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Genetic and environmental variation in the visual properties of bluefin killifish, *Lucania goodei*

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Abstract

Animals use their sensory systems to detect information about the external environment in order to find mates, locate food and habitat and avoid predators. Yet, there is little understanding of the relative amounts of genetic and/or environmental variation in sensory system properties. In this paper, we demonstrate genetic and environmental variation in opsin expression in a population of bluefin killifish. We measured expression of five opsins (which correlates with relative frequency of corresponding cones) using quantitative, real-time polymerase chain reaction for offspring from a breeding study where offspring were raised under different lighting conditions. Sire (i.e. genetic) effects were present for opsin found in yellow photopigment. Dam effects were present for opsins that create violet, blue and red photopigment. Lighting conditions affected expression of all opsins except SWS2A and mimicked the pattern found among populations. These results highlight the fact that sensory systems are both plastic and yet readily evolvable traits.

Introduction

Sensory systems are the means by which animals detect external information and enter that information into their nervous systems for processing. As such, sensory system properties are incorporated into many areas of evolutionary theory including sexual selection (West-Eberhard, 1984; Ryan, 1990; Endler, 1992), foraging ecology, population divergence and speciation (Endler, 1992; Schluter & Price, 1993). Yet despite this, we have little understanding of the degree to which there is genetic and/or environmental variation in sensory systems. The magnitude of variation in sensory systems and the extent to which that variation is genetic and/or environmental has important implications.

The presence of genetic variation implies that either natural or sexual selection can favour a change in the population mean of sensory system properties. This means that behaviours correlated with sensory systems, such as mate choice or foraging behaviour (West-Eberhard, 1984; Ryan, 1990; Endler, 1992, 1993; e.g. Rowe *et al.*, 2004) will also be subject to natural and/or sexual selection. Furthermore, in the case of sexual selection, genetic variation in sensory systems will allow for the build-up of genetic covariances between both (i) sensory system properties and male display trait and (ii) sensory system properties and viability. These covariances are critical parameters for the Fisherian and good-genes models of sexual selection (Lande, 1981; Pomiankowski, 1987; Iwasa & Pomiankowski, 1991).

Environmental variation in sensory systems implies that animal perceptions of their surroundings will change as a result of environmental conditions. In the case of foraging behaviour, this means that the profitability of various prey types may vary as a function of their detectability (Stephens & Krebs, 1986). In the case of sexual selection, plastic sensory systems may result in a reduction in the strength of sexual selection and a change in the direction of selection on male traits (Rodriguez & Greenfield, 2003). If environmental conditions are highly variable, plastic sensory systems

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may result in fluctuating selection on male traits which will break down the gametic disequilibria between genes for sensory systems, display trait, and viability and reduce the potential for divergence among populations (Lande, 1981).

Surprisingly, there have been few studies that attempt to measure genetic and environmental variation in sensory systems (also see Endler *et al.*, 2001 for a demonstration of artificial selection on optomotor response). The absence of studies measuring both environmental and genetic effects is because of two factors. First, vision physiology has traditionally been difficult to measure. As a result, the sample sizes needed for proper quantitative genetic studies make these experiments prohibitively large. Secondly, evolutionary studies of vision have typically relied on the comparative method with the objective of determining the nature of selection by comparing the visual properties of animals living in different lighting environments (Lythgoe, 1984; Lythgoe *et al.*, 1994; Partridge & Cummings, 1999; Cummings & Partridge, 2001). There are two problems with this approach. First, habitat sorting, whereby animals choose a visual environment to match their visual capabilities, may inflate the correlation between environment and visual properties. Secondly, comparative studies lack the ability to determine whether correlations between visual properties and environmental conditions are the result of genetic differentiation or simple environmental variation (i.e. plasticity). Even at the among species level, purely environmental effects can result in differences in species means (Leroi *et al.*, 1994).

The assumption that most variation is genetic in origin is problematic because, other studies have shown high levels of phenotypic plasticity in visual properties. For example, in studies of mantis shrimp, Cronin and colleagues have shown that animals adjust the properties of their photoreceptor filters such that they are most sensitive to the predominant wavelengths in the environment (Cronin *et al.*, 2001; Cronin & Caldwell, 2002; Cheroske *et al.*, 2003). In cichlids, variation in lighting conditions results in phenotypic plasticity in the production of cones, the properties of nurons in the retina and the properties of the crystalline lens (Kroger *et al.*, 1999, 2001a, b; Wagner & Kroger, 2000). There are also many studies showing ontogenetic variation in the production of cones (i.e. concordant with changes in lighting habitats) (Loew & Wahl, 1991; Shand, 1993; Kunz *et al.*, 1994; Shand, 1997; Flamarique, 2000, 2001; Allison *et al.*, 2003; Dann *et al.*, 2003). Unfortunately, although these studies have examined environmental variation, they have ignored genetic variation in visual properties and genetic variation in plasticity.

In this study, we quantify the extent to which variation in visual properties is attributable to genetic, environmental, and the interaction between genetic and environmental effects in the bluefin killifish, *Lucania goodei*. This is a compelling system to study. *Lucania goodei* is a small freshwater fundulid that occurs under a wide range of lighting environments ranging from tea-stained swamps that have reduced transmission of UV/blue wavelengths to crystal clear springs that have high transmission of UV/blue wavelengths (Fuller, 2002). Both male colouration and visual properties vary across populations in relation to lighting conditions (Fuller, 2002; Fuller *et al.*, 2003, 2004).

Males with blue anal fins are more abundant in tea-stained swamps, whereas males with red anal fins (and to a lesser extent, males with yellow anal fins) are more abundant in clear springs (Fuller, 2002). There is genetic and environmental variation as well as an interaction between genetic and environmental variation in male colour pattern expression. Yellow vs. red is controlled in large part by a single locus where yellow is dominant over red (Fuller & Travis, 2004). The expression of yellow vs. red can be masked by the expression of blue. In general, males are more likely to express blue colouration when raised under swamp conditions, but there is heritable variation in male response to environmental lighting conditions (Fuller & Travis, 2004).

Visual properties of animals also differ between spring and swamp habitats. Swamp animals are less sensitive to UV/blue wavelengths and possess fewer UV and violet cones than animals from spring populations (Fuller *et al.*, 2003). These differences in cone frequency match differences in opsin expression (Fuller *et al.*, 2004), the protein that determines spectral sensitivity of cones. In this study, we measure opsin expression for offspring derived from a paternal half-sib mating study where animals were raised under different lighting conditions to determine whether variation attributable to genetics, environment, or their interaction can be detected.

Methods

Breeding design

Lucania goodei were collected in Broward Co., FL, USA (location available upon request). This site is a swamp population. We chose four sires with distinctly different colour patterns (see Fuller & Travis, 2004). One male was yellow on the posterior region of the dorsal fin, blue on the anal fin and yellow on the pelvic fins, and is referred to as the 'Y/B' sire. The second male was yellow on the posterior region of the dorsal fin, yellow on the anal fin with a slight tinge of blue at the base and yellow on the pelvic fins, and is referred to as the 'Y/Y' sire. The third male was red on the posterior region of the dorsal fin, red on the anal fin and red on the pelvic fins, and is referred to as the 'R/R' sire. The fourth male was red on the posterior region of the dorsal fin, blue on the anal fin and red on the pelvic fins, and is referred to as the 'R/B' sire. We crossed each sire with three to four random dams, divided each clutch between clear water conditions (which mimics the lighting environment

found in springs) and tea-stained water conditions (which mimic the lighting environments found in swamps), and raised them to adulthood in a greenhouse. Water was treated with a buffer to keep the pH > 7. For the tea-stained treatment, we added instant, decaffinated tea to the water two to three times each week. Analyses of light transmission verified that the tea treatment significantly reduced the transmission of UV and blue wavelengths through the water column relative to clear water (Fuller & Travis, 2004). This experiment ran from August 2001 to December 2002. Further details on animal husbandry can be found elsewhere (Fuller & Travis, 2004).

Quantitative, real-time polymerase chain reaction

We use opsin expression to infer qualitative differences in cone abundance. The opsin protein is a major determinant of the spectral sensitivity of a given cone type (Yokoyama & Yokoyama, 1996). *Lucania goodei* possess five main types of cones (UV, violet, blue, yellow and red) which express five different types of photopigment. The spectral properties of the photopigment are determined by five separate cone opsin genes. These are very short-wavelength sensitive (SWS1) short-wavelength sensitive (SWS2B, SWS2A), rhodopsin like (RH2) and long-wavelength sensitive (LWS). These are all distinct from the rod opsin gene (RH1). There is no evidence for co-expression of opsins in the cones.

There have been at least two major gene duplications within the SWS family (Yokoyama & Yokoyama, 1996; Yokoyama, 1997; Carleton & Kocher, 2001). The first gave rise to the SWS1 and SWS2 gene families. The second occurred within the SWS2 family and gave rise to SWS2A and SWS2B. In combination with 11-cis retinal (derived from vitamin A1), the genes produce the following pigments: SWS1 – UV photopigment [maximum absorbance (λ_{max}) = 359 nm]; SWS2B – violet photopigment (λ_{max} = 405 nm); SWS2A – blue photopigment (λ_{max} = 455 nm); RH2 – yellow photopigment (λ_{max} = 539 nm); and LWS – red photopigment (λ_{max} = 573 nm, for *L. goodei*). *Lucania goodei* has at least two different LWS loci (genbank accession numbers AY296741, AY296740). Preliminary evidence indicates that these two opsin proteins do not differ in their spectral properties (N. Blows & S. Yokoyama, pers. comm.). Because these two loci have large regions of identical sequence, we were able to design primers and probes that were common to both alleles (see below).

As the map of genotype to phenotype is straightforward for these proteins, we can use differences in opsin expression to infer qualitative differences in cone frequency (Carleton & Kocher, 2001; Fuller *et al.*, 2004). Comparisons among populations have shown that animals from the spring population, which have a higher frequency of UV and violet cones, also have higher expression of SWS1 and SWS2B opsins (Fig. 1a)

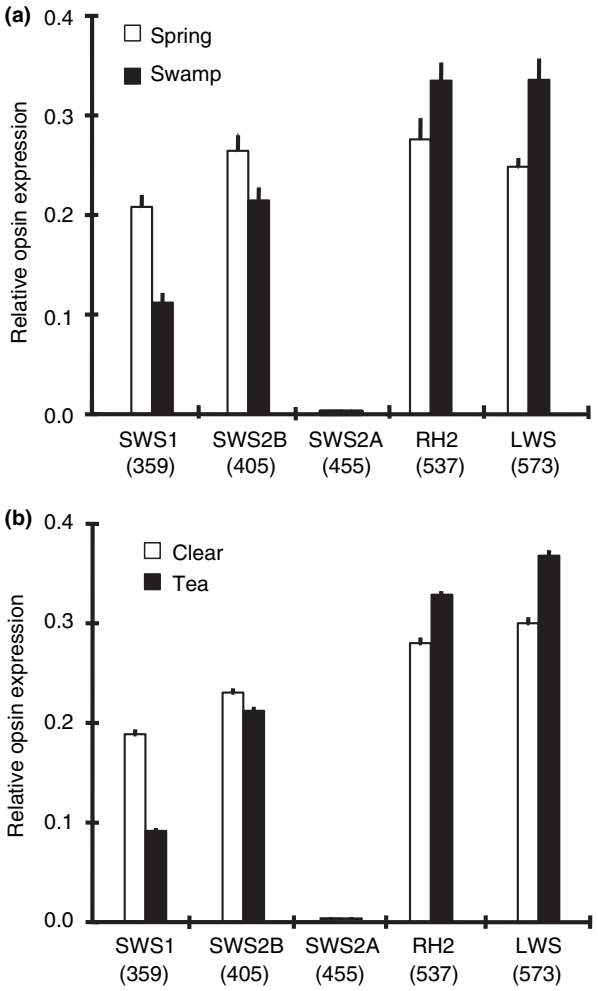


Fig. 1 (a) Relative expression of opsins expressed in animals from a spring and a swamp population, $n = 10$ for each population. Figure reprinted from Fuller *et al.* (2004) with permission from *Journal of Comparative Physiology A*. (b) Relative opsin expression for animals raised in tea-stained and clear-water treatments; $n = 78$ for tea-stained water, $n = 80$ for clear water. Mean values and standard errors of the raw data are shown for each opsin (λ_{max}).

(Fuller *et al.*, 2004). In contrast, swamp animals, which have a higher frequency of yellow and red cones, also have a higher frequency of RH2 and LWS opsins (Fig. 1a). Differences among individuals in opsin expression reflect qualitative differences in cone abundances (i.e. more vs. less), but are not precise parameter estimates for actual cone abundances. In particular, the frequency of blue cones in the retina (8%) does not match the relative SWS2A opsin expression (0.1%) which is likely an experimental artifact of poor reverse transcription efficiency of this gene (Fuller *et al.*, 2004). In this study, we assessed the environmental and genetic effects on opsin expression by comparing offspring from different paternal half-sib families raised under different

lighting environments (clear or tea-stained water) (Fuller & Travis, 2004).

We measured opsin expression for four to six adult animals (two to three males and two to three females) from each treatment combination. For each individual, we obtained cDNA by reverse transcribing RNA isolated from eye tissue. We created primers and probes that were unique to each opsin gene (see Fuller *et al.*, 2004 for details). For each quantitative, real-time polymerase chain reaction (qRT-PCR) reaction, we placed 0.2 μL of cDNA mixture in a 30 μL reaction with the appropriate primers, probes and taqman mix. The amount of fluorescence was monitored over 40 cycles (94 °C, 15 s/55 °C, 30 s/65 °C, 1 min) using the ABI Prism 7700 Sequence Detection System at Florida State University. We determined the relative abundance of each opsin based on its critical cycle number (C_{ti}) which was determined when the fluorescence exceeded a threshold set close to the background flourescence (Carleton & Kocher, 2001). Relative opsin expression was calculated as a fraction of total opsin genes for an individual according to the following:

$$\frac{T_i}{T_{all}} = \frac{\frac{1}{(1+E_i)^{C_{ti}}}}{\sum \frac{1}{(1+E_i)^{C_{ti}}}}.$$

T_i/T_{all} is the proportional gene expression for a given gene i. E_i is the PCR efficiency for each primer/probe set, and C_{ti} is the critical cycle number for each gene. PCR efficiencies were quantified with a multigene construct (Fuller *et al.*, 2004). Relative opsin expression data were log-transformed for analysis.

Statistical analysis

We used analysis of variance (ANOVA) to examine the effects of sire, environment, dam nested within sires [dam (sire)] and the interactions between environment and sire, and between environment and dam(sire) on log-transformed relative opsin expression, log (T_i/T_{all}). Dam (sire) and the interaction between environment and dam(sire) were treated as random effects. Initial analyses included the interaction between environment and dam (sire). If the term did not produce an $F > 1$, then it was subsequently dropped from the model. In cases where the F-value was >1, we examined ANOVA models both with and without the term [environment × dam (sire)] to determine whether its inclusion significantly altered the interpretation of the other terms. For individual ANOVAS, because of the unbalanced design, the sire effect was tested using an error term estimated by the Satterthewaite approximation which is very similar to the dam (sire) mean square (Sokal & Rohlf, 1995). We examined the distribution of residuals to determine whether they upheld the assumptions of homoscedasticity and normality. All analyses were performed using SAS V.8 (SAS Institute, Cary, NC, USA). All graphs show mean values and standard errors calculated on the untransformed data.

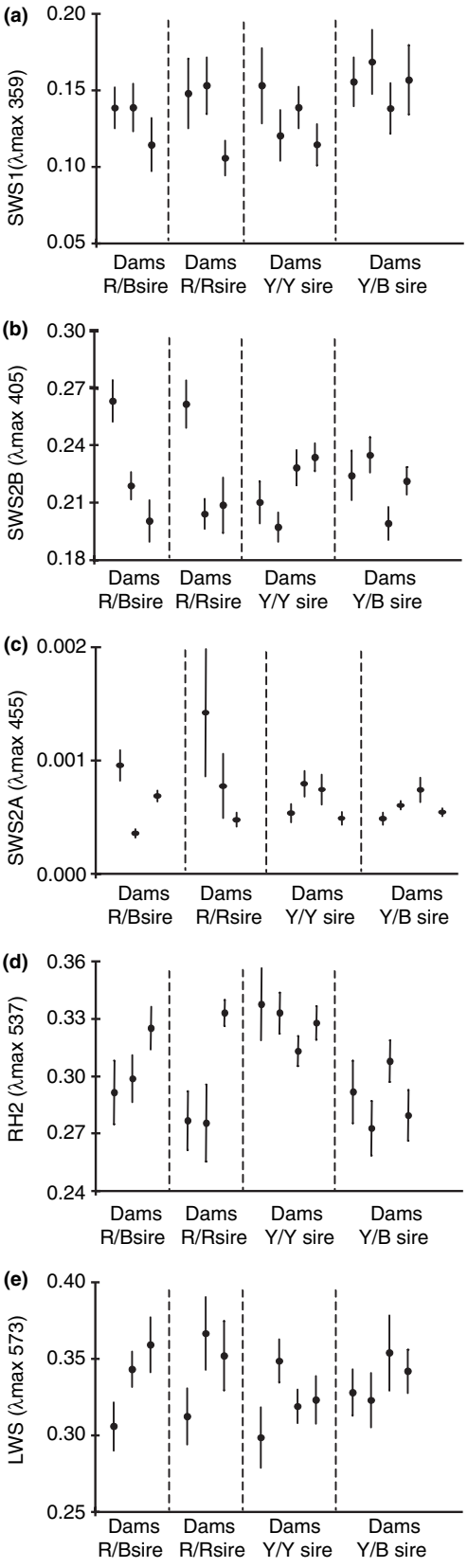
Results

We found effects of sires, dams within sires [dams (sires)], and the environment on opsin expression, but little evidence for interaction between sires and environment (Table 1) or between dams (sires) and the environment. In general, the interaction between dams (sires) and the environment was not statistically significant, and inclusion of the term in the ANOVA model did not affect the significance of the other terms with the exception of the LWS opsin expression. The interaction between environment and dams (sires) was marginally significant for LWS ($F_{10,130} = 1.85$, $P = 0.058$). Inclusion of this term in the model, rendered the overall dam (sires) effect statistically nonsignificant ($F_{10,10} = 1.55$, n.s.) but did not alter the environmental effect ($F_{1,11.5} = 44.44$, $P < 0.0001$). The F-value for the interaction between dams (sires) and environment was <1 for SWS2B and RH2, and was dropped from the model. For SWS1 and SWS2A, the interaction produced an $F > 1$, but was not statistically significant. Furthermore, inclusion of the term did not affect the statistical significance of the other terms.

Table 1 Analysis of variance on ln (relative opsin expression).

Opsin	Effect$_{(num,\ denom)}$	MS	F	P
SWS1 (λ_{max} 359)	Sire $_{(3,10.2)}$	0.038	1.78	0.2128
	Dam (sire) $_{(10,140)}$	0.021	1.70	0.0869
	Environment $_{(1,140)}$	3.792	299.87	<0.0001
	Sire × environment $_{(3,140)}$	0.002	0.18	0.9122
SWS2B (λ_{max} 405)	Sire $_{(3,10.5)}$	0.002	0.09	0.9612
	Dam (sire) $_{(10,140)}$	0.024	5.71	<0.0001
	Environment $_{(1,140)}$	0.041	9.84	0.0021
	Sire × environment $_{(3,140)}$	0.005	1.13	0.3380
SWS2A (λ_{max} 455)	Sire $_{(3,9.7)}$	0.026	0.12	0.9439
	Dam (sire) $_{(10,140)}$	0.217	4.63	<0.0001
	Environment $_{(1,140)}$	0.111	2.37	0.1259
	Sire × environment $_{(3,140)}$	0.010	0.21	0.8900
RH2 (λ_{max} 537)	Sire $_{(3,10.3)}$	0.034	5.96	0.0125
	Dam (sire) $_{(10,140)}$	0.006	0.87	0.5619
	Environment $_{(1,140)}$	0.206	31.48	<0.0001
	Sire × environment $_{(3,140)}$	0.004	0.56	0.6443
LWS (λ_{max} 573)	Sire $_{(3,10.2)}$	0.004	0.43	0.7355
	Dam (sire) $_{(10,140)}$	0.010	2.69	0.0047
	Environment $_{(1,140)}$	0.303	78.29	<0.0001
	Sire × environment $_{(3,140)}$	0.002	0.58	0.6306

Degrees of freedom in the numerator and denominator for each effect are indicated in parentheses. MS refers to mean square. Only the results for LWS opsin expression are affected by the inclusion of the environment × dam (sire) term (see text for details).



Environmental effects were greatest for opsins sensitive to extreme wavelengths (SWS1 and LWS) and were manifested as overall shifts towards increased expression of either short-wavelength sensitive opsins (SWS1 and SWS2B) or long-wavelength sensitive opsins (RH2 and LWS). Animals raised in tea-stained water had higher expression of RH2 and LWS opsins whereas animals raised in clear water had higher expression of SWS1 and SWS2B opsins (Fig. 1b). The pattern of phenotypic plasticity (Fig. 1b) resembles the pattern observed between swamp and spring populations (Fig. 1a) (Fuller *et al.*, 2004) where swamp animals expressed higher levels of RH2 and LWS opsins and spring animals expressed higher levels of SWS1 and SWS2B opsins.

We detected genetic variation in the expression of RH2. There was significant variation among sires in RH2 opsin expression (Table 1, Fig. 2d). Offspring from the Y/Y sire had higher RH2 opsin expression than offspring from the Y/B sire. We also detected maternal effects in the expression of SWS2B, SWS2A and LWS opsins (Fig. 2b,c,e). The dam (sires) effect can be influenced by both additive genetic, nonadditive genetic (i.e. dominance and epistasis) and nongenetic environmental effects (i.e. maternal environment and parental care) (Falconer & Mackay, 1996; Lynch & Walsh, 1998). The fact that we detected dam effects more often than sire effects was not surprising given our experimental design. The critical *F*-value for the sire effect ($F_{crit} = 3.7$) was nearly twice that of dams ($F_{crit} = 1.9$).

Discussion

Our results demonstrate clear genetic and environmental variation in opsin expression as shown by the effects of sires and lighting treatments. Previously, opsin expression has been found to correlate with relative cone frequency in the retina (Fuller *et al.*, 2004). The presence of genetic variation in visual system properties indicates that sensory systems are both plastic and yet readily evolvable traits that will be subject to the effects of natural and sexual selection. Furthermore, genetic variation in sensory systems implies that it is possible for sensory system properties to coevolve with male colour patterns.

The prevalence of maternal effects on opsin expression is more difficult to interpret. At present, we cannot empirically determine whether this variation is attributable to additive genetic, nonadditive genetic (i.e. dominance or epistasis) or environmental effects. Clearly, environmental, maternal effects are common across a

Fig. 2 Relative opsin expression across dams nested within sires. For each dam mean, data are pooled between the two environments. (a) SWS1, (b) SWS2B, (c) SWS2A, (d) RH2 and (e) LWS opsins. Mean values and standard errors of the raw data are shown. Statistical analyses were performed on log-transformed data. R/B, R/R, Y/Y and Y/B refer to the colour morph of the sires.

wide range of taxa (Lynch & Walsh, 1998; Mousseau & Fox, 1998), including fish (Heath & Blouw, 1998). Within Fundulidae (to which *L. goodei* belongs) large, nongenetic maternal effects have been found in enzymatic activity conferring resistance to pollutants in the mummichog, *Fundulus heteroclitus* (Meyer & Di Giulio, 2002; Meyer *et al.*, 2002). Given that opsin expression is quite plastic (as seen in the dramatic effects of light treatment), it is conceivable that the effects of dams reflect another plastic response to some cue present in the maternal environment.

On the contrary, there are reasons to doubt that there are large-nongenetic environmental effects that differ across dams. First, many maternal environmental effects typically arise through parental care, but *L. goodei* eggs are fertilized externally and receive no parental care aside from the effects of maternal provisioning of eggs (Fuller & Travis, 2001). Also, we removed eggs from spawning substrates within 24 h of fertilization and later divided offspring between the water treatments, thus, precluding maternal effects because of a common rearing environment. Any maternal effects would have to be large and persist in the presence of different lighting environments.

Genetic variation in opsin expression

The finding of genetic variation in the expression of some (but not all) opsins raises the question of how complex sensory systems evolve. In our study, we detected genetic effects because of sires and possible genetic effects because of dams. Although our experiment is too small to quantify precise levels of genetic variation in different opsins, the implications of variation in expression in some, but not all opsins are unclear. Does low genetic variation in the expression of one opsin (e.g. UV opsins) lower the evolvability of the whole system? Most likely, the answer is no. According to theory, the perception of colour relies on the comparison of output from multiple cone types, and nearly all proposed measures of colour incorporate spectral data across multiple axes corresponding to the various cone types (Endler, 1991; Chittka *et al.*, 1992; Chittka, 1992; Vorobyev *et al.*, 1998; Rowe *et al.*, 2004). Hence, genetic variation in the production of some cone types should create genetic variation in the visual system as a whole. However, experimental work is needed to verify this expectation.

Environmental variation in opsin expression

The pattern of differential opsin expression between clear and tea-stained environments bore striking resemblance to the pattern between spring and swamp populations (Fig. 1). This raises the question of whether the among-population variation is because of differences in environment, genetics or an interaction between the two. A close inspection of Fig. 1 shows that the two graphs are not identical which leaves possible a role for genetic differentiation between the two populations. Still, the similarity between these two patterns suggests that a large proportion of the variation among populations may be due to environmental effects.

The possibility that environmental variation is largely attributable for among population and among species variation in sensory systems has important implications for speciation. Conceptual models of speciation have emphasized the diversifying effects of sensory systems (Lande, 1981; Endler, 1992, 1993; Boughman, 2002). These models were based on the critical observation that different species (and different populations within species) living under different environmental conditions differ in their visual system properties (Lythgoe, 1984; Endler & Houde, 1995; Boughman, 2001; Cummings & Partridge, 2001). This observation led to the hypothesis that differences in sensory system properties will create differences in mating preferences that will lead to prezygotic isolation and speciation (Endler, 1992, 1993; Seehausen *et al.*, 1997, 1999; Boughman, 2002). However, if the majority of variation in sensory systems is environmental, then any associated preference (and hence prezygotic isolation) will also change with spatial and temporal variation in environmental conditions. Hence, environmental conditions must be very stable for plastic preferences to lead to speciation. Such a scenario is possible (West-Eberhard, 2003), but again empirical work is needed to verify this expectation. We do not mean to imply that all variation in sensory systems is because of environmental effects. Obviously, genetic differentiation in sensory systems does occur (Endler *et al.*, 2001; Terai *et al.*, 2002). However, assuming that all variation among populations in sensory systems is because of genetic differentiation is unfounded. We must determine the relative importance of genetics, environment and their interaction on sensory system divergence and on the extent to which sensory systems can act as diversifying agents in speciation.

Environmental variation in visual sensitivity may also cause the direction of sexual selection to be highly variable. Environmentally induced differences in colour perception will be further compounded by differential transmission of wavelengths which also alters the brightness and contrast of male colour patterns (Endler, 1992; Fuller, 2002; Leal & Fleishman, 2004). The result is that the types of male traits favoured by sexual selection should vary both spatially and temporally with lighting conditions. Selection on male traits to maximally stimulate female sensory systems need not result in constant, direct sexual selection (see Svensson & Sinervo, 2004 for an example of variable selection gradients).

The critical assumption of this study is that the variation in opsin expression creates meaningful variation in the visual experience and behaviour of individual *L. goodei*. We are currently testing this assumption. Studies in other organisms have demonstrated a link between variation in vision physiology and variation in

behaviour. Studies on sticklebacks have shown that animals living in different lighting environments differ in the excitability of retinal ganglion cells (Mcdonald & Hawryshyn, 1995) and in optomotor responses (Boughman, 2001) (a behavioural assay of visual sensitivity). These differences in visual properties are associated with differences in mating behaviour (Boughman, 2001). Whether this variation is genetic or environmental is unknown, but it suggests that differences in visual physiology can result in differences in behaviour.

In conclusion, this study found substantial within population genetic and environmental variation in sensory systems. The presence of genetic variation in sensory systems implies that changes in sensory systems (and correlated behaviours) may themselves be the result of selection and may potentially coevolve with male traits. The fact that sensory systems are highly plastic suggests that the intensity and/or direction of sexual selection may vary as a result of environmental conditions. Sensory systems are readily evolvable traits that should respond to selection.

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