

## Sensory Drive in Cichlid Speciation

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**ABSTRACT:** The role of selection in speciation is a central yet poorly understood problem in evolutionary biology. The rapid radiations of extremely colorful cichlid fish in African lakes have fueled the hypothesis that sexual selection can drive species divergence without geographical isolation. Here we present experimental evidence for a mechanism by which sexual selection becomes divergent: in two sibling species from Lake Victoria, female mating preferences for red and blue male nuptial coloration coincide with their context-independent sensitivities to red and blue light, which in turn correspond to a difference in ambient light in the natural habitat of the species. These results suggest that natural selection on visual performance, favoring different visual properties in different spectral environments, may lead to divergent sexual selection on male nuptial coloration. This interplay of ecological and sexual selection along a light gradient may provide a mechanism of rapid speciation through divergent sensory drive.

*Keywords:* cichlid fish, color evolution, sensory drive, sexual selection, speciation.

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It is widely acknowledged that female mate choice for male ornamental traits can maintain and strengthen reproductive isolation between recently diverged species, even without postzygotic barriers to gene flow (Andersson 1994). The role of sexual selection in the emergence of repro-

ductively isolated populations, and hence in the speciation process itself, is less well understood and much more controversial (Arnegard and Kondrashov 2004). Especially when female choice selects for “good genes,” it is hard to see how variation in mating preferences can evolve, let alone drive species divergence (Kirkpatrick and Nuismer 2004; but see Edelaar et al. 2004; Reinhold 2004). However, intraspecific variation in female preferences has been demonstrated in several taxa (e.g., Godin and Dugatkin 1995; Coleman et al. 2004), and more examples may emerge as research effort into the evolution of signal perception increases (Jennions and Petrie 1997).

The extremely species-rich cichlid communities of the East African lakes Malawi and Victoria have been presented as possible examples of speciation driven by sexual selection (Dominey 1984; McKaye 1991; Seehausen 2000; Danley and Kocher 2001). This hypothesis was inspired by the widespread occurrence of intra- and interspecific variation in male nuptial coloration and corresponding female mating preferences, often associated with only slight ecological differentiation and no intrinsic postzygotic isolation between species (Albertson et al. 1999; Seehausen 2000).

Haplochromine cichlids express considerable interspecific variation in color vision (van der Meer and Bowmaker 1995; Smit and Anker 1997). Seehausen et al. (1997) proposed that if such variation occurred within populations, together with directional sexual selection by female mate choice for brightly colored, conspicuous males, it might constitute disruptive sexual selection on male coloration and possibly cause speciation. Several recent studies have presented evidence for divergent sensory drive in species pairs that use visual signals in sexual communication (Boughman 2001; Fuller 2002; Leal and Fleishman 2004), indicating that it may be a potent driving force in speciation (Endler and McLellan 1988; Endler et al. 2001; Boughman 2002).

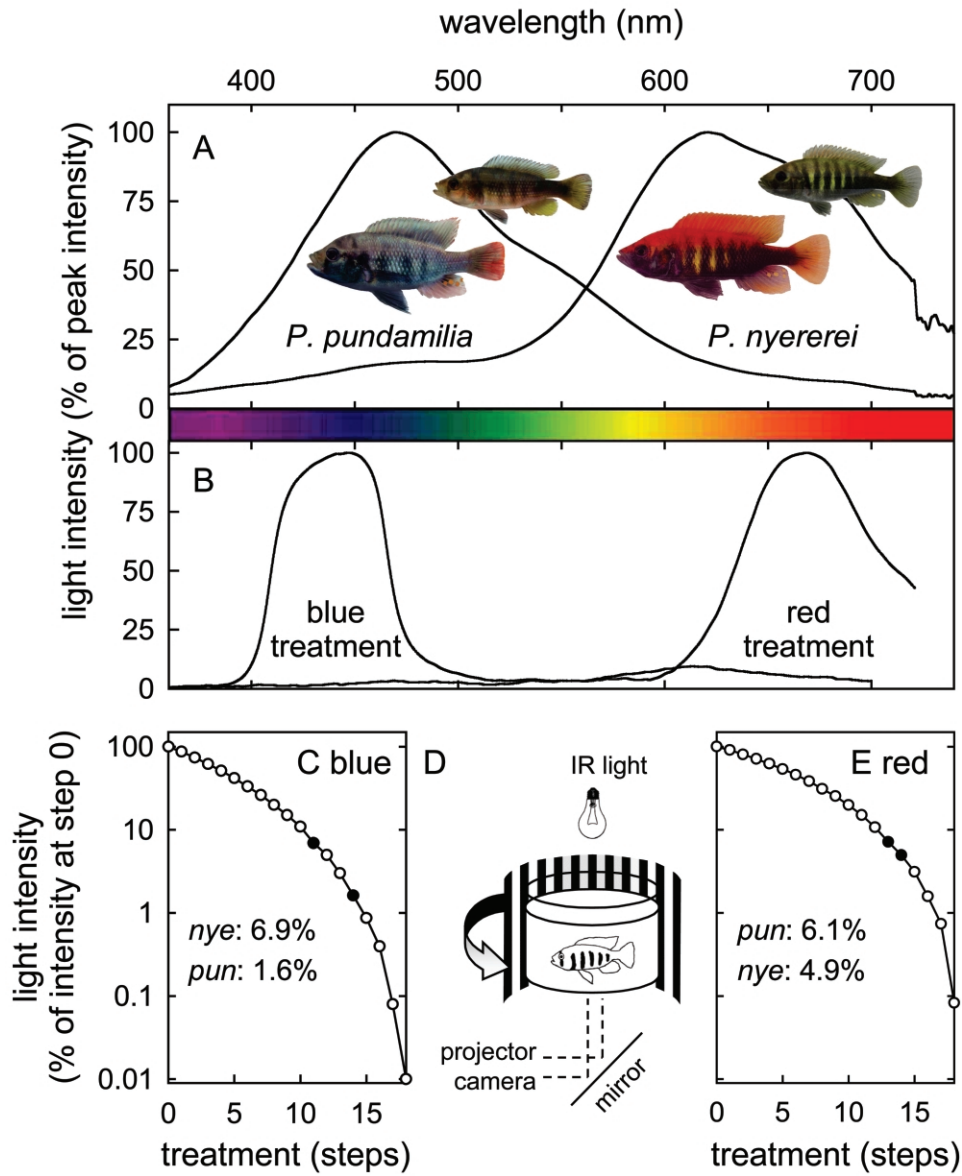
We investigate the divergence of a species pair that represents the dominant pattern of color variation among sympatric closely related Lake Victoria cichlids (Seehausen et al. 1999). *Pundamilia pundamilia* and *Pundamilia nyererei* are anatomically similar, but *P. pundamilia* males are metallic blue and *P. nyererei* males are bright red (fig. 1A).

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**Figure 1:** Male nuptial coloration in *Pundamilia* and the light treatments in the optomotor response test. *A*, *Pundamilia pundamilia* and *Pundamilia nyererei* males and females with the reflection spectra of male nuptial coloration. *B*, Transmission spectra of the blue and red light treatments used in the optomotor response test. *C*, *E*, Treatment light intensities, from step 0 to step 18, expressed as a percentage of the treatment light intensity in step 0. Group medians for both species (filled symbols) are given in each panel. *D*, Experimental setup.

They behave as reproductively isolated species in some populations but interbreed in locations where the water is very turbid (Seehausen et al. 1997). Females of both species are cryptically colored and can be distinguished only with difficulty. They have assortative mating preferences and use male coloration as a choice criterion (Seehausen and van Alphen 1998). The hypothesis that sensory

drive has been involved in the divergence of this species pair (Seehausen et al. 1997) predicts that the photic environments in the microhabitats of the two species differ, that the visual systems of the two species have diverged in adaptation to these different photic environments, and that, within a species, females prefer more conspicuous over less conspicuous males. The latter has been dem-

onstrated in one of the two species: the red coloration of *P. nyererei* males is subject to directional sexual selection by female choice (Maan et al. 2004).

Here we report data consistent with divergent adaptation of the visual systems of the two species. First, we quantify the photic habitats of both species in nature. Although geographically *P. nyererei* is entirely sympatric with *P. pundamilia*, it breeds in deeper water (Seehausen and Bouton 1997). Because the turbid Lake Victoria waters selectively absorb and scatter light of short wavelengths, the intensity and spectrum of ambient light change rapidly with depth (De Beer 1989). Second, we test whether the two species differ in visual properties in the direction predicted by the difference in spectral environment. We use the optomotor response test to measure the context-independent behavioral responses to colored light of both species.

## Methods

### *The Fish*

Fish were collected in February 2003 at Makobe Island (Seehausen and Bouton 1997) in the western Speke Gulf of Lake Victoria (Tanzania; water transparency: Secchi reading =  $221 \pm 7$  cm (mean  $\pm$  SE); 84 measurements in 2000–2003). At this island, *Pundamilia pundamilia* and *Pundamilia nyererei* inhabit a continuous rocky slope from 0.5 to 7 m water depth. *Pundamilia pundamilia* is most abundant at 0.5–2 m; *P. nyererei* is most abundant at 4–7 m. Both species occur at 2–4 m depth (Seehausen and Bouton 1997; M. E. Maan, personal observation). Their main habitats are not separated by any barrier (such as stretches of sand or mud), nor are they isolated by distance (the distances between locations within each habitat are not shorter than those between the habitats). Individuals of both species are regularly observed and caught in the entire 0.5–7-m depth range.

Sensitivity thresholds were determined in October–December 2003. Because we were interested in correspondence between visual sensitivity and female preference, we used only females. *Pundamilia nyererei* females ( $n = 11$ ) were caught in gill nets at a 4–7-m depth; *P. pundamilia* females ( $n = 14$ ) were collected using hook and line at a  $\sim$ 1-m depth. Fish were shipped to the Netherlands and kept at  $25^\circ \pm 2^\circ\text{C}$  and a 12L : 12D photoperiod. Tanks were illuminated with high-frequency fluorescent light tubes (Philips TLD 58 W, light color 830, 1,100 lux). Shortly before an experiment, we measured fish standard length and inserted a microchip into the abdominal cavity for individual identification (12-mm glass tags, UKID122GL, Biomark); the species identity of

the subjects was not known to the observer during the experiments.

### *Spectrophotometry*

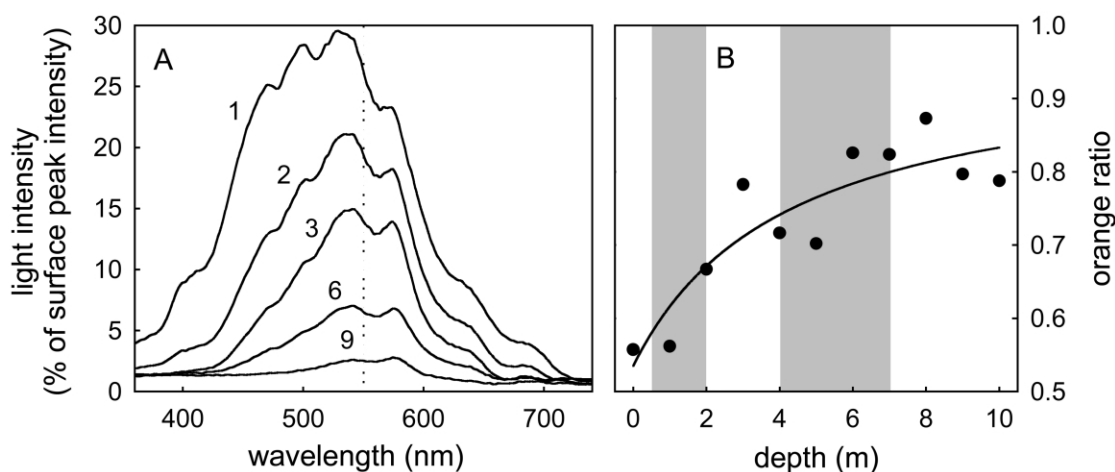
Reflection spectra of male nuptial coloration were measured using an Avantes PS 2048 spectrophotometer with SpectraWin 6.1 software (Avantes). We used one sexually active male of each species and measured reflectance in daylight in clear water, holding the probe of the spectrophotometer at a distance of 5 mm perpendicular to the fish skin and holding the fish underwater. Light reflectance was calibrated using a dark reference (covering the probe completely) and a light reference (reflectance off a white piece of plastic, also underwater); no additional illumination was used. For *P. pundamilia*, we measured reflectance off the blue sides of the fish; for *P. nyererei*, we measured the red dorsum (which is more important in female choice than the yellow coloration on the sides of the males; Maan et al. 2004). We normalized reflectance spectra by the peak reflectance to facilitate species comparison.

Treatment light spectra were measured using the same equipment and holding the probe in the middle of the experimental tank illuminated by the treatment light and filled with water to 15 cm. With decreasing light intensity, the spectral curves became less steep, but the wavelength of maximum intensity did not change (wavelength of top 5% intensity [mean  $\pm$  SE]: blue,  $447.9 \pm 1.3$  nm; red,  $670.2 \pm 0.7$  nm).

We measured light transmission at Makobe Island with an Ocean Optics PS 1000 spectrophotometer with a 10-m optical fiber cable (100  $\mu\text{m}$ ), using SpectraWin 4.16 software (Avantes). We quantified the spectral composition at different depths by calculating the “orange ratio,” the light intensity in the 550–700-nm range (yellow, orange, red) divided by the intensity in the 400–550-nm range (blue, green; Endler and Houde 1995).

### *Optomotor Experiment*

The optomotor response test exploits the optokinetic response, the tendency of fish to follow a moving light stimulus. The method has been successfully employed in a variety of fish species (e.g., guppies: Anstis et al. 1998; zebrafish: Krauss and Neumeyer 2003; goldfish: Schaerer and Neumeyer 1996; sticklebacks: Boughman 2001; and cichlids: van der Meer 1994; Kröger et al. 2003). Fish were placed individually in a cylindrical tank (diameter 20 cm, water depth 15 cm; fig. 1D). A screen with vertical black and white bars (35 mm wide) rotated around the tank at 8.33 rpm. Trials started with an acclimatization period of 10 min, during which the bar pattern rotated and the tank



**Figure 2:** Photoc habitats in the study population at Makobe Island. *A*, Transmission light spectra at different depths. Numbers indicate depth in meters. The dotted line indicates the 550-nm threshold that is used to calculate the orange ratio. *B*, Increase in orange ratio with water depth. Shaded areas indicate *Pundamilia pundamilia* (0.5–2 m) and *Pundamilia nyererei* (4–7 m) breeding habitats.

containing the test fish was illuminated with a small adapting light (230 lux), an infrared light source (875 nm, intensity 17 mW/sr; Agilent Technologies) above the tank, and the maximum intensity of treatment light. Treatment light (fig. 1*B*) was provided by a slide projector (GAF 131) with either a blue (436 nm) or a red (656 nm) narrowband filter (Spindler & Hoyer). To narrow wavelength ranges, we added a colored Lee filter (113, magenta) and density filters (Lee 209; one density filter for the blue treatment and two for the red treatment). Light intensity was adjusted in 18 discrete steps by lowering the voltage feeding of the slide projector (fig. 1*C*, 1*E*). The response of the fish was observed using an infrared camera with a monitor. After the habituation period, the adapting light was switched off. If the fish continued following the rotating bar pattern within 15 s for at least 10 s, the treatment light intensity was lowered by one step. This was repeated until the swimming response had disappeared. To confirm this threshold, the light intensity was increased by two steps and again lowered stepwise, this time reversing the rotating direction once at each light intensity level. The sensitivity threshold was defined as the lowest light intensity at which the fish responded to reversal of the rotation direction by reversing the swimming direction. The sensitivities that could be measured therefore ranged from 0 (maximum light intensity) to 18 (minimum light intensity). During the test procedure, the adapting light source was switched on for 1 min every 90 s, to ensure that the fish were light adapted (Smit and Anker 1997). Each individual was tested five times in each light treatment, and the median sensitivity threshold of the test series was used for statistical analysis.

#### Data Analysis

Species differences were analyzed using independent-sample *t*-tests (normal data) and Mann-Whitney *U*-tests (nonnormal data) in SPSS 10.0. To disentangle the effects of body size and species identity, we analyzed generalized linear models (GLMs) in R (<http://www.r-project.org>; Ihaka and Gentleman 1996) with a Poisson distribution. Also in R, the orange ratio at Makobe Island was analyzed in GLMs with binomial distribution. Significance was determined by *F*-tests examining the change in deviance after removal of variables. Test statistics were adjusted for overdispersion and underdispersion (Venables and Ripley 2002).

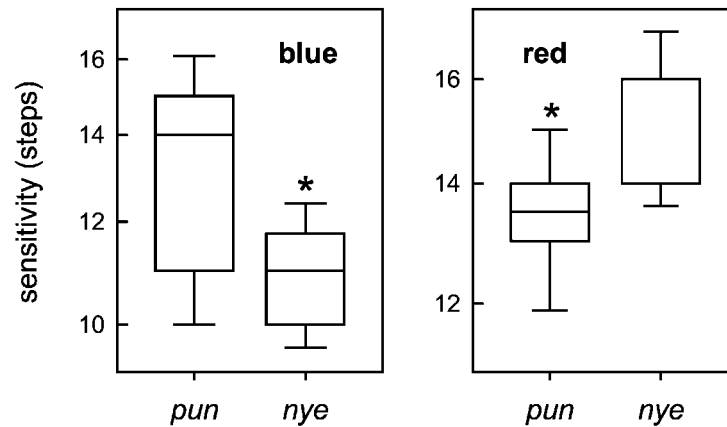
## Results

### The Photoc Environment

At Makobe Island, the proportion of long wavelengths (i.e., >550 nm) in the light spectrum increased rapidly with depth ( $F = 24.9$ ,  $df = 1, 9$ ,  $P = .0008$ ; fig. 2). As a result, the light spectrum in the habitat where *Pundamilia nyererei* dominates (4–7 m depth) was significantly more redshifted (orange ratio = 0.75) than that in the habitat where *Pundamilia pundamilia* is most abundant (0.5–2 m depth; orange ratio = 0.57):  $F = 8.79$ ,  $df = 1, 4$ ,  $P = .04$ .

### The Sensitivities to Colored Light

In both blue and red light, there were significant differences in optomotor response between the two species (fig. 3). In blue light, *P. pundamilia* females performed signif-



**Figure 3:** Performance of *Pundamilia pundamilia* (*pun*,  $n = 14$ ) and *Pundamilia nyererei* (*nye*,  $n = 11$ ) females in the optomotor response test. *Left*, Blue light; *right*, red light. Boxes represent medians with first and third quartiles; error bars indicate tenth and ninetieth percentiles; asterisks indicate  $P < .02$ .

icantly better than *P. nyererei* females ( $n = 14$  and  $11$ , respectively; Mann-Whitney  $U$ -test:  $Z = 2.86$ ,  $P = .004$ ). In red light, the pattern was reversed ( $Z = 2.53$ ,  $P = .011$ ). The minimum intensity of blue light that *P. pundamilia* responded to was 2.7% of (or  $1/37.7$ ) the minimum intensity of blue light that *P. nyererei* responded to. The minimum intensity of red light that *P. nyererei* responded to was 23.7% of (or  $1/4.2$ ) the minimum intensity of red light that *P. pundamilia* responded to. Together, the blue and red optomotor response thresholds categorized 23 out of the 25 individuals tested into two nonoverlapping groups, one with individuals having high sensitivity to red light and low sensitivity to blue light (all *P. nyererei*) and the other with individuals having high sensitivity to blue light and low sensitivity to red light (all *P. pundamilia*). Thus, if mate choice in nature corresponds to visual sensitivities as measured by optomotor response thresholds, these results are consistent with assortative mating for 23 of 25 individuals (92%).

On average, *P. pundamilia* females were larger than *P. nyererei* females (standard length [mm, mean  $\pm$  SE]: *P. pundamilia*,  $84.7 \pm 1.1$ , and *P. nyererei*,  $79.7 \pm 1.1$ ; independent-sample  $t$ -test:  $t = 3.11$ ,  $df = 23$ ,  $P = .005$ ; weight (g): *P. pundamilia*,  $18.9 \pm 0.7$ , and *P. nyererei*,  $13.8 \pm 0.5$ ;  $t = 5.48$ ,  $df = 23$ ,  $P < .001$ ). The performance in the experiment was not correlated with body size in either species (Spearman rank correlations between weight and standard length and red and blue sensitivity: all  $r_s < 0.41$ ,  $P > .21$ ). GLMs including species, standard length, and weight showed that sensitivity threshold was best explained by species identity (red: estimate [species] =  $0.11 \pm 0.036$ ,  $F = 9.47$ ,  $df = 1, 23$ ,  $P = .0053$ ; blue: estimate [species] =  $-0.23 \pm 0.061$ ,  $F = 14.11$ ,  $df = 1, 23$ ,  $P =$

.001). Models did not improve by including body size information (all  $F < 0.062$ ,  $df = 1, 22$ ,  $P > .81$  for the difference between models).

## Discussion

We investigated the hypothesis that divergent natural selection on visual properties has contributed to the divergence of female mating preferences between sibling species of Lake Victoria cichlid fish, *Pundamilia pundamilia* and *Pundamilia nyererei* (Seehausen et al. 1997). This hypothesis was inspired by the observations that the species differ strikingly in male nuptial coloration, that the cryptically colored females use this difference as a basis for species-assortative mate choice (Seehausen and van Alphen 1998), and that female mate choice exerts directional sexual selection on male coloration in at least one of the two species (*P. nyererei*; Maan et al. 2004). Moreover, the spectral characteristics of the Lake Victoria waters create a heterogeneous light environment (De Beer 1989) with potentially steep selection gradients.

We quantified the spectral habitats of *P. pundamilia* and *P. nyererei* at Makobe Island and found that the two species indeed inhabit significantly different light environments. Relative to the shallow-breeding *P. pundamilia*, *P. nyererei* experiences a narrower and redshifted ambient spectrum. In optomotor experiments, we tested whether this difference in light environment coincides with a difference in sensitivity to colored light. Our data demonstrate that the species indeed differ in behavioral responses to color stimuli outside the mate choice context: *P. pundamilia* females responded to lower intensities of blue light than did *P. nyererei* females. Conversely, *P. nyererei* females responded

to lower intensities of red light than did *P. pundamilia* females.

Since we used wild-caught fish collected from different spectral environments, the differences we found could be due to phenotypic plasticity (Kröger et al. 2003). There are, however, strong indications of heritable differences in the visual systems of the two species. First, *P. nyererei* has a larger number of long-wavelength-sensitive (LWS) cones than *P. pundamilia*, and this difference is maintained in fish that are bred in identical laboratory conditions (Carleton et al. 2005). Second, the gene sequence of the LWS opsin gene differs between the species, corresponding to a 3–4-nm shift of maximum absorbance toward longer wavelengths in *P. nyererei* (Carleton et al. 2005).

Several earlier studies have demonstrated differences in absorbance spectra between cone pigments extracted from retinas of different haplochromine species (van der Meer and Bowmaker 1995), in cone opsin gene and protein sequences (Carleton and Kocher 2001; Terai et al. 2002), and in opsin gene expression (Carleton and Kocher 2001). Our study provides the first evidence that differences between sibling species in opsin protein sequences, opsin expression patterns (Carleton et al. 2005), and female mating preferences for different male colors (Seehausen and van Alphen 1998) are accompanied by differences in context-independent behavioral responses to light of different wavelengths. This is an important but previously untested prediction of the sensory-drive speciation hypothesis.

Many animals use only long-wavelength-sensitive (LWS) cones for the perception of movement (e.g., goldfish: Schaerer and Neumeyer 1996), and this may hold for cichlid fish as well (but see Kröger et al. 2003). In the case of *Pundamilia*, the difference in optomotor response between *P. pundamilia* and *P. nyererei* could be due to differences in expression level or in the peak sensitivity of a single cone pigment, most likely LWS (Carleton et al. 2005). By contrast, color assessment in the mate choice context may involve the joint action of all cone types (three different cone pigments). Further, behavioral responses to visual stimuli are mediated by information processing in the brain. For these reasons, further work is required to investigate how variation in *Pundamilia* optomotor responses relates to variation in female preferences for male nuptial coloration.

Either way, our data are consistent with the hypothesis that the visual systems of *P. pundamilia* and *P. nyererei* have evolved under divergent natural selection exerted by the spectral depth gradient in the natural habitat of the fish and that this in turn mediates divergent or disruptive sexual selection on male nuptial coloration. Increased sensitivity to light of longer wavelengths (longer wavelength of maximum sensitivity in the LWS cones, i.e., longer  $\lambda_{\max}$ ,

and/or a larger proportion of LWS-expressing cones) is advantageous in deeper water, while shorter  $\lambda_{\max}$  and a larger proportion of short-wavelength-sensitive (SWS) cones are favored in shallow water. Consequently, if females prefer conspicuous males (Maan et al. 2004; Pauers et al. 2004), males that reflect mainly on the blue end of the spectrum have an advantage in shallow water, where selection favors shorter  $\lambda_{\max}$  and a larger proportion of SWS-expressing cones. In deeper water, where selection favors longer  $\lambda_{\max}$  and a larger proportion of LWS-expressing cones, red males are likely to have higher mating success.

Fish visual systems tend to be adapted to the spectral environment (Ali 1975; Loew and Lythgoe 1978; Levine and MacNichol 1982; van der Meer and Bowmaker 1995; Cummings and Partridge 2001; Jokela et al. 2003). The relationship between spectral environment and sexual color signals, however, is often negative (Marchetti 1993; Boughman 2001; Fuller 2002; Leal and Fleishman 2004): wavelengths that dominate in the ambient light spectrum are not used in visual signals. This maximizes color signal conspicuousness through background contrasting. In *Pundamilia*, however, male nuptial coloration exploits the available extremes in the ambient spectrum to maximize contrast against the green-yellow background light (fig. 2). Thus, the blue *P. pundamilia* inhabits a broad-spectrum environment where blue wavelengths are available to generate contrast. The red *P. nyererei* inhabits a redshifted photic environment and exploits the long-wavelength extreme of the ambient spectrum to maximize contrast against the background light. This difference with other taxa may be due to the steepness of the spectral gradient in Lake Victoria. In the *P. nyererei* habitat at Makobe Island, light intensity in the short-wavelength range is so low that blue signals are not conspicuous or are even invisible there.

We conclude that the interaction of divergent ecological selection on the visual system along a spectral light gradient and directional sexual selection for bright male color may result in divergent or disruptive sexual selection on male coloration through female mate choice. Consistent with sensory-drive speciation models (Endler 1992; Boughman 2002), this mechanism may have driven the divergence of *P. pundamilia* and *P. nyererei*. The geographically sympatric and ecologically parapatric distribution of the two species suggests that this process may have occurred without geographical isolation. The same mechanism is also likely to contribute to the maintenance of reproductive isolation after speciation. Given the abundance of blue-red sister species and polymorphisms among Lake Victoria cichlid fish (Seehausen et al. 1999), we postulate that similar mechanisms may have been involved in other cases of rapid speciation that resulted in sympatric

sister species that differ in male nuptial coloration and depth distribution. Likewise, divergent selection on visual properties may have contributed to the cichlid radiations in other African lakes. In Lake Malawi, for example, which has a higher water transparency and shorter wavelength of maximum transmission than Lake Victoria, blue-yellow, rather than blue-red, species pairs or morphs predominate (McElroy et al. 1991; Deutsch 1997; Seehausen et al. 1999). This corresponds to patterns of opsin gene expression in these fish (Carleton and Kocher 2001).

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