.74	−0.546
	25.8	*2.26*			*24.5*	*0.55*	
Head length	32.0	0.93	0.184	Preorbital depth	21.0	3.11	0.307
	31.6	*1.42*			*25.8*	*2.26*	
*Brood 3 (6, 16)							
Preorbital depth	20.6	2.46	0.816	Lower jaw length	29.1	1.84	−0.723
	22.9	*1.48*			*29.2*	*1.68*	
Vertical eye diam.	28.0	1.67	−0.358	Vertical eye diam.	28.0	1.67	−0.417
	25.5	*1.38*			*25.5*	*1.38*	
Lower jaw length	29.1	1.84	−0.293	Preorbital depth	20.6	2.46	−0.308
	29.2	*1.68*			*22.9*	*1.48*	

Figure 4. Plot of standard length (SL) versus lower jaw length/SL of *Labeotropheus fulleborni* brood 1.

Table 2.
Head and body morphometric measures and highest variable loadings of *Melanochromis auratus* broods. Means and standard deviations for individuals fed brine shrimp are listed on the first line, and those fed flake food are on the second line. Asterisks indicate significant differences ($P < 0.05$) between feeding groups, and sample sizes are given in parentheses.

Sheared PCII Character	Mean	Std. Dev.	Loading	Sheared PCIII Character	Mean	Std. Dev.	Loading
Percent head length				**Percent head length**			
*Brood 1 (6, 16)							
Snout length	32.0	1.10	0.569	Preorbital depth	19.7	1.00	−0.905
	31.7	*1.89*			*17.7*	*1.00*	
Lower jaw length	28.0	0.83	−0.344	Cheek depth	68.2	1.73	0.241
	29.0	*1.48*			*70.1*	*1.06*	
Head depth	89.9	2.68	−0.322	Head depth	89.9	2.68	0.200
	88.1	*3.53*			*88.1*	*3.53*	
*Brood 2 (14, 20)							
Preorbital depth	17.3	1.78	−0.855	Horizontal eye diam.	31.7	1.26	−0.567
	19.0	*1.66*			*28.2*	*1.28*	
Lower jaw length	28.6	1.07	0.233	Snout length	28.2	1.80	0.538
	30.4	*0.93*			*31.6*	*1.12*	
Cheek depth	70.6	1.39	0.214	Vertical eye diam.	29.8	1.05	−0.426
	69.4	*2.12*			*26.9*	*1.18*	
*Brood 3 (9, 8)							
Horizontal eye diam.	16.9	2.25	−0.655	Preorbital depth	28.0	1.77	0.531
	18.6	*1.68*			*28.0*	*1.89*	
Preorbital depth	28.0	1.77	0.481	Vertical eye diam.	28.0	2.02	0.510
	28.0	*1.89*			*28.2*	*1.39*	
Lower jaw length	26.8	1.68	−0.172	Cheek depth	29.4	1.17	−0.452
	28.9	*0.86*			*30.1*	*1.78*	

formed by plotting SPCAII versus SPCAIII for head morphometrics were not significantly ($P > 0.05$) different (table 6; fig. 8a).

For the *M. pyrsonotos* brood in which one-half of the brood was fed live brine shrimp and the other half fed brine shrimp flake food, the minimum polygon clusters formed by plotting SPCAII vs. SPCAIII of the head morphometrics were significantly ($P < 0.05$) different (table 7; fig. 8b).

Size, as indicated by standard length, was different for many feeding modes (table 8). *Herichthys cyanoguttatum* and *L. fulleborni* fed flake food were significantly ($P < 0.05$) larger than those fed live brine shrimp, as were two of three broods of *M. auratus*. The third brood of *M. auratus* was not significantly different between feeding modes. The part of one brood of *M. prysonotos* fed live brine shrimp was significantly larger than the siblings that were fed flake food; there was no significant difference ($P > 0.05$) in the feeding modes of the other two broods. The portion of the brood of *M. prysonotos* fed live brine shrimp was significantly

Table 3.
Head and body morphometric measures and highest variable loadings on *Metriclima prysonotus*. Means and standard deviations for individuals fed brine shrimp are listed on the first line, and those fed flake food are on the second line. Asterisks indicate significant differences ($P < 0.05$) between feeding groups, and sample sizes are given in parentheses.

Sheared PCII Character	Mean	Std. Dev.	Loading	Sheared PCIII Character	Mean	Std. Dev.	Loading
Percent head length				**Percent head length**			
*Brood 1 (12, 12)							
Postorbital head	52.6	6.92	−0.028	Preorbital depth	20.0	2.23	0.570
length	50.8	7.69			19.9	3.77	
Snout length	26.6	2.34	−0.025	Snout length	26.6	2.34	0.537
	25.4	4.37			25.4	4.37	
Head length	33.8	1.29	−0.023	Postorbital head	52.6	6.92	−0.378
	34.1	1.89		length	50.8	7.69	
*Brood 2 (22, 13)							
Preorbital depth	22.4	2.51	−0.791	Snout length	28.8	3.07	0.687
	21.5	2.91			26.2	2.63	
Snout length	28.8	3.07	0.506	Vertical eye diam.	25.5	2.67	−0.474
	26.2	2.63			27.0	2.26	
Lower jaw length	27.0	2.96	0.301	Preorbital depth	22.4	2.51	0.309
	25.0	3.33			21.5	2.91	
*Brood 3 (5, 5)							
Preorbital depth	21.1	2.87	−0.878	Cheek depth	23.7	2.14	0.644
	18.1	2.34			24.6	4.67	
Lower jaw length	30.5	1.27	0.274	Snout length	32.5	1.69	−0.624
	31.7	1.30			30.2	2.07	
Horizontal eye	28.3	0.47	0.236	Lower jaw length	30.5	1.27	0.284
diam.	30.9	1.64			31.7	1.30	

($P < 0.05$) larger than the portion fed brine shrimp flake food. The portion of the brood of *M. prysonotos* fed commercial flake food was significantly ($P < 0.05$) larger than that portion fed flake brine shrimp.

DISCUSSION

In many cases, there was no overlap between the clusters formed when the sheared second principal components were plotted against the sheared third principal components of the two feeding modes of certain broods (e.g., figs. 1, 2). Historically, allopatric populations, which exhibited such differentiation, were regarded as separate species (Stauffer and McKaye, 2001). Thus, feeding mode induced phenotypic plasticity resulted in full siblings that were as different morphologically as sister species. Hanken (1983) demonstrated that relatively minor alterations in non-skeletal head regions of salamanders may effect a major change in overall head morphology. The
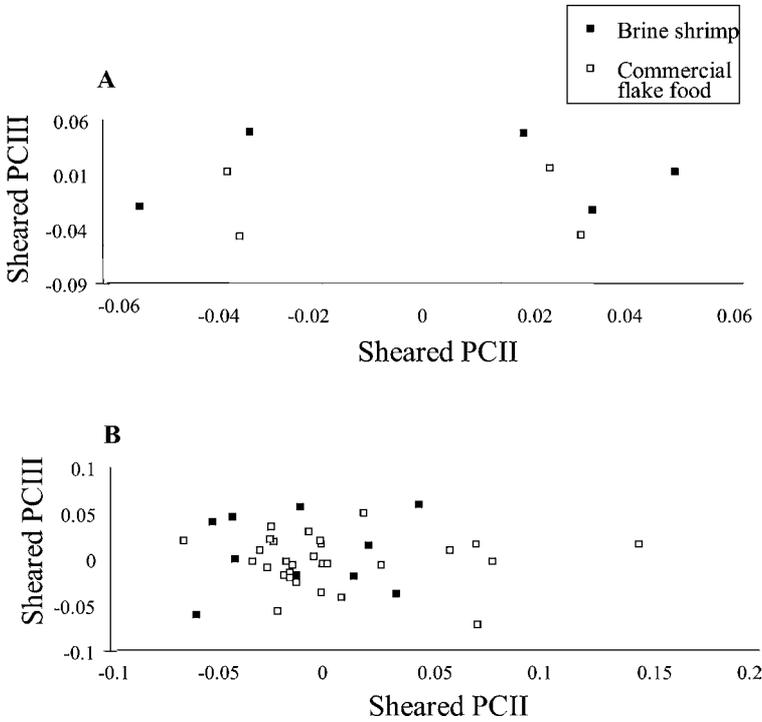
Figure 5. Plot of sheared PCII versus PCIII of the head morphometric data of *T. mariae* brood 1 (A) and brood 2 (B) fed brine shrimp and flake food.
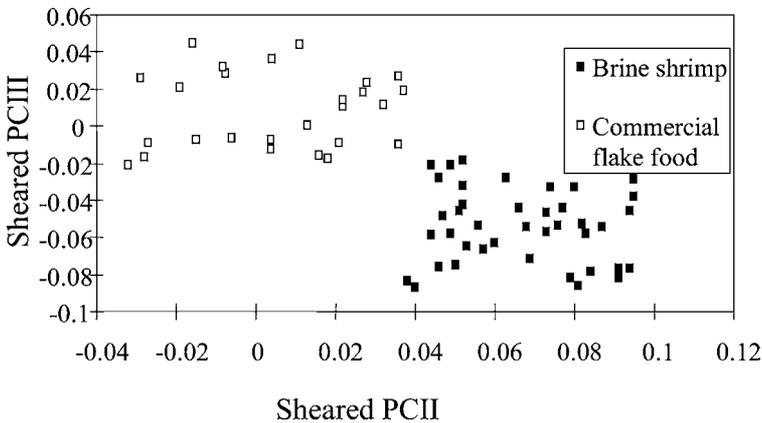

Figure 6. Plot of sheared PCII versus sheared PCIII of the head morphometric data of *H. cyanoguttatum* brood 1 fed brine shrimp and flake food.

direction of the plasticity is similar to that found by Meyer (1987), with those individuals fed brine shrimp having longer, narrower heads than those fed flake food. In particular, lower-jaw length and preorbital depth were typically smaller and postorbital head length and snout length typically larger in the brine-shrimp groups than

Table 4.
Head and body morphometric measures and highest variable loadings of *Tilapia mariae* broods. Means and standard deviations for individuals fed brine shrimp are listed on the first line, and those fed flake food are on the second line. Asterisks indicate significant differences ($P < 0.05$) between feeding groups, and sample sizes are given in parentheses.

Sheared PCII Character	Mean	Std. Dev.	Loading	Sheared PCIII Character	Mean	Std. Dev.	Loading
Percent head length				**Percent head length**			
*Brood 1 (5, 4)							
Lower jaw length	26.1	1.41	−0.633	Preorbital depth	18.4	1.07	0.540
	31.6	*2.74*			*22.4*	*1.70*	
Horizontal eye diam.	38.4	1.96	0.502	Horizontal eye diam.	38.4	1.96	−0.525
	31.5	*3.68*			*31.5*	*3.68*	
Vertical eye diam.	35.7	1.96	0.354	Postorbital head	38.6	1.85	0.464
	30.8	*2.26*		length	*38.9*	*1.24*	
*Brood 2 (29, 12)							
Lower jaw length	23.6	1.88	−0.896	Preorbital depth	19.5	1.71	−0.838
	26.4	*2.89*			*22.3*	*1.53*	
Postorbital head	38.5	2.37	0.224	Postorbital head	38.5	2.37	0.357
length	*38.4*	*1.18*		length	*38.4*	*1.18*	
Preorbital depth	19.5	1.71	0.220	Cheek depth	31.8	2.06	0.344
	22.3	*1.53*			*31.7*	*1.77*	

Table 5.
Head and body morphometric measures and highest variable loadings of *Herichthys cyanoguttatum* broods. Means and standard deviations for individuals fed brine shrimp are listed on the first line, and those fed flake food are on the second line. Asterisks indicate significant differences ($P < 0.05$) between feeding groups, and sample sizes are given in parentheses.

Sheared PCII Character	Mean	Std. Dev.	Loading	Sheared PCIII Character	Mean	Std. Dev.	Loading
Percent head length				**Percent head length**			
*Brood 1 (40, 26)							
Preorbital depth	17.2	2.06	−0.740	Postorbital head	44.5	2.34	−0.725
	21.7	*3.35*		length	*42.1*	*3.05*	
Postorbital head	44.5	2.34	0.373	Snout length	28.8	2.09	0.359
length	*42.1*	*3.05*			*33.8*	*3.32*	
Lower jaw length	27.3	1.19	0.342	Preorbital depth	17.2	2.06	−0.320
	28.6	*2.08*			*21.7*	*3.35*	

the flake-food groups. The hypothesis that changes in head morphology are due to the mode of feeding rather than dietary nutrition was supported by the results of the feeding experiments using the brine shrimp flake food. The head morphology of the *M. pyrsonotos* brood fed brine shrimp flakes and commercial flakes was not signif-
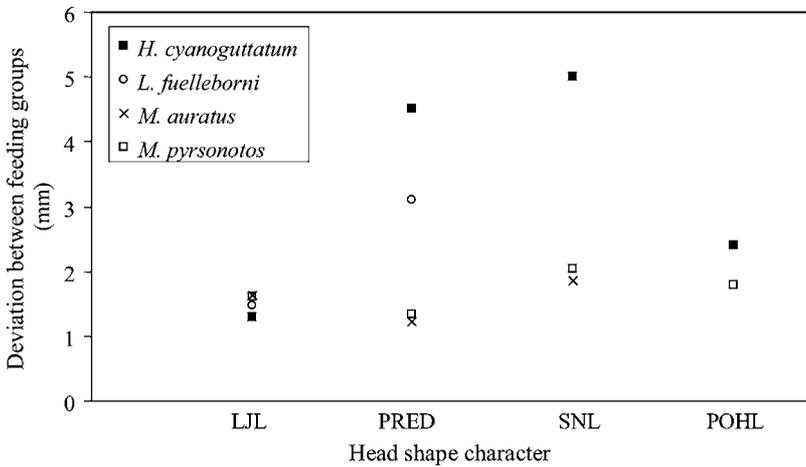
Figure 7. Plot of the mean deviation (mm) between feeding groups for four head-shape characters in *Labeotropheus fulleborni, Melanochromis auratus, Metriaclima pyrsonotos* and *Hererichthys cyanoguttatum* (LJL = lower jaw length, PRED = pre-orbital depth, SNL = snout length, and POHL = postorbital head length).

Table 6.

Head and body morphometric measures and highest variable loadings of *Metriaclima pyrsonotos.* Means and standard deviations for individuals fed brine shrimp flake food are listed on the first line, and those fed commercial flake food are on the second line. Asterisks indicate significant differences ($P < 0.05$) between feeding groups, and sample sizes are given in parentheses.

Sheared PCII Character	Mean	Std. Dev.	Loading	Sheared PCIII Character	Mean	Std. Dev.	Loading
Percent head length				**Percent head length**			
*Brood 1 (16, 10)							
Preorbital depth	22.7	3.00	−0.804	Vertical eye diam.	32.5	1.69	0.738
	20.8	*2.60*			*30.2*	*2.07*	
Snout length	34.8	4.27	0.397	Horizontal eye diam.	27.6	1.61	0.483
	28.7	*2.76*			*28.9*	*2.40*	
Postorbital head length	40.6	0.72	0.253	Lower jaw length	32.4	1.62	−0.403
	39.9	*1.88*			*32.8*	*2.47*	

icantly different ($P > 0.05$; same feeding mode), whereas significant ($P < 0.05$) differences existed between the brood fed brine shrimp and brine shrimp flakes (different feeding modes).

Moreover, one could argue that the changes reported herein could be a result of changes in scale, which result in allometric growth (Strauss, 1984). Certainly other fishes, such as dwarf *Coregonus* species, exhibit changes in body shape which may be related to differences in size (Shields and Underhill, 1993), as well as changes in spawning times and life span (Swardson, 1949, 1950; Fenderson, 1964; Lindsey et al., 1970; Smith and Todd, 1984). Although we observed differences in size between

Table 7.

Head and body morphometric measures and highest variable loadings of *Metriaclima pyrsonotos*. Means and standard deviations for individuals fed brine shrimp are listed on the first line, and those fed brine shrimp flake food are on the second line. Asterisks indicate significant differences ($P < 0.05$) between feeding groups, and sample sizes are given in parentheses.

Sheared PCII Character	Mean	Std. Dev.	Loading	Sheared PCIII Character	Mean	Std. Dev.	Loading
Percent head length				**Percent head length**			
*Brood 1 (6, 6)							
Preorbital depth	24.0	1.99	−0.624	Snout length	32.8	1.50	0.654
	20.3	*2.10*			*31.6*	*2.70*	
Horizontal eye diam.	26.8	2.95	−0.479	Cheek depth	34.0	1.97	−0.518
	27.6	*2.26*			*35.7*	*2.36*	
Snout length	32.8	1.50	0.370	Lower jaw length	33.3	1.91	−0.340
	31.6	*2.70*			*35.3*	*2.28*	

Table 8.

Comparisons of standard lengths (mm) between feeding broods.

Species	Live brine shrimp	Commercial flake food	Flake brine shrimp
Herichthys cyanoguttatum[*]	29.2	48.0	
Labeotropheus fulleborni[*]	41.4	61.0	
Labeotropheos fulleborni[*]	60.0	83.4	
Labeotropheos fulleborni[*]	41.0	64.3	
Melanochromis auratus	15.9	15.7	
Melanochromis auratus[*]	34.1	40.1	
Melanochromis auratus[*]	42.6	47.3	
Metriaclima prysonotos[*]	31.6	25.4	
Metriaclima prysonotos	36.3	35.7	
Metriaclima prysonotos	39.6	33.6	
Metriaclima prysonotos[*]		59.7	44.4
Metriaclima prysonotos[*]	55.8		48.0
Tilapia mariae[*]	47.2	89.7	
Tilapia mariae[*]	39.1	56.7	

[*]Indicates significant differences between feeding modes ($P < 0.05$).

feeding modes within broods, the fact that there was no relationship between any of the head morphometrics and standard length (e.g., fig. 4) refutes this hypothesis. Moreover, significant differences in standard length were observed for both broods of *T. marie;* however, no differences in shape of individuals exposed to different feeding modes was observed for this species.

The magnitude of head shape plasticity observed in the New World substrate-spawning cichlid, *H. cyanoguttatum*, was greater than that observed in the Old World haplochromine cichlids. Thus, these data suggest that mouth brooding may constrain the plasticity of jaw morphology in the latter; however, the comparison
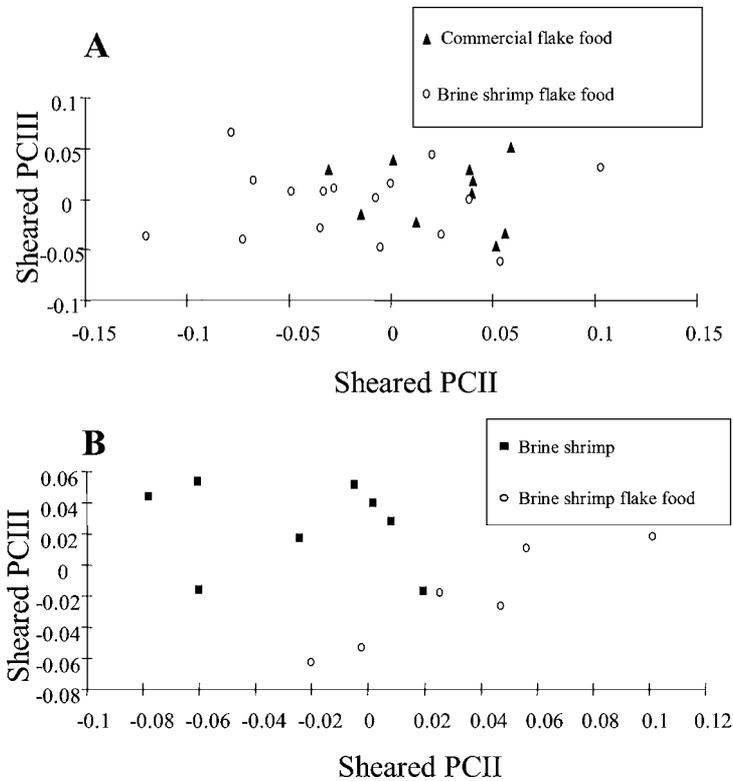
Figure 8. Plot of sheared PCII versus PCIII of the head morphometric data of *Metriaclima pyrsonotos* fed commercial flake food and brine-shrimp flake food (A) and brine shrimp and brine-shrimp flake food (B).

with *T. mariae* may indicate that New World cichlids simply exhibit more plasticity than do Old World cichlids. Similar experiments should be conducted on Lake Tanganyika mouth brooders vs. substrate spawners.

Implications for alpha-level taxonomy

Because of the current lack of detectable fixed genetic differentiation among closely related Lake Malaŵi cichlids (McKaye et al., 1982; Moran and Kornfield, 1993; Stauffer et al., 1993), most haplochromine cichlids are described on the basis of morphology alone. For example, characteristics of the pharyngeal bone and jaw morphology have often played an important part in species descriptions of Old World cichlids (Greenwood, 1981). Stauffer and Boltz (1989) described a new species of *Metriaclima* from Lake Malaŵi and found that the characters differentiating it from congeners (cheek depth, post-orbital head length, pre-orbital depth, and size of the dentigerous area of the pharyngeal bone) were ones that could be influenced by feeding mode (Kornfield et al., 1982; Meyer, 1987; Wimberger, 1991, 1992; Stauffer et al., 1995). Similar results were found in the genus *Petrotilapia*

(Marsh, 1983; Stauffer and van Snik, 1996). Conversely, Sturmbauer and Meyer (1993) note that heterospecific populations are particularly prone to homoplasy with respect to character states associated with foraging. Therefore, it is necessary to study the ecology, behavior, genetics, and breeding coloration of these species in order to substantiate their specific status as suggested by morphological data (Stauffer and McKaye, 1986; Stauffer and Boltz, 1989).

Implications for rapid radiation of haplochromine cichlids

Wimberger (1991) considered phenotypic plasticity an evolutionary factor that results in morphological diversification. Vertebrate resource polymorphisms may significantly contribute to population divergence and speciation (Smith and Skulason, 1996). Skulason and Smith (1995) suggest that resource polymorphisms are important entities in the initial phases of speciation and Day et al. (1994) concluded that phenotypic plasticity is evolutionarily labile. Rice and Hostert (1993) further suggest that if traits important in resource use are associated with those important in isolation, then reproductive isolation can occur via genetic hitchhiking. Certainly, differences in mouth shape, eye size (Lindsey, 1981) gill-raker morphology (Magnuson and Heitz, 1971; Chapman et al., 2000), and pharyngeal-mill morphology (Liem, 1974, 1979), can all contribute to feeding diversification, which in turn can lead to habitat preferences and isolation of selected morphs. In his discussion of ecological speciation, Schluter (1996) suggests that mating preferences may diverge if the selection criteria are associated genetically with phenotypic traits. Differences in phenotypes can be as dramatic as those found in four sympatric morphs of the arctic char, *Salvelinus alpinnus* (Hindar, 1994), trophic morphs of the tiger salamander, *Ambystoma tigrinum* (Collins, 1981), and larval morphs of the spadefoot toad, *Scaphiopus* spp. (Pomeroy, 1981). Morphological plasticity, however, must be linked with parameters that promote genetic isolation (e.g., behavioural barriers, habitat isolation) in order for it to influence speciation rates (Lovell, 1989). Robinson and Wilson (1994) provide such evidence by stating that genetic differentiation is linked to phenotypic differences in 19 of 48 lacustrine fish species. Moreover, McPhail (1984, 1994) and Lavin and McPhail (1987) have demonstrated that phenotypic differences between benthic and pelagic forms of sticklebacks persist when different morphs are cultured in the laboratory and provided with the same diet.

The driving mechanism for the speciation events which led to the explosive radiation of the haplochromine cichlids in the Great Lakes of Africa is undiscovered; the two most widely proposed methods are allopatric speciation accelerated by fluctuation in lake levels (Fryer, 1959; Marlier, 1959; Fryer and Iles, 1972; Greenwood, 1974, 1981, 1982; McKaye and Gray, 1984) and intrinsic isolating mechanisms such as assortative mating (Kosswig, 1947, 1963; Bush, 1975; McKaye, 1978, 1980; McKaye and Stauffer, 1986, Stauffer et al., 2002). Irrespective of the mechanism primarily responsible for the high diversity, the relationship between phenotypic morphs and speciation is currently unknown. Unquestionably, a colonising species possessing a high degree of phenotypic plasticity may have a selective advantage be-

cause of the ability to exploit different resources in differing environments (Lewontin, 1965), and phenotypic plasticity may be an important factor which allows so many species to coexist in the African lakes. A necessary first step, in assessing the relationship, if any, between polymorphism and speciation is to determine the extent that environmental influences have on the morphology of natural populations. For example, one New World cichlid, *H. minckleyi*, has achieved trophic radiation through polymorphism (Sage and Selander, 1975; Kornfield et al., 1982). A strong pharyngeal bone with molariform teeth was found in the form feeding on snails, whereas a less developed pharyngeal bone with villiform teeth was found in the form feeding on softer food items (Kornfield et al., 1982). In this case, the environment was not only the broker of selection, but was also the agent of development that directed the range of phenotypes that were created (West-Eberhard, 1989).

The observed plasticity in the rock-dwelling Malaŵi cichlids may have facilitated their extensive trophic radiation and subsequent explosive speciation. Lake Malaŵi is the most speciose lake in the world with regard to fishes (Kocher et al., 1993). Certainly variation, which supplies the raw material for evolutionary change, originates with both the genotype and the phenotype (Stearns, 1989). While some argue that phenotypic plasticity retards evolution (Wright, 1931), Dobshansky (1951) theorised that phenotypic modulation provided the necessary changes during evolution. Plasticity can be considered as an evolutionary factor that results in morphological diversification (Wimberger, 1991). If the environmental stimulus directing the plasticity is fluctuating, selection for maintenance of plasticity may occur. If the environmental stimulus is constant and directional, however, genetic assimilation of the new phenotype could occur over time (Waddington, 1975; Chapman et al., 2000). Trophic polymorphism has been proposed as an intermediate step towards speciation (Sage and Selander, 1975). Polymorphism and genetic assimilation of plastic traits may be a speciation mechanism in Old World haplochromine cichlids. Although additional studies of the phenotypic plasticity of Old World *Tilapia* species are needed, the absence of explosive radiation, as observed in Malaŵi haplochromine species, in the substrate spawning *Tilapia* species may be related to the reduced level of plasticity observed in *T. mariae*.

Alternatively, other authors (Wimberger, 1994) have suggested that although phenotypic plasticity itself does not contribute to speciation, if coupled with factors promoting reproductive isolation of morphs, such as assortative mating, speciation may result. Sexual selection has been suggested as a factor in the accelerated speciation of many of the Lake Malaŵi cichlids (Dominey, 1984; McKaye, 1991), and if sexual selection for particular trophic morphs occurs, speciation can be accelerated (Dominey, 1984; O'Donald and Majerus, 1985). If Wimberger (1994) is correct, phenotypic plasticity may have provided the raw material on which assortative mating cued.

Many authors have postulated that behavioural characteristics are frequently the initial part of the phenotype which evolves (Mayr, 1963, 1974; Corning, 1974; Wyles et al., 1983; Weislo, 1989). West-Eberhard (1989) summarised several

reasons why plastic traits may initiate new directions in the evolution of a species and concluded that labile plastic traits, such as behaviour, are more likely to result in a favorable variant. Stauffer et al. (1995) postulated that colour forms of many of the Lake Malaŵi rock-dwelling cichlids as well as the bowers (spawning platforms) of the sand-dwelling cichlids are manifestations of behavioural characteristics and can be used to delimit sibling species; such circumstantial evidence supports the theory that phenotypic plasticity aided in the rapid radiation of the Old World cichlids.

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