Mechanisms of rapid sympatric speciation by sex reversal and sexual selection in cichlid fish

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Abstract

Mechanisms of speciation in cichlid fish were investigated by analyzing population genetic models of sexual selection on sex-determining genes associated with color polymorphisms. The models are based on a combination of laboratory experiments and field observations on the ecology, male and female mating behavior, and inheritance of sex-determination and color polymorphisms. The models explain why sex-reversal genes that change males into females tend to be **X**-linked and associated with novel colors, using the hypothesis of restricted recombination on the sex chromosomes, as suggested by previous theory on the evolution of recombination. The models reveal multiple pathways for rapid sympatric speciation through the origin of novel color morphs with strong assortative mating that incorporate both sex-reversal and suppressor genes. Despite the lack of geographic isolation or ecological differentiation, the new species coexists with the ancestral species either temporarily or indefinitely. These results may help to explain different patterns and rates of speciation among groups of cichlids, in particular the explosive diversification of rock-dwelling haplochromine cichlids.

Introduction

Cichlid fishes in the African great lakes speciated more rapidly than any other vertebrates in the history of the earth. One or a few ancestral species in Lake Victoria 12,400 years ago produced more than 500 modern species of haplochromine cichlids (Meyer et al., 1990; Johnson et al., 1996; Seehausen, 1996), whereas other groups of cichlids speciated much more slowly (Seehausen, 2000). Key morphological innovations promoted adaptive diversification of cichlids (Galis & Drucker, 1996). However, closely related species of haplochromine cichlids usually are rather similar ecologically (Bouton, Sechausen & Van Alphen, 1997; Seehausen & Bouton, 1997; Genner et al., 1999) and frequently are sympatric with conspicuous differences in coloration (Seehausen & van Alphen, 1999). Sexual selection played a major role in cichlid speciation (Seehausen, Van Alphen & Witte, 1997; Knight et al., 1998; van Oppen et al., 1998; Turner, 1998; Wilson, Noack-Kunnann & Meyer, 2000) as possibly did changes in sex determination (Hickling, 1960; Hammerman & Avtalion, 1979; Trewavas, 1983; Crapon de Caprona & Fritzsch, 1984; Seehausen, Van Alphen & Lande, 1999).

For example, field observations and laboratory experiments on a highly polymorphic cichlid species from Lake Victoria, *Neochromis omnicaeruleus*, suggest that this represents one original species and two incipient species which are sympatric and ecologically indistinguishable, but partially isolated reproductively by both male and female mating preferences (Seehausen, Van Alphen & Lande, 1999). In each incipient species some **X** chromosomes carry a dominant sex-reversal gene, *W*, that changes males to females; such chromosomes are labelled **W** and are visibly marked by blotched coloration all over the body and fins (either black and white blotched or orange and black

blotched). Each incipient species also is polymorphic for a recessive autosomal gene, M, that suppresses W. Polymorphic sex chromosomes (indicated by bold letters **W**, **X**, **Y**), as first described in the platyfish (Orzack et al., 1980; Bull, 1983), occur frequently within and among other species of African cichlids (Hickling, 1960; Hammerman & Avtalion, 1979; Trewavas, 1983; Crapon de Caprona & Fritzsch, 1984).

In many species of haplochromine cichlids blotched coloration occurs in much higher frequency in females than in males (Table 1). The ancestral coloration of the sexes for species in Table 1 is 'plain' blue or yellow in males, whereas females are cryptically brownish, with both sexes having dark vertical bars. With homomorphic **X** and **Y** chromosomes (a nondegenerate **Y** chromosome) the alternative mechanisms of **X**-linkage and recessivity, or partial sex-limited expression, of blotch genes remains a possible explanation for some of these species. However, breeding experiments with *N. omnicaeruleus* (Seehausen, Van Alphen & Lande, 1999), *Pseudotropheus zebra* (Knight, 1999) and *Paralabidochromis chilotes* from Zue (O. Sechausen, unpublished) demonstrated that blotch (both black and white, and orange and black types) is semi-dominant and strongly associated by tight linkage or pleiotropy with dominant **X**-linked sex-reversal genes, suggesting that W factors may be widespread in haplochromine cichlids.

These observations motivated us to construct population genetic models to investigate the potential for speciation by sexual selection on linked color and sex-determining genes.

X-linkage of sex reversal

Dominant female determiners, W, are likely to be **X**-linked (creating **W** chromosomes) for the following reason. Suppose that the ancestral species is male heterogametic as for most animals, with **XX** females and **XY** males (White, 1973), but that the sex chromosomes are homomorphic as in many fishes including cichlids (Kornfield, 1991). The **Y** chromosome tends to accumulate deleterious recessive mutations tightly linked to the male-determining allele, y, which initially, before the appearance of W, is always heterozygous (Charlesworth, 1991). After W appears, matings between **XY** males and **WY** females produce **YY** sons, and by recombination progeny genotypes that carry W and are homozygous for the y allele, with reduced fitness.

Recombination on the sex chromosomes therefore inhibits invasion of the population by the W allele, depending on the recombination rate. Thus tight linkage of the W allele to the original female determiner, x, facilitates the invasion of W, which then needs only a moderate selective advantage to invade (see Appendix).

A stable polymorphism of W, or any other gene, linked to the sex-determining locus that interacts with it to affect fitness will favor reduced recombination between them (Bull, 1983; Charlesworth, 1991). Suppressed recombination on the **Y** chromosome is thought to be one of the initial steps in the evolution of degenerate **Y** chromosomes (Charlesworth, 1991). A nonrecombining region on the sex chromosomes carries color markers in guppies (Haskins et al., 1970) and in the platyfish (Kalman, 1970). For this reason, and to simplify the models, we assumed a region of no recombination on the sex chromosomes, although this has not been demonstrated in cichlids. This part of the model is then equivalent to the three sex chromosome system (**W**, **X**, **Y**) in the platyfish (Orzack et al., 1980; Bull, 1983). A sufficient condition for stable polymorphism of all three sex chromosomes under random mating is a fitness advantage to **W**- females and a disadvantage of **YY** males (Orzack et al., 1980), neither of which has been demonstrated in cichlids, although they appear to be necessary ingredients for stable sympatric speciation in our model.

To this basic sex-determining system we add a novel blotched color mutation, indicated by a prime ′, linked to the **W** chromosome. There are then four types of sex chromosomes, **W**, **W′**, **X**, and **Y** inherited as alleles at a single locus. We also introduce a second unlinked locus with two alleles, m and M, that is a recessive suppressor of **W**, such that **WY**MM and **W′Y**MM are male. A third unlinked locus with two alleles, c and C, determines male and female mating preferences based on the color of potential mates. The details of this genetic system are based primarily on observations on *N. omnicaeruleus* (Seehausen, Van Alphen & Lande, 1999), supported by data on other cichlid species cited above. In some variants of the model we introduced the blotched color mutation on **X** chromosomes instead of **W** chromosomes, or allowed recombination on the sex chromosomes between W and blotch loci. The next section describes the operation of sexual selection by male and female mating preferences, and how these are affected by sex-ratio selection.

Table 1. Sex differences in frequency of blotched phenotypes in haplochromine cichlids

Lake species	Island population	Phenotype of blotch[a]	Female frequency Percentage (sample size)	Male frequency Pecentage (sample size)	Reference	Comment
Lake Victoria						
Neochromis omnicaeruleus	Makobe	WB	25.6	0.3		0% WB homozyg. female
		OB	33.3[b] (516)	0.8 (2082)	Seehausen et al., 1999	3% OB homozyg. female
	Ruti	OB	0.6 (50)	0 (300)	O.Seehausen, unpublished	
Neochromis greenwoodi		OB	8–61[b] (244)	0–3 (283)	Seehausen and Bouton, 1996	
Neochromis 'unicuspid scraper'		OB	40 (5)	0 (12)	Seehausen and Bouton, 1996	
Paralabidochromis chilotes		WB	13 (8)	0 (17)	Greenwood, 1981	
	Zue	WB	2 (44)	0 (51)	O.Seehausen, unpublished	
	Ruti	WB	100 (3)	0 (3)	O.Seehausen, unpublished	
Paralabidochromis chromogynos		WB	100 (22)	0 (7)	Greenwood, 1981	100% WB heterozyg. female
Hoplotilapia retrodens		WB	37	3		
		OB	31 (35)	0 (32)	Greenwood, 1981	
Macropleurodus bicolor		WB	30 (50)[c]	4 (50)[c]	Greenwood, 1981	
Ptyochromis sauvagei		WB	25 (42)[c]	0 (42)[c]	Greenwood, 1981	
			+ + +	+	O.Seehausen, unpublished	
'Haplochromis' barbarae		WB	50			
		OB	38 (8)	0 (1)	Greenwood, 1981	
'Haplochromis' cronus		WB	30 (3)	0 (5)	Greenwood, 1981	
Lipochromis obesus			Some (48)[c]	0 (48)[c]	Greenwood, 1981	
Lipochromis melanopterus		OB	10 (10)	0 (10)	O.Seehausen, unpublished	
Harpagochromis altigenis		WB	24 (12.5)[c]	0 (12.5)[c]	Greenwood, 1981	
Lake Kivu						
'Haplochromis' vittatus		WB	2 (319)[c]	1 (319)[c]	Snoeks, 1994	
'Haplochromis' adolphifrederici		WB	45 (11)	9 (11)	Snoeks, 1994	
'Haplochromis' paucidens		WB	59 (100)	2 (43)	Snoeks, 1994	
'Haplochromis' occultidens		WB	7 (15)	8 (12)	Snoeks, 1994	
Lake Malawi						
Pseudotropheus zebra	Nkhata	OB	++	+	Holzberg, 1978	
	Nkukute	OB	20 (432)[d]	0 (many)	Knight, 1999	Includes 4% O females[e]
	Fisheries	OB	38 (570)	0.07 (many)	Knight, 1999	Includes 21% O females
Pseudotropheus 'zebra gold'		OB	++	+	Holzberg, 1978; Knight, 1999	
Pseudotropheus callainos	Tanzania	OB	100 (many)	100 (many)	Spreinat, 1995	Both sexes almost all O[f]
Pseudotropheus estherae	Minos	OB	100 (many)	No exact figure	Konings, 1995	Almost 100% O females
	Nkungu Reef	OB	100 (many)	No exact figure	Konings, 1995	Almost 100% O females

[a]OB = orange blotched; WB = black and white blotched (Seehausen et al., 1999).

[b]Variable among populations: high in clear water, low in murky water.

[c]In the reference separate sample sizes are not provided for females and males; half the total sample is attributed to each sex here.

[d]Observations were done Scuba diving.

[e]What is referred to as O (orange) by many authors in Lake Malawi are (at least partly) homozygous OB.

[f]Referred to as W (white) by most authors, which is homologus to O (homozygous OB).

Male and female mating preferences

We generalized a model of female mate choice in polygamous species (Lande, 1981) to incorporate mating preferences by both sexes, as observed in *Neochromis omnicaeruleus* (Seehausen, Van Alphen & Lande, 1999). The importance of developing models of sexual selection where both sexes choose mates is discussed by Bergstrom and Real (2000). We suppose that mating preference by both sexes depends on the colors of potential mates (Seehausen, Van Alphen & Lande, 1999). The probability of mating between male and female genotypes is assumed to be proportional to the product of their frequencies and their mating preferences, suitably normalized so that: (i) All females mate and each female genotype produces the same expected number of zygotes. This implies that female mating preferences are selectively neutral with respect to natural and sexual selection (Lande, 1981). (ii) All male genotypes spend equal total time or effort in courtship display. Male mating preferences are manifested by courting different female types disproportionately to the female frequencies in the population, which can directly affect male mating success. The model therefore entails that male mating preferences experience direct sexual selection.

Mating preferences of both sexes, as well as color morphs, may be subject to indirect sex-ratio selection through their associations with sex-determining genes when there is a biased sex ratio in the population. Sex-ratio selection operates by favoring genotypes that produce more progeny of the rarer sex and hence more grandchildren (Fisher, 1958; Hamilton, 1967). For example, in a population with a female-biased sex ratio, the average male contributes more autosomal genes to the next generation than the average female, because every individual receives equal autosomal contributions from its mother and father.

Denote the relative preference of female genotype j for male genotype i as ψ_{ij}, and the relative preference of male genotype i for female genotype j as δ_{ij}. With the adult frequencies of female and male genotypes (after viability selection) written as p_j^* and q_i^* respectively, the frequency of matings between female genotype j and male genotype i is $\delta_{ij}^* \psi_{ij}^* p_j^* q_i^*$ where

$$\delta_{ij}^* = \delta_{ij} / \sum_k \delta_{ik} p_k^* \quad \text{and}$$

$$\psi_{ij}^* = \psi_{ij} / \sum_k \delta_{kj}^* \psi_{kj} q_k^*.$$

These normalizations imply $\sum_j \delta_{ij}^* p_j^* = 1$ and $\sum_i \psi_{ij}^* \delta_{ij}^* q_i^* = 1$ which guarantee assumptions (i) and (ii) above are satisfied. We further assume that the relative preferences of both sexes are functions of male and female colors, z_i and z_j, and preference phenotypes y_i and y_j in males and females that may differ between the sexes, $\delta_{ij} = pref[y_i z_j]$ and $\psi_{ij} = pref[y_j z_i]$, with preference function $pref[x] = x$ for $x > 0$ and $-1/x$ for $x < 0$ with $pref[0] = 1$. Parameters for discrete phenotypes were always set such that $|x|$ was never less than unity except when $x = 0$.

Dynamics of genotype frequencies under non-random mating were calculated using deterministic numerical methods, employing the Kronecker direct product to build up genomic segregation matrices from those for unlinked loci, following the method of Lande and Wilkinson (1999), with special modifications for unlinked sex-determining loci (the suppressor locus, *M*). Computations were accelerated using the sparseness of genomic segregation matrices, containing mostly zeros, by symbolically computing the recursion equations (Wolfram, 1999) to delete zero terms before numerical iteration.

Results

We found that an initial mating preference against novel colors actually facilitates their establishment, both by increasing the association between a novel color and the mating preference for it, and by providing a pool of preferred mates in the novel color morphs. A preference for the ancestral phenotype and against novel phenotypes may often exist to prevent maladaptive hybridization between preexisting species. In results reported here, the initially common allele c causes a preference for the ancestral phenotype, and the initially rare allele C causes a preference for the novel color.

In the first mechanism, **YY** males have little or no fitness disadvantage. This may occur if the effective size of the ancestral population is large enough so that deleterious mutations have not been fixed on the **Y** chromosome. Invasion of **W** and the appearance of **YY** homozygotes would then cause rapid purging of polymorphic deleterious recessive mutations from the **Y** chromosome by natural selection. In Figure 1 natural selection favoring *W* and the high fitness of **YY** males allow *W* to increase to almost 50% in females, converting sex determination in the population from male heterogamety (**XX** females and **XY**
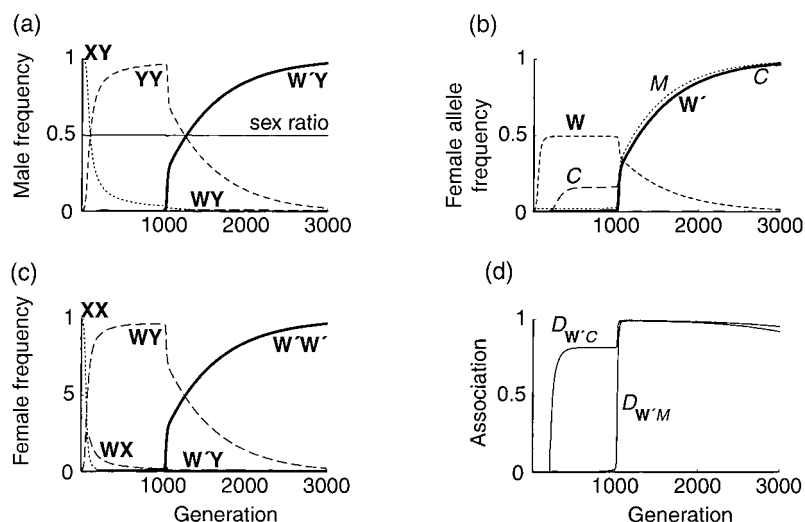
Figure 1. Change from male to female heterogamety in allopatry (with geographic isolation), followed by sympatric speciation and reversion to male heterogamety when **YY** males are fully viable. A dominant female-determining chromosome **W** invades because of a 10% fecundity advantage in females. The sex ratio (proportion of males in the population) decreases slightly during the transition from male to female heterogamety and back again (panels *a, c*). (Some rare sex chromosome genotypes are not indicated). The reversion to male heterogamety is initiated by appearance of a novel color ′ linked to **W**, with an initial frequency of 0.002 at generation 200, as if by a new mutation in a finite population, and the creation of colored males by *M*, a recessive suppressor of **W** (panel *b*). Color is additive with heterozygote phenotype $z = 0.5$ and homozygote $z = 1.0$ compared to $z = 0$ in ancestors. Mating preferences also are additive with alleles *c* and *C* having effects -30 and $+30$ respectively in both sexes. This produces, for example, ancestral mating preferences (*cc*) favoring the ancestral color over blotch heterozygotes by 30 : 1, and derived mating preferences (*CC*) favoring blotch heterozygotes over the ancestral phenotype by 1 : 30 in both sexes. Initial frequencies of *M* and *C* are 0.02 and 0.002 respectively. Association between alleles at different loci is measured by the standardized linkage disequilibrium, *D*, relative to its maximum value [Hartl & Clark, 1997] in females (panel *d*). After sudden sympatric speciation at around generation 1000 the new colored species replaces the ancestral species on a time scale of hundreds of generations.

males) to female heterogamety (**WY** females and **YY** males). During the transition the population sex ratio is nearly unbiased (Bull, 1983). Once *W* becomes established, a novel color mutation ′ is introduced at a low frequency. Color mutations linked to an **X** chromosome (or any autosome) rapidly disappear because of a disadvantage in males from preexisting female mating preferences against new phenotypes. In contrast, without a suppressor, color mutations arising on **W** chromosomes are restricted to females on which sexual selection does not act (because all females mate and are equally fecund). Males with mating preferences for the novel color morph attain greater mating success by disproportionately courting colored females that tend to be avoided by ancestral males (Figure 1(b)). This sexual selection on male mating preference is necessary for the initial increase and quasiequilibrium of **W′** and *C*, which become partially associated. The recessive suppressor *M* creates rescued males with the novel color, **W** ′*YMM*. These are the preferred mates of *C*-females, which causes *M* to slowly increase until a critical frequency is reached, triggering sudden simultaneous jumps to intermediate

nearly equal frequencies of **W′**, *M*, and *C* with almost complete association among them. This marks the origin of two distinct species with a high degree of reproductive isolation (Figure 1(d)). Sympatric speciation can thus occur rapidly, within several dozen generations. However, coexistence of the two species is transient: on a time scale of several hundred generations **W′** replaces **W** and, as the suppressor *M* approaches fixation, the population reverts from female heterogamety back to male heterogamety. In summary, this mechanism initially produces an allopatric shift from male heterogamety to female heterogamety, followed by rapid but transient sympatric speciation and replacement of the old species by the new one, with reversion to male heterogamety.

In the second mechanism, **YY** males have low fitness due to fixation of recessive deleterious mutations on the **Y** chromosome in small populations. Figure 2 illustrates results in which all **Y** chromosomes carry a recessive lethal mutation so that **YY** males are inviable. Initially, **W** chromosomes increase by natural selection, skewing the population sex ratio toward females, reaching a quasiequilibrium
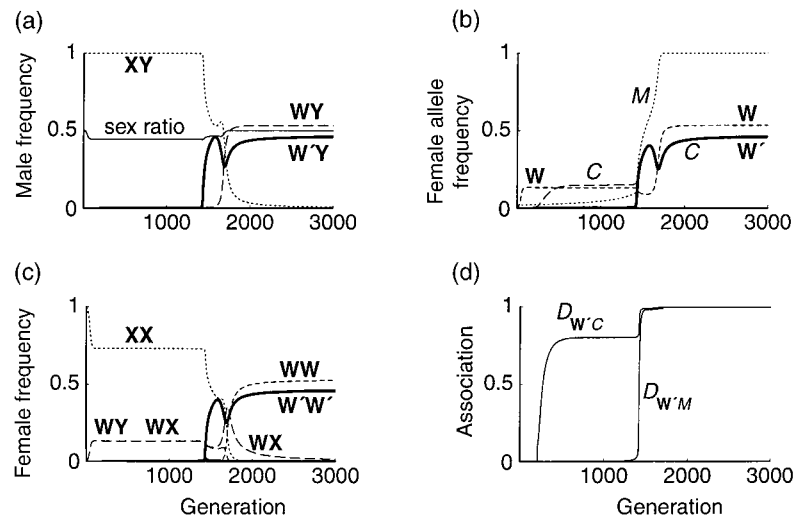
Figure 2. Sympatric speciation by sexual selection on color and sex reversal with a suppressor when **YY** males are inviable. Parameters are otherwise identical to Figure 1 except that mating preferences are asymmetric between the sexes with new mating preferences, *C*, in females being only half as strong as in males (Seehausen, van Alphen & Lande, 1999). The sex ratio is substantially female-biased at the first quasiequilibrium until rescued males with the novel color **W′Y** *MM* become common (panel *a*). After sudden sympatric speciation at around generation 1500 the new species may replace the ancestral one (as in Figure 1) or the two may coexist indefinitely in a stable equilibrium (panels *b–d*), depending on the parameters.

balanced against sex-ratio selection. Matings between **W**-females and **XY** males produce female-biased progeny. (When **YY** males are inviable, **WX** mothers produce 3/4 daughters and **WY** mothers produce 2/3 daughters.). This becomes increasingly detrimental under sex-ratio selection as the population becomes more female-biased. Female mating preferences again select against new color mutations except those arising on **W** chromosomes which are restricted to females. Sexual selection on male mating preference establishes a quasiequilibrium of **W′** and *C*, which become partially associated. Now, in addition to being the preferred mates of *C*-females, rescued males with the novel color, **W′Y** *MM*, are favored by sex-ratio selection since they tend to produce more even progeny sex ratios than ancestral males. The recessive suppressor *M* gradually increases to a critical frequency whereupon rescued males with the novel color suddenly increase from rare to common (Figure 2(a)). A simultaneous rapid increase in **W′**, *C*, and *M* occurs with evolution of almost complete associations among all three genes (Figure 2(b)–(d)). **W′** and *C* achieve a stable polymorphic equilibrium while *M* becomes fixed. Two subpopulations with distinct colors undergoing strong assortative mating have suddenly emerged and can coexist indefinitely in a stable equilibrium, with occasional hybridization producing rare recombinant genotypes. Sympatric speciation can thus occur rapidly, in a few dozen generations, with no geographic barriers to gene flow and no ecological differentiation.

Models with recombination between color and sex reversal revealed a requirement for strongly suppressed recombination to maintain the initial association created by mutation to **W′**. Our models thus explain observations of **X**-linked sex reversal that is common in fish (Hickling, 1960; Hammerman & Avtalion, 1979; Orzack et al., 1980; Trewavas, 1983; Crapon de Caprona & Fritzsch, 1984; Seehausen et al., 1999) and the association between sex reversal and color observed in rapidly speciating cichlids (Fryer & Iles, 1972; Holzberg, 1978; Seehausen, van Alphen & Lande, 1999). Models with a dominant suppressor of sex reversal displayed similar dynamics.

Discussion

These models may help to explain why some groups of cichlids in African lakes have speciated much more rapidly than others. The most rapidly speciating groups in Lakes Malawi and Victoria are nearshore rock-dwelling haplochromine cichlids, which are territorial habitat specialists with limited dispersal (Markert et al., 1999). Such species in spatially structured populations with small effective sizes are more

likely to have recessive deleterious **Y**-linked mutations fixed by random genetic drift and hence **YY** males with relatively low viability. The tilapiine cichlids speciated much more slowly, are far less specialized to particular habitats, and have much larger effective local population sizes (Sodsuk, McAndrew & Turner, 1995). The same holds for many offshore haplochromines. These latter groups are thus more likely to have **YY** males with relatively high viability, predisposing them to speciation by repeated reversal of heterogametic sex while maintaining a nearly unbiased sex ratio (Figure 1). The smaller the disadvantage to **YY** males, the closer an advantageous **W** comes to replacing **X** and completing the initial allopatric shift from male to female heterogamety; this relaxes selection for reduced recombination on the sex chromosomes, diminishing the likelihood of the second phase of sympatric speciation in Figure 1. By comparison, the rock-dwelling haplochromines appear predisposed to sympatric speciation by sex-ratio distortion and sexual selection while maintaining male heterogamety (Figure 2). These predictions accord with observations that species of the tilapiine genus *Oreochromis* often differ in the heterogametic sex, are usually allopatric, and frequently similar in color (Hickling, 1960; Hammerman & Avtalion, 1979; Trewavas, 1983; Crapon de Caprona & Fritzsch, 1984). In contrast, rock-dwelling haplochromines are usually male heterogametic (Kornfield, 1991), with sister species often sympatric, and usually conspicuously distinguished by color of one or both sexes (O.Seehausen, unpublished results).

These mechanisms of sympatric speciation restore the ancestral species to its original color, mating behavior and sex determination. The new species carries both sex reversal and its suppressor, restoring the original mode of sex determination, as may have occurred in the history of other sex-determining systems (Wilkins, 1995). In the process of sympatric speciation the new species also has acquired novel color and mating preferences that differentiate it from the ancestral species. The process can therefore repeat in either species with new sex determiners, colors and mating preferences. This potential for repeated rapid speciation without geographic isolation or ecological differentiation may help to explain the explosive diversification of rock-dwelling haplochromine cichlids.

Several recent models have been proposed to explain sympatric speciation in cichlids. One set of models relies on ecological differentiation in conjunction with sexual selection and/or assortative mating (van Doorn, Noest & Hogeweg, 1998; Dieckmann & Doebeli, 1999; Kondrashov & Kondrashov, 1999), which appears inconsistent with the strong ecological similarity often observed between closely related sympatric species of cichlids (Bouton, Seehausen & van Alphen, 1997; Seehausen & Bouton, 1997; Genner et al., 1999; Seehausen, van Alphen & Lande, 1999). Other models of sympatric speciation depend only on sexual selection but differ from our model in the following respects. Wu's (1985) model is driven by random genetic drift such that reproductive isolation evolves slowly, on a time scale on the order of the inverse of the mutation rate per locus. The model of Turner and Burrows (1995) produces two species that coexist within a single ecological niche from one that was initially at a balance between female mating preferences and stabilizing natural selection. The model of Higashi et al. (1999) begins with a large variance in female mating preference and produces only a single speciation event, after which genetic variance in the male character is exhausted in both species (see however Takimoto, Higashi & Yamamura, 2000). Each of these models may therefore explain only a limited amount of sympatric speciation.

Our models are consistent with repeated events of rapid sympatric speciation by sexual selection without ecological differentiation, as seems to have occurred in rock-dwelling haplochromine cichlids. In contrast to previous models, our models are based on empirical observations on male and female mating preferences and the genetics of color and sex determination in cichlids (Seehausen, van Alphen & Lande, 1999). The unique feature of our models is the action of sexual selection on sex-determining genes associated with color markers in hypothetical chromosomal regions with restricted recombination. All of the mechanisms described by these various models may have contributed to the explosive diversification of cichlids, but their relative importance has yet to be determined.

Experiments are now underway to test the generality of sex-reversal and its suppression among closely related species of rock-dwelling cichlids. We also intend to investigate recombination on the sex chromosomes of cichlids and to measure the fitness of blotched morphs and **YY** males in the field and in the laboratory. Preliminary theoretical analysis suggests that population subdivision into small neighborhoods or demes, as in rock-dwelling cichlids, can allow **W** chromosomes to invade a subdivided population by interdeme selection without an individual selection advantage, because demes with a more female-biased

sex ratio export more emigrants (cf. Hamilton, 1967). It would be interesting to determine whether this mechanism can facilitate rapid sympatric speciation by sex reversal and sexual selection.

Appendix. Condition for invasion of X-linked W allele with yy lethal

Assuming that homozygotes for the male-determining allele, yy, are lethal, with a dominant sex-linked female determining allele, W, one viable male and four viable female sex-chromosome genotypes exist, with frequencies summing to one, $q + p_1 + p_2 + p_3 + p_4 = 1$ and relative fitnesses (male viability, female viability times fecundity) as follows.

	Male		Female		
Genotype	$\dfrac{yw}{xw}$	$\dfrac{xw}{xw}$	$\dfrac{xw}{xW}$	$\dfrac{yw}{xW}$	$\dfrac{yW}{xw}$
Frequency	q	p_1	p_2	p_3	p_4
Fitness	1	1	ω	ω	ω

For a recombination rate r between the (x, y) locus and the (w, W) locus, in a randomly mating population with discrete non-overlapping generations the recursion equations are

$$\begin{pmatrix} p_1' \\ p_2' \\ p_3' \\ p_4' \end{pmatrix} = \frac{q}{4\overline{w}} \begin{pmatrix} 2 & 1 & r & 1-r \\ 0 & 1 & 1-r & r \\ 0 & 1 & 1-r & r \\ 0 & 0 & r & 1-r \end{pmatrix} \begin{pmatrix} p_1 \\ \omega p_2 \\ \omega p_3 \\ \omega p_4 \end{pmatrix}$$

where prime denotes values in the next generation, and the mean relative fitness of all matings is $\overline{w} = q\{p_1 + \omega[p_2 + \frac{3}{4}(p_3 + p_4)]\}$. When all Ww genotypes are rare the linearized equations give the condition for invasion of W as $\left(3 - 2r + \sqrt{1 + 4r^2}\right) \omega > 4$. With

no linkage ($r = 1/2$) this becomes $\omega > 1.172$ and with tight linkage ($r \ll 1/2$) it is $\omega > 1 + r/2$ approximately.

References

Bergstrom, C.T. & L.A. Real, 2000. Towards a theory of mutual mate choice: lessons from two-sided matching. Evol. Ecol. Res. 2: 493–508.

Bouton, N., O. Seehausen & J.J.M. van Alphen, 1997. Resource partitioning among rock-dwelling haplochromines (Pices: Cichlidae) from Lake Victoria. Ecol. Freshwater Fish 6: 225–240.

Bull, J.J., 1983. Evolution of Sex-determining Mechanisms. Benjamin/Cumings, London.

Charlesworth, B., 1991. The evolution of sex chromosomes. Science 251: 1030–1033.

Crapon de Caprona, M.D. & B. Fritzsch, 1984. Interspecific fertile hybrids of haplochromine cichlidae (Teleostei) and their possible importance for speciation. Neth. J. Zool. 34: 503–538.

Dieckmann, U. & M. Doebeli, 1999. On the origin of species by sympatric speciation. Nature 400: 354–357.

Fisher, R.A., 1958. The Genetical Theory of Natural Selection. Dover, New York, 2nd edn.

Fryer, G. & T.D. Iles, 1972. The Cichlid Fishes of the Great Lakes of Africa. Their Biology and Evolution. Oliver & Boyd, Edinburgh.

Galis, F. & E.G. Drucker, 1996. Pharyngeal biting mechanics in centrarchid and cichlid fishes: insights into a key evolutionary innovation. J. Evol. Biol. 9: 641–670.

Genner, M.J., G.F. Turner, S. Barker & S.J. Hawkins, 1999. Niche segregation among Lake Malawi cichlid fishes? Evidence from stable isotope signatures. Ecol. Lett. 2: 185–190.

Greenwood, P.H., 1981. The Haplochromine Fishes of the East African Lakes. Kraus International Publications, Munich.

Hamilton, W.D., 1967. Extraordinary sex ratios. Science 156: 477–488.

Hammerman, I.S. & R.R. Avtalion, 1979. Sex determination in *Sarotherodon* (*Tilapia*). Part 2: The sex ratio as a tool for the determination of genotype: a model of autosomal and gonosomal influence. Theor. Appl. Genet. 55: 177–187.

Hartl, D.L. & A.G. Clark, 1997. Principles of Population Genetics. Sinauer, Sunderland, MA, 3rd edn.

Haskins, C.H., P. Young, R.E. Hewitt & E.F. Haskins, 1970. Stabilised heterozygosis of supergenes mediating certain Y-linked colour patterns in populations of *Lebistes reticulatus*. Heredity 25: 575–588.

Hickling, C.F., 1960. The Malacca *Tilapia* hybrids. J. Genetics 57: 1–10.

Higashi, M., G. Takimoto & N. Yamamura, 1999. Sympatric speciation by sexual selection. Nature 402: 523–526.

Holzberg, S., 1978. A field and laboratory study of the behaviour and ecology of *Pseudotropheus zebra* (Boulenger), an endemic cichlid of Lake Malawi (Pices; Cichlidae). Z. Zool. Syst. Evol.-Forsch. 16: 171–186.

Johnson, T.C., C.A. Scholtz, M.R. Talbot, K. Kelts, R.D. Ricketts, G. Ngobi, K. Beuning, I. Ssemmanda & J.W. McGill, 1996. Late Pleiostocene desiccation of Lake Victoria and rapid evolution of cichlid fishes. Science 273: 1091–1093.

Kallman, K., 1970. Sex determination and the restriction of sex-linked pigment patterns to the X and Y chromosomes in populations of a poeciliid fish, *Xiphophorus maculatus*, from Belize and Sibun Rivers of British Honduras. Zoologica 55: 1–16.

Kondrashov, A.S. & F.A. Kondrashov, 1999. Interactions among quantitative traits in the course of sympatric speciation. Nature 400: 351–354.

Konings, A., 1995. Remarkable observations on the Red Zebra. The Cichlids Yearbook 5: 42–47.

Kornfield, I., 1991. Genetics, pp. 103–128 in Cichlid Fishes, Behavior, Ecology and Evolution, edited by M.H.A. Keenleyside. Chapman & Hall, London.

Knight, M.E., 1999. Sexual selection and speciation in Lake Malawi cichlids. PhD thesis, University of Southampton, UK.

Knight, M.E., G.F. Turner, C. Rico, M.J.H. van Oppen & G.M. Hewitt, 1998. Microsatellite paternity analysis on captive Lake Malawi cichlids supports reproductive isolation by direct mate choice. Mole. Ecol. 7: 1605–1610.

Lande, R., 1981. Models of speciation by sexual selection on polygenic traits. Proc. Natl. Acad. Sci. USA 78: 3721–3725.

Lande, R. & G. Wilkinson, 1999. Models of sex-ratio meiotic drive and sexual selection in stalk-eyed flies. Genet. Res. 74: 245–253.

Markert, J.A., M.E. Arnegard, P.D. Danley, & T.D. Kocher, 1999. Biogeography and population genetics of the Lake Malawi cichlid *Melanochromis auratus*: habitat transience, philopatry and speciation. Mole. Ecol. 8: 1013–1026.

Meyer, A., T.D. Kocher, P. Basasibwaki & A.C. Wilson, 1990. Monophyletic origin of lake Victoria cichlid fishes suggested by mitochondrial DNA sequences. Nature 347: 550–553.

Orzack, S.H., J.J. Sohn, K.D. Kallman, S.A. Levin & R. Johnston, 1980. Maintenance of the three sex chromosome polymorphism in the platyfish, *Xiphophorus maculatus*. Evolution 34: 663–672.

Seehausen, O., 1996. Lake Victoria Rock Cichlids–Taxonomy, Ecology and Distribution. Verduijn Cichlids, Zevenhuizen, The Netherlands.

Seehausen, O., 2000. Exposive speciation rates and unusual species richness in haplochromine cichlid fishes: effects of sexual selection. Adv. Ecol. Res. 31: 237–274.

Seehausen, O. & N. Bouton, 1996. Polychromatism in rock dwelling Lake Victoria cichlids: types, distribution, and observations on their genetics. The Cichlids Yearbook 6: 36–45.

Seehausen, O. & N. Bouton, 1997. Microdistribution and fluctuations in niche overlap in a rocky shore cichlid community in Lake Victoria. Ecol. Freshwater Fish 6: 161–137.

Seehausen O, & J.J.M. van Alphen, 1999. Can sympatric speciation by disruptive sexual selection explain rapid evolution of cichlid diversity in Lake Victoria? Ecol. Lett. 2: 262–271.

Seehausen, O., J.J.M. van Alphen & F. Witte, 1997. Cichlid fish diversity threatened by eutrophication that curbs sexual selection. Science 277: 1808–1811.

Seehausen, O., J.J.M. van Alphen & R. Lande, 1999. Color polymorphism and sex-ratio distortion in a cichlid fish as a transient stage in sympatric speciation by sexual selection. Ecol. Lett. 2: 367–378.

Snoeks, J., 1994. The haplochromines (Teleostei, Cichlidae) of Lake Kivu (East Africa). Annales Sciences Zoologique Museum Royal de l'Afrique Centrale 270: 1–221.

Sodsuk, P.U., B.J. McAndrew & G.F. Turner, 1995. Evolutionary relationships of the Lake Malawi *Oreochromis* species: evidence from allozymes. J. Fish Biol. 47: 321–333.

Spreinat, A., 1995. Lake Malawi Cichlids from Tanzania. Verduijn Cichlids, Zevenhuizen, The Netherlands.

Takimoto, G., M. Higashi & N. Yamamura, 2000. A deterministic genetic model for sympatric speciation by sexual selection. Evolution 54: 1870–1881.

Trewavas, E., 1983. Tilapiine Fishes of the Genera *Sarotherodon, Oreochromis* and *Danakilia*. British Museum [Natural History], London.

Turner, G.F. & M.T. Burrows, 1995. A model of sympatric speciation by sexual selection. Proc. Roy. Soc. Lond. B 260: 287–292.

Turner, G.F., 1998. Explosive speciation in African cichlid fishes, pp. 217–229 in The Evolution of Biological Diversity, edited by A.E. Magurran & R.M. May. Oxford University Press, Oxford.

van Doorn, G.S., A.J. Noest & P. Hogeweg, 1998. Sympatric speciation and extinction driven by environment dependent sexual selection. Proc. Roy. Soc. Lond. B 265: 1915–1919.

van Oppen, M.J.H., G.F. Turner, C. Rico, R.L. Robinson, J.C. Deutsch, M.J. Genner & G.M. Hewitt, 1998. Assortative mating among rock-dwelling cichlids fishes supports high estimates of species richness from Lake Malawi. Mole. Ecol. 7: 991–1001.

White, M.J.D., 1973. Animal Cytology and Evolution. Cambridge University Press, Cambridge, 3rd edn.

Wilkins, A.S., 1995. Moving up the hierarchy - a hypothesis on the evolution of a genetic sex determination pathway. Bioessays 17: 71–77.

Wilson, A.B., K Noack-Kunnmann & A. Meyer, 2000. Incipient speciation in sympatric Nicaraguan crater lake cichlid fishes: sexual selection versus ecological differentiation. Proc. Roy. Soc. Lond. B 267: 2133–2141.

Wolfram, S., 1999. Mathematica. Cambridge University Press, Cambridge, 4th edn.