

Mechanisms of species divergence through visual adaptation and sexual selection: Perspectives from a cichlid model system

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Abstract The theory of ecological speciation suggests that assortative mating evolves most easily when mating preferences are directly linked to ecological traits that are subject to divergent selection. Sensory adaptation can play a major role in this process, because selective mating is often mediated by sexual signals: bright colours, complex song, pheromone blends and so on. When divergent sensory adaptation affects the perception of such signals, mating patterns may change as an immediate consequence. Alternatively, mating preferences can diverge as a result of indirect effects: assortative mating may be promoted by selection against intermediate phenotypes that are maladapted to their (sensory) environment. For Lake Victoria cichlids, the visual environment constitutes an important selective force that is heterogeneous across geographical and water depth gradients. We investigate the direct and indirect effects of this heterogeneity on the evolution of female preferences for alternative male nuptial colours (red and blue) in the genus *Pundamilia*. Here, we review the current evidence for divergent sensory drive in this system, extract general principles, and discuss future perspectives [*Current Zoology* 56 (3): 285–299, 2010].

Key words Cichlid, Sexual selection, Species divergence, Visual adaptation

1 The Ecology of Speciation

Unraveling the mechanisms that generate species diversity has major implications for both fundamental science and the conservation of natural ecosystems. The previous century was dominated by the view that animal speciation requires geographic isolation (Mayr, 1942, 1963). The past two decades have seen a shift towards the idea that one species can split in two even without geographic barriers, as a result of adaptation to different environmental conditions (Bolnick and Fitzpatrick, 2007; Bush, 1994; Coyne and Orr, 2004; Lande, 1982; Nosil et al., 2002; Schliewen et al., 1994; Schluter, 2001). While this scenario is supported by observations of divergent adaptation between parapatric, and sometimes sympatric natural populations, the link between adaptation and reproductive isolation is not well understood (Hendry, 2009; Nosil et al., 2009; Schluter, 2009).

Without physical isolation, adaptive divergence in sexually reproducing populations is constrained by the homogenizing effect of interbreeding (Darwin, 1859; Felsenstein, 1981; Futuyma and Mayer, 1980; Mayr, 1963). One theoretical solution is the evolution of selec-

tive mating among locally adapted individuals, which may occur through either direct or indirect mechanisms. First, ecological adaptation may have immediate consequences for mating patterns, for example when environmental conditions influence the time or place of mating. Theoretical models show that such mechanisms can rapidly drive speciation (Dieckmann and Doebeli, 1999; Fry, 2003; Kondrashov, 1983; Udovic, 1980). However, the traits that would mediate this process have been labelled ‘magic’: extremely powerful in driving fast speciation, but assumed to be exceedingly rare in nature (Gavrilets, 2004; Hendry et al., 2007; Maynard Smith, 1966). And yet, empirical studies have identified several possible examples. Perhaps the most convincing case is the formation of host races in phytophagous insects, driven by adaptation to host plants that are separated in space (Berlocher and Feder, 2002; Caillaud and Via, 2000) or time (Feder and Filchak, 1999; Groman and Pellmyr, 2000). Additional evidence comes from size-assortative mating in sticklebacks (McKinnon et al., 2004) and colour-assortative mating in *Heliconius* butterflies (Jiggins, 2008; Kronforst et al., 2006). Second, divergence in mating patterns can occur through indi-

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rect selection. While less straightforward theoretically, divergent ecological selection can promote the evolution of linkage disequilibrium between initially independent adaptive and mating traits, even without geographical isolation (Gavrilets, 2004; Kondrashov and Kondrashov, 1999; Servedio, 2008). Evidence for this mechanism comes from studies that demonstrate female mating preferences for the mating signals produced by locally adapted males, for example in treefrogs (Gerhardt, 1994), North-American crossbills (Smith and Benkman, 2007; Smith et al., 1999; Snowberg and Benkman, 2007), treehopper insects (Cocroft et al., 2008; Rodriguez et al., 2006) and laboratory populations of *Drosophila* (Rundle et al., 2009; Rundle et al., 2005).

In this paper, we explore the potential contribution of sensory adaptation to either of these mechanisms of speciation. When mate choice is mediated by perceptual processes, heterogeneous sensory environments can promote the divergence of sexual signals and preferences, and thereby reduce geneflow between populations.

2 Mechanisms of Mate Selection

Currently, the relative importance of direct and indirect mechanisms of divergent evolution in mate choice, and hence speciation, are unknown, and empirical examples of divergence driven by direct ecological effects on sexual selection by female choice are rare. Most studies of 'magic trait' speciation focus on scenarios in which assortative mating is mediated by a single trait, which is expressed in both sexes (host preference, body size, coloration). In such cases, the probability that two individuals mate is directly related to their similarity with regard to this trait. Theory predicts that mechanisms like these are most conducive to speciation (Felsenstein, 1981). However, they can account for only a small number of cases of selective mating in nature. In particular, they do not explain the widespread occurrence of sexual dimorphism and the spectacular diversity in male ornamentation in the animal kingdom, ranging from elongated fins and feathers to bright colours and elaborate birdsong (Andersson, 1994). These phenomena derive from mechanisms of selective mating that are mediated by two independent traits: a sexual preference, which is often expressed only in females, and a preferred trait, typically limited to males. Such mechanisms may be less favourable to speciation, but their evolutionary consequences are substantial. In particular, female preferences for male ornaments can gen-

erate large differences in mating success among males (i.e. sexual selection), thereby increasing the frequency of such traits in populations and changing their genetic composition.

There is overwhelming empirical evidence for both direct and indirect ecological selection on female mating preferences. Direct selection occurs for example when predation risk influences choosiness (Hedrick and Dill, 1993; Johnson and Basolo, 2003; Kim et al., 2009), or when environmental conditions affect female perception of male signals (Boughman, 2001; Endler, 1992; Hebets et al., 2008). Indirect selection occurs when female preferences are mediated by male traits that indicate some aspect of ecological performance, such as parasite resistance or foraging ability (Andersson, 1994; Jennions et al., 2001; Møller and Alatalo, 1999). In both direct and indirect scenarios, environmental heterogeneity in ecological conditions can affect male traits, female preferences or both, contributing to population divergence (Lorch et al., 2003; Reinhold, 2004; Van Doorn et al., 2009).

3 Divergent Sensory Drive

Variation in sensory environments exerts selection on sexual communication in two ways (Endler, 1992; Fuller et al., 2005b). First, (male) sexual signals are subject to environmental selection for greater detectability. Optimal signal design depends on the background against which signals are perceived and the signal propagation properties of the environment (Guilford and Dawkins, 1991). For visual signals, conspicuousness often additionally depends on the ambient light spectrum that is available for reflection. As a result of these effects, different signal properties are expected to evolve in different environments. Second, the same environmental conditions that affect signal design also exert selection on sensory properties. Natural selection for sensory performance in a particular environment, or for detecting particular targets (e.g. Madden and Tanner, 2003; Rodd et al., 2002; Smith et al., 2004), will generate sensory biases that may pleiotropically affect mating preferences (Endler, 1992; Ryan, 1990). Thus, different sensory environments may generate different mating preferences as a by-product of adaptation.

To evaluate the potential role of sensory drive in speciation, the above distinction is important. Pleiotropic effects of sensory adaptation would generate direct selection on mating preferences, essentially constituting a 'magic trait' scenario in which ecological adaptation immediately restricts interbreeding between

diverging populations. In contrast, environmental selection on sexual signals alone does not promote reproductive isolation, unless preferences diverge as well. Therefore, distinguishing between direct and indirect divergent selection in natural systems is a crucial step in determining the role of sensory drive in speciation. Freshwater fishes are emerging as rewarding model systems for studying this question (e.g. sticklebacks, (Boughman, 2001); silversides (Gray et al., 2008); bluefin killifish (Fuller et al., 2005a); cichlids (Carleton and Kocher, 2001; Seehausen et al., 2008)). In the present paper, we evaluate the current evidence for direct and indirect effects of sensory adaptation on species divergence in the genus *Pundamilia*, a species-rich group within the adaptive radiation of haplochromine cichlids in Lake Victoria. We review roughly a decade of research in this system and integrate the available knowledge into a hypothetical scenario for *Pundamilia* divergence.

4 Haplochromine Cichlids

Haplochromines are an extremely species-rich lineage of cichlid fish. Hundreds of species have evolved in East-African lakes within a very short time (e.g. less than 15,000 years for Lake Victoria (Stager and Johnson, 2008)). Consequently, the haplochromines have become an important model system for speciation research (Joyce et al., 2005; Kocher, 2004; Meyer et al., 1990; Seehausen, 2006; Seehausen et al., 1997; Verheyen et al., 2003).

Haplochromine species can often be distinguished by the bright colours of reproductively active males, while females are generally grey or brown. All species are female mouthbrooders; males do not contribute to broodcare. Male coloration affects both inter- and intraspecific female mate choice (Kidd et al., 2006; Knight and Turner, 2004; Maan et al., 2004; Pauers et al., 2004; Seehausen and Van Alphen, 1998), indicating that sexual selection for coloration may be important for species differentiation. At the same time, haplochromines show extensive variation in colour vision, apparently as an adaptation to their diverse visual environments (Carleton and Kocher, 2001; Carleton et al., 2005; Hofmann et al., 2009; Parry et al., 2005; Spady et al., 2005; Sugawara et al., 2005; Terai et al., 2002; Terai et al., 2006; Van der Meer and Bowmaker, 1995). Moreover, species diversity and water transparency are correlated (Seehausen et al., 1997), suggesting a link between visual environments and the processes of speciation and coexistence. Together, these observations raise the ques-

tion how sensory adaptation, visual communication and sexual selection interact in the course of haplochromine speciation.

5 Sensory Drive in *Pundamilia* Speciation

Pundamilia pundamilia and *Pundamilia nyererei* are two closely related haplochromine species that co-occur at many islands in Lake Victoria (Seehausen, 1996) (Fig. 1). Morphologically similar, the two species differ strikingly in male coloration: *P. pundamilia* males are metallic blue-grey, *P. nyererei* males are bright red dorsally with yellow flanks. Females of both species are cryptically brown and are difficult to distinguish. Mate-choice experiments in the laboratory established that females exert species-specific preferences for either blue or red male coloration (Haesler and Seehausen, 2005; Seehausen and Van Alphen, 1998; van der Sluijs et al., 2008; Verzijden and ten Cate, 2007). Field observations and laboratory experiments in one of the two species, *P. nyererei*, showed that females also exert intraspecific directional sexual selection on male coloration (Maan et al., 2004; Maan et al., 2010). These findings suggest that female preferences for male coloration not only mediate current reproductive isolation between *P. pundamilia* and *P. nyererei*, but may have contributed to the process of divergence as well.

Research on *Pundamilia* has focused on the Mwanza Gulf, in the south-east of Lake Victoria (Fig. 1; Table 1). Here, *Pundamilia* species inhabit locations with water transparencies ranging from about 50 to about 250cm Secchi readings (Seehausen, 2009). For comparison, Secchi readings in the two other great East-African lakes, Malawi and Tanganyika, may exceed 1500cm. In very turbid locations (Secchi reading around 50 cm), *Pundamilia* populations do not separate into a distinct blue and a distinct red form but constitute a single population, in which variation in both male coloration and female preferences is unimodally distributed (Seehausen et al., 2008). In locations where the water is relatively clear (Secchi readings 60-250cm), *Pundamilia* populations fall into two distinct forms that show significant differentiation in neutral genetic markers (microsatellites: multilocus $F_{st} > 0.01$, $P < 0.05$; Table 1). One of these species contains blue males and blue-preferring females *P. pundamilia* and the other has red males and red-preferring females *P. nyererei*. The importance of visual communication for species differentiation is further confirmed by laboratory studies: under light conditions that preclude colour discrimination, behavioural colour

preferences disappear and mating isolation breaks down (Seehausen and Van Alphen, 1998; Selz, 2009¹).

In addition to geographical variation in water clarity, *Pundamilia* populations experience depth-related gradients in the intensity and spectral composition of the ambient light. While light conditions in shallow water resemble those at the surface, the high levels of suspended and dissolved organic material in the lake result in rapidly changing light conditions with increasing depth. Absorbance and scattering, particularly of shorter wavelengths, generate darker and more red-shifted vis-

ual environments in deeper waters (Levring and Fish, 1956; Lythgoe, 1984). The distribution of *P. pundamilia* and *P. nyererei* covaries with this transition: at all sites where the two species are genetically distinct, *P. nyererei* breeds in deeper waters than *P. pundamilia*. As a result, *P. pundamilia* inhabits a bright, broad-spectrum visual environment, but the deeper habitat of *P. nyererei* has a roughly three-fold lower light intensity and a spectrum that is significantly shifted towards longer wavelengths (Maan et al., 2006a)(Fig. 2).

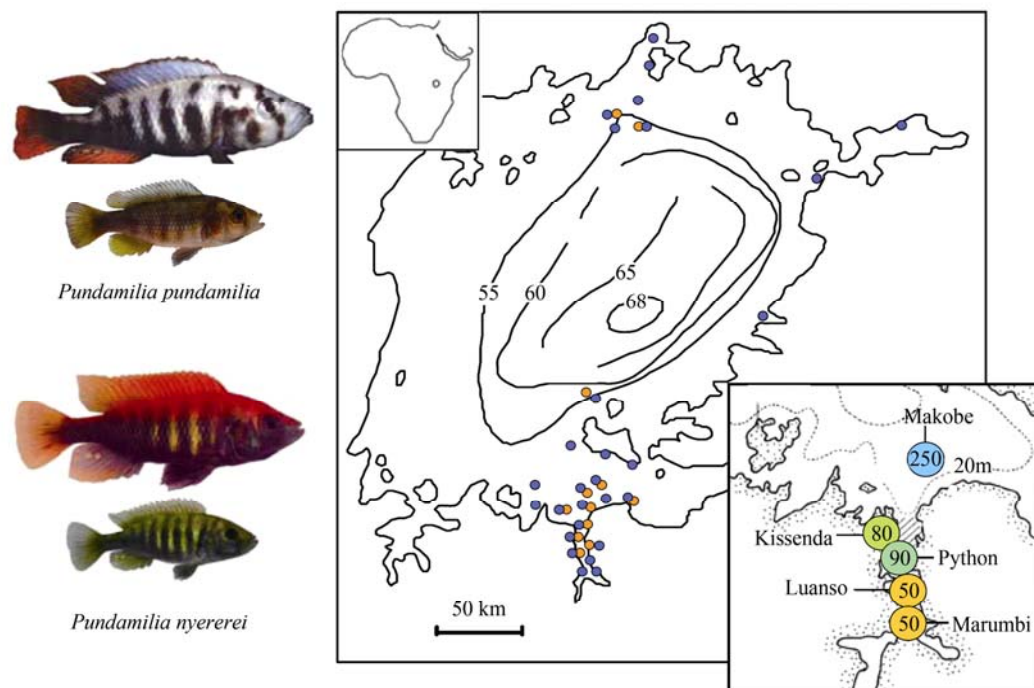


Fig. 1 Male and female *P. pundamilia* and *P. nyererei* (from Makobe Island)

Large map: distribution of known records of the two species in Lake Victoria. Small inset map: five sampling locations in the Mwanza Gulf: Marumbi, Luanso, Python, Kissenda and Makobe. Water transparencies at the islands (cm Secchi disk readings) are given inside the circles (low transparency=brown; high transparency=blue). Note that Kissenda island lies inside a bay, hence the lower transparency there than that at Python island, despite Kissenda's greater proximity to the clear water areas (Figure modified from Seehausen, 2009).

Table 1 Differentiation between *P. pundamilia* and *P. nyererei* at five sampling locations in southeast Lake Victoria

	a) Water transparency ¹	b) Fst ¹			c) RR/RG ²	
		msat	SWS2A	LWS	<i>P. pundamilia</i>	<i>P. nyererei</i>
Marumbi	53±8	0.000		0.000		
Luanso	50±10	0.002		0.000		
Kissenda	78±24	0.010	0.1	0.648		
Python	96±21	0.014		0.826	0.81	1.47
Makobe	225±67	0.026	0.437	0.890	0	0.15

a) Water transparency (cm Secchi; mean ±SD). b) Genetic differentiation at neutral loci (11 microsatellites) and at the SWS2A and LWS opsin loci. c) The ratio of identical double cones (both cones expressing LWS opsin) to non-identical double cones (one cone expressing LWS, the other RH2). Bold script indicates significant differentiation. ¹Seehausen et al., 2008; ²Carleton et al., 2005.

¹ Selz O, 2009. Interspecific female mate choice in Lake Victoria cichlids: the role of male nuptial hue. unpublished MSc Thesis.

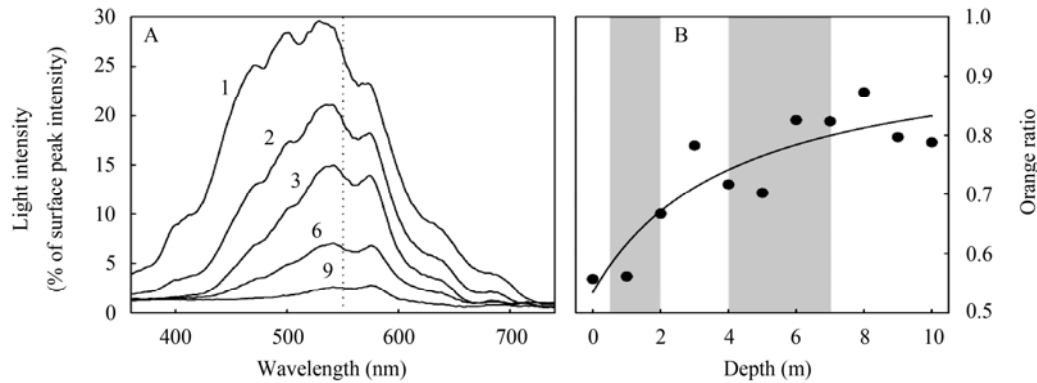


Fig. 2 Photic habitats of *P. pundamilia* and *P. nyererei* at a clear-water site, Makobe Island

A. Transmission light spectra at different depths. Numbers indicate depth in meters. The dotted line indicates the 550 nm threshold which is used to calculate the “orange ratio”, which measures the relative contribution of long wavelengths to the ambient spectrum, and is calculated by dividing the light intensity in the 550–700 nm range (yellow, orange, red) by the light intensity in the 400–550 nm range (blue, green) (Endler and Houde, 1995). B. The increase in orange ratio with water depth. Shaded areas indicate *P. pundamilia* (0.5–2 m) and *P. nyererei* (4–7 m) breeding habitats (From Maan et al., 2006a)

6 Sensory Drive in *Pundamilia*: Direct Selection?

One way in which divergent sensory drive can contribute to speciation is through pleiotropic effects of sensory adaptation on mate choice. This hypothesis makes two main predictions, that recent work in the *Pundamilia* system has started to address: 1) the two species differ in spectral sensitivity in a way that corresponds to the species difference in visual environment and male coloration; and 2) spectral sensitivity affects colour preferences in a mate choice context, such that females with long-wavelength-biased visual systems prefer red males, while females with short-wavelength-biased visual systems prefer blue males.

6.1 Divergence in colour vision

Vertebrate colour vision is shaped by the light absorbance properties of the pigments expressed in retinal cones. These pigments consist of opsin proteins bound to a vitamin-A-based chromophore. In addition to neural processing, variation in colour vision derives from variation in opsin amino acid sequences and opsin expression patterns. Moreover, major shifts in spectral sensitivity can result from differential chromophore usage. Current evidence indicates that there are biologically meaningful differences between the two *Pundamilia* species in several of these determinants of colour perception (Table 1).

Pundamilia express four different opsin genes: short-wavelength-sensitive (SWS) 2A and 2B, middle-wavelength-sensitive (MWS or Rh2) and long-wavelength-sensitive (LWS) (Carleton et al., 2005; Hofmann et al., 2009). In three out of five studied communities, all from

relatively clear waters, *P. nyererei* and *P. pundamilia* are significantly differentiated at the LWS opsin locus (Table 1; Seehausen et al., 2008). Most *P. nyererei* individuals carry a sequence variant that differs in three non-synonymous substitutions from the allele that is most frequent in *P. pundamilia*, and that is predicted to shift spectral sensitivity by about 15 nm towards longer wavelengths. In two populations from clear water, sequencing of SWS2A revealed significant divergence as well. However, all of the variable nucleotide positions in SWS2A were either synonymous or located in introns, suggesting that these mutations are neutral. Because LWS and SWS are located on the same chromosome, it is possible that sequence divergence in SWS is a by-product of divergent selection on LWS.

While both species express the same set of opsin genes, the levels of expression differ between locations and between species within locations. Realtime-PCR analysis revealed that both species express less SWS and more MWS/LWS in more turbid locations (Carleton et al., 2005; Hofmann et al., 2009), consistent with adaptation to the more red-shifted light conditions there. In addition, the species differ in the composition of the retinal mosaic. Cichlid retinas contain single and double cones. Single cones contain SWS pigments, while double cones may consist of either two identical, LWS-expressing cones or a pair of two non-identical cones: one expressing MWS opsin and the other LWS opsin. Microspectrophotometry (MSP) of the cone outer segments in two clear-water populations revealed that *P. nyererei* retinas contain a larger proportion of identical double cones than *P. pundamilia* retinas, consistent with a red-shifted spectral sensitivity (Carleton et al., 2005;

Hofmann et al., 2009).

Finally, the light absorbance properties of opsin pigments are co-determined by the chromophore that they are bound to. In fish, chromophores are mainly derived from vitamin A1 (retinal) or A2 (3,4-dehydroretinal) (Bowmaker, 1995; Munz and McFarland, 1977). Variation in chromophore usage can have major consequences for spectral sensitivity: A2 usage is associated with a sensitivity shift towards longer wavelengths, with greater shifts (up to 60nm) for longer-wavelength opsins (Dartnall and Lythgoe, 1965; Toyama et al., 2008). Lake Victoria haplochromines mostly use A1-derived chromophores, but some species incorporate A2 as well (Sugawara et al., 2005; Terai et al., 2006; Van der Meer and Bowmaker, 1995). Chromophore usage has not been quantified for *Pundamilia*. However, MSP measurements suggest that, under identical laboratory conditions, *P. nyererei* may use greater proportions of A2 than *P. pundamilia* (Carleton et al., 2005).

Opsin sequences and expression patterns, together with chromophore usage, determine whether a visual stimulus *can* be perceived by an organism. Whether it *is* in fact perceived, how it is perceived, and whether it is translated into a behavioural response, is determined by neural processes that we know relatively little about. In the case of *Pundamilia*, we have tested species differences in colour vision at the behavioural level, using the optomotor response to assess spectral sensitivity thresholds. For individuals from a clear water community, we found species differences in the predicted direction: *P. pundamilia* was more sensitive to blue light and *P. nyererei* was more sensitive to red light (Maan et al., 2006a).

With species differences at the level of opsin sequences, opsin expression, and behavioural responses to coloured light, the evidence for divergence in visual systems is fairly convincing. But do these differences

influence female mating preference?

6.2 Colour vision predicts sexual colour preference

The second prediction of the direct selection hypothesis is a causal relationship between visual adaptation and female colour preference. Testing this prediction requires manipulation of spectral sensitivity and subsequent evaluation of colour preferences in a mate-choice context. Seehausen et al. (2008) provide an initial attempt at this type of manipulation. They crossed *P. pundamilia* and *P. nyererei* in the laboratory, generating an F2 hybrid generation with recombinant opsin genotypes, ranging from completely *P. pundamilia*-like to completely *P. nyererei*-like and several different intermediate genotypes. For a group of 12 F2 hybrid females, they then sequenced the two opsin genes that were significantly divergent between the species, SWS2A and LWS, and determined the behavioural mating preferences of the same individuals. Analysis revealed a significant correlation between opsin genotype and preference ($F_{2, 9}=4.72$, $P=0.0396$; Fig. 3). However, the substitutions that differentiate the two species at the SWS2A locus are not predicted to have any direct effect on colour vision (see above), implying that this relationship might be due to variation at LWS alone. Yet, the correlation between LWS genotype and preference was not significant ($P=0.13$), indicating a role of additional factors in determining mating preference, possibly located on the same chromosome that carries LWS and SWS2A. Clearly, further work is necessary to resolve the causal relationship between colour vision and mating preference. A larger number of females need to be tested, and analyses ought to include other levels of variation in the visual system, such as differential opsin expression and chromophore usage. Finally, mate choice experiments ought to be carried out in light environments that resemble those in nature.

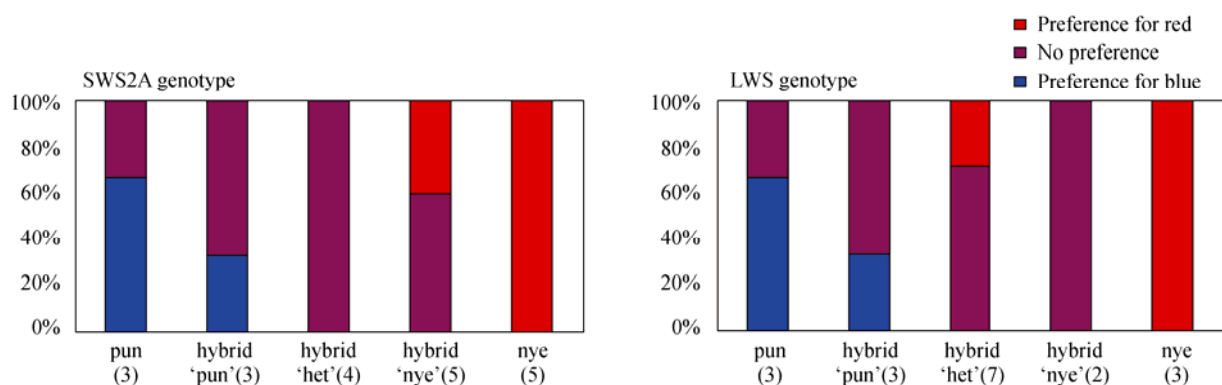


Fig. 3 Opsin genotypes and female mate preference of F2 offspring of *P. pundamilia* (pun) and *P. nyererei* (nye) and F2 hybrids SWS2A and LWS genotypes are categorised as pundamilia-like ('pun'), heterozygote ('het') or nyererei-like ('nye'). Bars indicate female preferences in two-way mate choice experiments, with preferences for *P. pundamilia* males indicated in blue; preferences for *P. nyererei* males in red; and females without significant preferences in grey (Data from Seehausen et al., 2008).

7 Sensory Drive in *Pundamilia* Speciation: Indirect Selection?

As an alternative to direct selection, *Pundamilia* female mating preferences may diverge through indirect selection (Seehausen et al., 2008). In such a scenario, correlations between light environment and male coloration would be largely driven by adaptation by males, and divergence of female preferences follows. As discussed above, variation in visual environments may exert selection not only on visual systems, but also on visual signals. Based on the results obtained for *P. nyererei* (Maan et al., 2004) as well as many other organisms (Ryan and Keady-Hector, 1992), we may hypothesise that *Pundamilia* females share a general preference for conspicuous males, generating selection on males to evolve colour signals that maximise conspicuousness in their local light environment. This mechanism could explain the observed correlation between male coloration and water depth: variation in ambient light spectrum could favour different colour signals at different depths, independent of variation in female spectral sensitivity. Preference divergence would then require additional mechanisms, such as Fisherian coevolution, frequency-dependent sexual selection, or female choice for locally adapted males. Below, we discuss the evidence for this indirect scenario in more detail.

7.1 Males maximise local conspicuousness

To stand out against the background, animals often use signals that contrast with the colours or sounds that dominate in their environment (Bradbury and Vehrencamp, 1998). Visual signals that depend on light reflectance, however, are constrained by the wavelength spectrum of the incident light. The spectral properties of Lake Victoria waters generate a red-shift in ambient light in the first 10m of the water column, resulting in a greenish-yellowish background colour. Theoretically, blue colour signals could achieve high contrast against such a background. However, the low penetration of short wavelengths in deeper waters restricts blue reflectance, precluding the production of sufficiently intense signals in this spectral range. The red and yellow coloration of *P. nyererei* may represent a compromise: taking advantage of the abundant long wavelengths in the incident light, but still generating colour contrast against the dominant background colour (Fig. 4).

Colour variation between populations of *P. nyererei* is consistent with this hypothesis, as males tend to be more orange at sites with more turbid waters, and more red in clearer waters (Maan et al., 2010). Quantitative

analysis of male conspicuousness in different environments is necessary to test this idea more systematically. Also, while our argumentation explains why the blue *P. pundamilia* phenotype is restricted to shallow waters, it does not explain why red and yellow phenotypes should be restricted to deeper waters. These colours should generate conspicuous signals in shallow waters as well. Probably, the near absence of red coloration in shallow water is the result of additional selective pressures, such as increased predation on conspicuous individuals (Maan et al., 2008a).

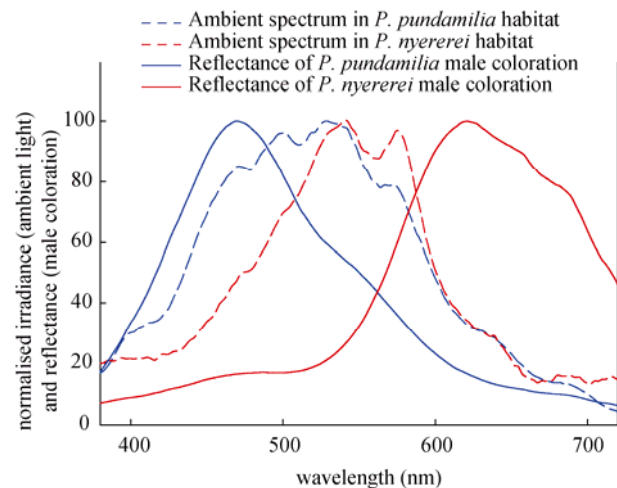


Fig. 4 Reflectance of male coloration of *P. pundamilia* and *P. nyererei* and underwater light spectra in the species' habitat

Data are from the clear-water site at Makobe Island (Modified from Maan et al., 2006a).

Additional evidence for the adaptation of male colours to signaling conditions comes from a qualitative correlation between *Pundamilia* male nuptial coloration and the steepness of the rocks in the breeding habitat. Specifically, among the species with red male body coloration, the presence of red on the flanks decreases and that on the dorsal body surface increases with steepness of the rocks. This may be explained by variation in the angle at which males and females interact. Male *Pundamilia* are highly territorial, and their territories are centered around crevices in the rocky substrate. On flat or gently sloping slopes, females observe territorial males at an approximately horizontal viewing angle. On nearly vertical rocks, females observe males from above. It should hence pay to concentrate the display colors dorsally on the body, while displaying on the flanks should pay in environments with a horizontal floor (Seehausen, 1996).

Thus, while we have indications that male colours co-evolve with light and signaling conditions, more

quantitative work is required to quantify the extent to which the distribution of colour phenotypes, between locations and along depth gradients within locations, can be explained by these conditions, taking into account variation in habitat features and haplochromine colour vision.

7.2 Preference-trait coevolution

Divergence of female preferences may follow divergence in male traits as a result of Fisherian runaway. Such coevolution may be part of any sexual selection process (Mead and Arnold, 2004). On its own however, while theoretically possible (Higashi et al., 1999; Takimoto et al., 2000), divergent Fisherian coevolution is unlikely to be sufficient to maintain reproductive isolation when species ranges are overlapping (e.g. Arnegard and Kondrashov, 2004; Payne and Krakauer, 1997; Turelli et al., 2001; Van Doorn et al., 2004). The reason is that occasional hybridization will quickly lead to a breakdown of linkage disequilibrium between preference and trait unless there is selection against hybrids.

Direct support for Fisherian coevolution in *Pundamilia* is absent. Experiments within a population with variable colour failed to find a phenotypic correlation between female preference and male coloration: variation in female colour preference did not predict the colour of the male offspring of these females, and male coloration did not predict the preference of female offspring of those males (Van der Sluijs, 2008; Van der Sluijs et al., 2010). However, these tests were conducted in a population from highly turbid waters, where such linkage disequilibrium may never have evolved, or may have been lost.

7.3 Frequency-dependent sexual selection

Competition for access to mates or territories may not only generate negative frequency-dependent selection on male coloration (Mikami et al., 2004; Seehausen and Schluter, 2004), but also on female preferences (Almeida and de Abreu, 2003; Van Doorn et al., 2004). When females compete over males, females expressing rare mating preferences could be at an advantage because they face weaker competition from other females. When female mate choice and male-male competition are based on the same male trait, frequency-dependent sexual selection on both preferences and traits can promote divergence. In *Pundamilia*, colour-mediated male competition (Dijkstra et al., 2007b) and female mate choice (Seehausen and Van Alphen, 1998) satisfy two prerequisites for this mechanism to occur. The third condition, competition among females, remains to be investigated. Male mate choice (as observed in several

haplochromine species, Pierotti et al., 2009; Seehausen et al., 1999; Werner and Lotem, 2003, 2006) could generate such competition, and female-female aggressive competition has been documented (Dijkstra et al., 2008).

7.4 Female choice for locally adapted males

The expression of sexual signals is often condition-dependent, and may thus reflect heritable variation in traits that affect fitness, such as foraging efficiency or parasite resistance. When different traits confer fitness advantages in different habitats, sexual selection may operate on these different traits in the different environments. It may then contribute to speciation by accelerating local adaptation (Lorch et al., 2003; Reinhold, 2004; Whitlock and Agrawal, 2009) and by reducing gene flow between populations adapting to divergent ecological regimes, similar to reinforcement (Bolnick and Fitzpatrick, 2007; Servedio and Noor, 2003; Van Doorn et al., 2009). Could the divergent colour preferences of female *Pundamilia* be driven by such a process?

P. pundamilia and *P. nyererei*, like other haplochromine cichlids, are female mouthbrooders and males do not contribute to brood care. Direct benefits are therefore unlikely to influence female choice, but female choice based on male coloration may confer indirect benefits through association of colour variation with heritable variation in fitness-related traits.

We do have some evidence to suggest that variation in male coloration is related to variation in ecological performance. First, the red and yellow coloration of *P. nyererei* males is based on carotenoids, that must be obtained from the diet and may constitute a limiting resource (Maan et al., 2006b). Female choice for males with bright red and yellow colours could thus be driven by selection for foraging ability or efficient carotenoid metabolism. Second, experimental evidence is consistent with the hypothesis that the expression of male nuptial coloration is subject to a trade-off with immune function (Dijkstra et al., 2007a), possibly contributing to the honesty of male colour signals. Consistent with this too, we found male coloration to be correlated with parasite load in a field study. In a clear-water community, higher colour scores among red males *P. nyererei* as well as among blue males *P. pundamilia* were associated with lower parasite loads (Maan et al., 2006b; Maan et al., 2008b). This implies that female preferences for strongly coloured males might exert sexual selection for lower parasite infection.

Sexual selection for heritable benefits can contribute to population divergence when variation in male trait

values reflects a gene-by-environment interaction component in fitness variation. Then, sexual signals can become 'markers' of local adaptation (Baptestini et al., 2009; Dieckmann and Doebeli, 1999; Doebeli and Dieckmann, 2003; Kondrashov and Kondrashov, 1999; Van Doorn et al., 2009). Some ecologically important traits are statistically associated with coloration in *Pundamilia*: wherever *P. pundamilia* and *P. nyererei* are distinct species, they diverge in their depth ranges, albeit *P. pundamilia* can be contained within the depth range of *P. nyererei* (Seehausen et al., 2008). Thus, the offspring from red males may tend to inherit traits that confer advantages in the deep-water habitat, while the offspring from blue males may inherit alleles that confer adaptation to shallow water.

Spectral sensitivity could be such an adaptation. In addition to direct effects of colour vision on female preferences, discussed above, divergence in spectral sensitivity could contribute to preference divergence indirectly, if females can increase their fitness by mating with males that express a locally adapted set of opsin genes. In Lake Malawi cichlids, spectral sensitivity affects foraging efficiency (Jordan et al., 2004) and covaries with foraging niche (Hofmann et al., 2009). In Lake Victoria, spectral sensitivity correlates predominantly with local light environment, determined by the interaction between water clarity and water depth (Hofmann et al., 2009; Seehausen et al., 2008; Terai et al., 2006). These associations between vision and environment indicate that assortative mating by visual system along environmental gradients could be favoured by natural selection.

Parasite resistance provides another candidate mechanism for habitat-dependent sexual selection. At an island where the two species are genetically distinct and occur at different depths, they carry a nearly identical set of macroparasite species, but infestation rates of individual parasites are significantly different (Maan et al., 2008b). *P. pundamilia* have high nematode loads, possibly related to the abundance of piscivorous birds in the shallow near-shore habitat, that serve as intermediate hosts for these parasites. In contrast, *P. nyererei* have higher loads of gill copepods, consistent with their more limnetic feeding style. Thus, differences in parasite exposure could promote habitat-specific parasite defenses, which in turn might generate selection for assortative mating, mediated by male colour 'markers'. However, this remains speculative until parasite communities are compared also at islands where the two species have overlapping depth ranges and are genetically less strongly differentiated.

8 A scenario for *Pundamilia* Divergence

The evidence discussed above suggests that visual adaptation plays a major role in the divergence of *P. pundamilia* and *P. nyererei*. Moreover, computer simulations confirm the feasibility of speciation by sensory drive along environmental gradients (Kawata et al., 2007). However, the relative importance of direct and indirect mechanisms remains to be determined. It seems likely that several mechanisms are acting simultaneously or in close succession. Comparative work in several populations indicates that divergence in male colour and female preferences precedes diet segregation (Seehausen, 2009), but coincides with differentiation in depth range and in visual pigment genes (Seehausen et al., 2008). This suggests that divergent selection on sensory systems between depth ranges could initiate divergence, while other sources of selection may increase in importance later.

Our hypothesised scenario for *Pundamilia* divergence is illustrated in Fig. 5. We suggest that the involvement of divergent sexual selection starts with a general female preference for conspicuously coloured males. Such preferences may be driven by both direct and indirect benefits (Schluter and Price, 1993). First, female choice is likely subject to direct natural selection, because mate searching and assessment entails energetic costs and exposure to predators. Brightly coloured males are easier to detect on longer distance, such that preferences for such males may contribute to female survival. Second, the production and maintenance costs of bright colours (predators, physiological trade-offs) warrant their reliability as indicators of fitness. In this way, preferences for brightly coloured males may contribute to offspring survival. Third, Fisherian coevolution could exert indirect sexual selection on female mating preferences.

When the coincidence of ecological opportunity and intraspecific competition increases the depth range at which individuals forage and mate, they become subject to divergent natural selection. Environmental heterogeneity along the depth gradient influences several traits: heterogeneity in visual environments generates selection on visual systems and, through sexual selection for conspicuousness, leads to selection on male coloration. Additionally, differential prey availability generates selection on feeding-related traits; differential predation intensity generates selection on traits related to predation risk; and diet- and habitat-related variation in parasite exposure generates selection on immune defense.

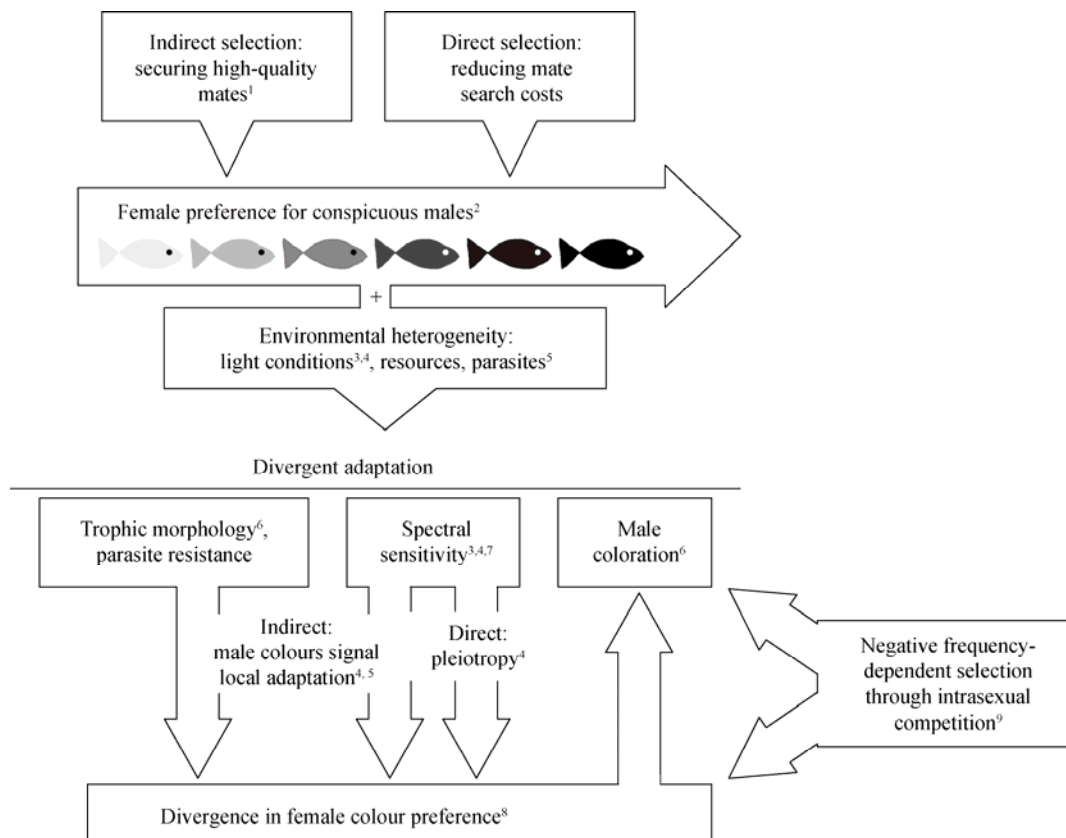


Fig. 5 An integrated scenario for *Pundamilia* divergence

1. Maan et al., 2006b; 2. Maan et al., 2004; 3. Maan et al., 2006a; 4. Seehausen et al., 2008; 5. Maan et al., 2008b; 6. Seehausen et al., 1998; Magalhaes et al., 2009; 7. Carleton et al., 2005; 8. Seehausen and Van Alphen, 1998; Stelkens et al., 2008; 9. Dijkstra et al., 2007b; Dijkstra et al., 2008.

To the extent that it outweighs homogenizing gene flow, this heterogeneous and multifarious selective regime induces clinal variation in ecological phenotypes that may split into two distinct phenotype clusters when assortative mating evolves. Here again, both direct and indirect mechanisms may play a role. First, visual adaptation may pleiotropically affect female colour preferences, rapidly generating an association between spectral sensitivity and male colour. Second, natural and sexual selection against hybrid and recombinant individuals may favour colour-mediated assortative mating preferences. For example, males with blue coloration but a deep water-adapted visual system, or vice versa, are likely to be selected against.

9 Perspectives

The divergence scenario outlined above leaves us with several empirical challenges. First, we assume that *Pundamilia* females exert selection on male conspicuousness and that male coloration evolves towards greater conspicuousness. While current evidence is consistent with this, more detailed characterization of fe-

male preference functions and male coloration is required. For example, the relative importance of colour and brightness contrast in determining the efficacy and attractiveness of male coloration should be established. Second, the evidence for direct selection is equivocal. Testing its importance requires additional experimental work on the relationship between spectral sensitivity and female colour preferences during mate choice. In addition, direct selection predicts that, in each habitat, male coloration evolves to become most conspicuous to visual systems that are adapted to that particular habitat. This prediction will be tested by integrated analysis of male colour, visual environment and spectral sensitivity along natural light gradients.

Third, there is extensive evidence for both genetically fixed and phenotypically plastic components of fish colour vision, also in cichlids (Cheng and Novales Flamarique 2004; Fuller et al. 2005; Wagner and Kroger 2005; Spady et al. 2006; Carleton et al. 2008; Temple et al. 2008). If haplochromine spectral sensitivity is plastic, migration between light environments could break down the association between visual genotype and male col-

oration, preventing speciation. Future work is therefore aimed at resolving the genetic and plastic contributions to spectral sensitivity.

Fourth, for indirect mechanisms to generate reproductive isolation, selection against hybrids should be strong (Servedio, 2008). This is because indirect mechanisms require the evolution of linkage disequilibrium between female preference, male signals, and the traits under divergent natural selection. Analysis of opsin sequence variation in *Pundamilia* and other haplochromines has revealed signatures of strong divergent selection on these genes (Seehausen et al., 2008; Terai et al., 2002). More direct evidence could be obtained by quantifying visual performance of hybrid opsin genotypes in parental visual environments. Likewise, divergent selection on other ecologically important traits (feeding morphology, parasite resistance) remain to be quantified. We do have experimental evidence for sexual selection against hybrids: females of one of the two species prefer conspecific males over hybrid males (van der Sluijs et al., 2008), and hybrid females either mate randomly or prefer males of either of the two parental colours (Haesler and Seehausen, 2005; Stelkens et al., 2008). Additional traits that are targets of disruptive selection could be detected by genome scans of sympatric hybridizing populations, and subsequent analysis of associations between marker loci under disruptive selection and phenotypic trait values. Such work is currently in progress in our lab. The critical test though, of whether indirect selection is sufficient to generate reproductive isolation, would estimate the strength of selection on the association between opsin genes, male colours and female preferences. This estimate is difficult to obtain and currently unavailable, but the maintenance of almost perfect associations between opsin genotype and heritable male colour phenotype, even at places where introgressive hybridization is common, suggest that strong selection does operate on these associations (Seehausen et al., 2008).

Finally, it is likely that other sources of selection on colour and preferences facilitate speciation in this system. Coexistence of different colours may be promoted by male aggression biases that generate negative frequency-dependent selection on coloration (Dijkstra et al., 2007b; Seehausen and Schluter, 2004). In addition, crossfostering experiments have shown that female preferences may be influenced by sexual imprinting (Verzijden and ten Cate, 2007), an effect that could be mediated by visual, chemical, or acoustic cues. One possibility is the involvement of MHC-mediated com-

munication, which could provide another link between ecological adaptation (to parasite exposure) and mate choice. Mate choice for MHC compatibility occurs in many systems (Milinski, 2006) and MHC evolution may well be relevant for haplochromine diversity (Blais et al., 2007).

Determining the relative importance of these mechanisms in the course of *Pundamilia* speciation will be a major focus of future studies.

10 Conclusion

By providing an ecological mechanism for divergent selection on both preferences and traits, sensory drive can be a powerful diversifying agent. The *Pundamilia* model system illustrates how direct and indirect selective pressures might contribute to this process. Dismantling these two will be important not only for reconstructing the evolutionary history of this species complex, but also for establishing how sensory drive contributes to speciation in general.

Our *Pundamilia* studies raise a fundamental question regarding the concept of 'speciation by sensory drive'. Clearly, when pleiotropic effects of perceptual divergence on selective mating are enough to drive speciation, this term is appropriate. We note that this mechanism integrates two previously disconnected paradigms in evolutionary biology: directional sexual selection by female choice on the one hand, and 'magic trait' speciation on the other. Support for this scenario in *Pundamilia* or other taxa would illustrate how divergent ecological adaptation not only promotes speciation in similarity-based mating systems, but also in taxa where selective mating entails female choice for male ornamental traits.

However, if the associations between sensory adaptation, female preference and male signal design arises through indirect mechanisms, then the nature of those indirect selective pressures should determine whether speciation is truly 'by sensory drive'. Assortative mating driven by natural selection for locally adapted visual systems implies that sensory adaptation and signal divergence alone are sufficient to generate reproductive isolation. Such a scenario could qualify as sensory drive speciation as well. If, on the other hand, divergence of mating preferences (also) requires other sources of selection, such as selection for parasite resistance, then the evolution of reproductive isolation can not be explained by sensory adaptation alone. In that case, perceptual processes may contribute to signal and preference divergence, but determining the mechanism by which

gene flow is reduced then requires evaluation of the relative importance of sensory drive and other selective pressures.

To evaluate the contribution of sensory processes to species divergence, we hope that future studies will address these distinctions.

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