

SENSORY TRADE-OFFS PREDICT SIGNAL DIVERGENCE IN SURFPERCH

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Unidirectional elaboration of male trait evolution (e.g., larger, brighter males) has been predicted by receiver bias models of sexual selection and empirically tested in a number of different taxa. This study identifies a bidirectional pattern of male trait evolution and suggests that a sensory constraint is driving this divergence. In this system, the inherent trade-off in dichromatic visual detection places limits on the direction that sensory biases may take and thus provides a quantitative test of the sensory drive model. Here I show that sensory systems with trade-offs in detection abilities produce bidirectional biases and that signal design properties match these biases. I combine species-specific measurements and ancestral estimates with visual detection modeling to examine biases in sensory and signaling traits across five fish species occupying optically diverse habitats in the Californian kelp forest. Species-specific divergence in visual pigments correlates with changes in environment and produces different sensory biases—favoring luminance (brightness) detection for some species and chromatic (color) detection for others. Divergence in male signals (spectral reflectance of orange, blue, and silver color elements) is predicted by each species' sensory bias: color divergence favors chromatic detection for species with chromatically biased visual systems, whereas species with luminance sensory biases have signals favoring luminance detection. This quantitative example of coevolution of communication traits varying in a bidirectional pattern governed by the environment is the first demonstration of sensory trade-offs driving signal evolution.

KEY WORDS: Color vision, receiver bias, sensory drive, signal evolution, surfperch.

A courtship signal's success depends upon its detectability (signal design) as well as the extractable information conveyed (signal content). Although debate rages as to the relative importance of each of these on signal evolution (e.g., Maynard Smith and Harper 2005; Ryan and Cummings 2005), it is often difficult to evaluate these components independently. Recent receiver bias models suggest that design constraints allow us to test the importance of design on signal evolution independent of content (Basolo 1990; Ryan 1990; Endler 1992; Christy 1995). One of these receiver bias models, the sensory drive hypothesis (Endler 1992), states that if specific environmental and sensory constraints can be identified, then testable predictions for the direction of signal evolution can be made. A powerful, yet previously untested, way to explore sensory drive predictions is to examine signal evolu-

tion in systems that experience sensory trade-offs—where tuning of sensory systems is constrained to detect certain signal features at a cost of others in different environments. This study examines signal design evolution in a group of closely related fish species constrained by sensory trade-offs.

Sensory system constraints can occur when receptor cells extract qualitatively different environmental features. Vision is one such system. Photoreceptors, the receptor cells of the visual system, are specialized neurons in the retina that transduce light energy into the energy of the nervous system and pass this information to different types of higher order neurons. Photoreceptors differ in their spectral sensitivity (the set of wavelengths of light they absorb) and higher order cells compare the output of different photoreceptor classes to extract information from stimuli such as color and brightness. Information extraction often involves mutually exclusive processes. Although there is ample variation across taxa, two of the most basic processes involve summing

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the output among photoreceptor classes to assess stimuli brightness (i.e., luminance component), and subtractive or inhibitory interactions between photoreceptor classes to assess color (i.e., chromatic component).

This fundamental difference in how luminance and chromatic properties are processed imposes a conflict in photoreceptor design for different detection pathways for some visual organisms. Animals with only two cone classes, known as dichromats, represent the most extreme example of this design trade-off in luminance versus chromatic detection. As a first approximation for dichromats living in spectrally narrow light environments, increasing the overlap of sensitivity between the two cone classes favors luminance detection, whereas increasing the spectral distance between the two (while still maintaining some overlap for comparison) improves chromatic detection (Lythgoe and Partridge 1991; Chiao et al. 2000; Cummings 2004). Although different environments will favor specific tuning, in spectrally narrow environments and nonwhite visual targets having two cone classes that are sensitive to different spectral regions will increase the difference signal in the chromatic channel while decreasing the luminance contrast; whereas having two cone classes with more spectral overlap will increase the brightness contrast for colored objects yet decrease the color contrast signal. Hence, spectral tuning of photoreceptors represents an apparent trade-off in discrimination performance—spectral placement that favors one discrimination channel will come at a cost to the other. Identifying the evolutionary direction species have taken in this sensory trade-off is one means to quantify receiver biases. We can quantify the evolutionary direction of a sensory trade-off by examining the direction of visual pigment divergence across extant taxa relative to the ancestral condition and evaluate the subsequent detection performance (gains in one detection channel relative to the other) in each species' habitat.

Surfperch, a group of dichromatic marine fish, are excellent candidates to quantify receiver biases resulting from a sensory trade-off as species-specific visual pigments, phylogenetic relatedness, visual task, and optical habitats are all well defined. Surfperch inhabit optically variable waters of the eastern Pacific and forage visually on small invertebrates associated with benthic algae (Tarp 1952). Changes in depth, degree of wave-induced focusing, percent canopy cover, water column productivity, and storm turbidity (McFarland and Loew 1983; Reed and Foster 1984; Wing et al. 1993) combine to make an underwater environment where target and background radiances change in chromatic and luminance properties on small spatial and temporal scales. Surfperch occupy species-specific niches in the nearshore environment governed by ecological competition for foraging resources (Hixon 1980; Schmitt and Holbrook 1990) resulting in species-specific optical habitats (Cummings 2004). The divergent surfperch habitats provide predictive power for the evolutionary direction species take in the luminance and chromatic trade-off.

Optical properties of different habitats can constrain the evolution of visual processes. Specifically, overall light intensity and variation in intensity levels are two environmental features that can constrain color or brightness detection. The shallower zones of the nearshore environment (such as the habitat of the reef surfperch, *Micrometrus aurora*) encounter higher intensities that favor color vision (DeValois and Jacobs 1984). Furthermore, environments with extreme intensity fluctuations, where background light flickering varies in time and space, are also expected to favor color over brightness discrimination (McFarland and Munz 1975; Mollon 1989; Maximov 2000). Color vision is favored in environments of extreme light fluctuations because the achromatic or luminance signal is too variable, and the opponency process of the chromatic pathway provides a nonflickering output (Maximov 2000). Consequently, species that experience extreme ranges in background intensities, passing from high to low light environments, are more likely to have greater reliability in chromatic detection processes. Surfperch forage mainly by roving through many different microhabitats (canopied and noncanopied; shallow and deep) in the nearshore environment and many of them experience great intensity changes across their daily ranges. *Hypsurus caryi*, in particular, can experience up to a fourfold log change in background intensities within minutes; and has the greatest variation in background luminance levels across all surfperch species surveyed (Cummings 2004). Furthermore, *H. caryi* is unusual in that it has less variation in chromatic signal-to-noise than luminance signal-to-noise ratios. This combination of environmental features is likely to favor a sensory system geared toward chromatic detection. Meanwhile, the relatively deeper habitats of some kelp forest surfperch such as *Embiotoca jacksoni*, *E. lateralis*, and *Damalichthys vacca* that do not experience as much luminance variation as *H. caryi* may favor luminance detection in their lower intensity environments.

This study examines the evolution of receiver and signal biases from a sensory drive context, and takes advantage of the inherent sensory trade-off found in dichromatic surfperch and their well-defined and divergent habitats to make specific quantifiable predictions about signal design evolution. Surfperch display a variety of colors (e.g., oranges, blues, silvers) during courtship communication (De Martini 1969). Such diversity of signal types allows multiple, independent tests of signal evolution driven by receiver biases by examining whether divergence in signal reflectance properties parallels the detectional biases of each species' visual system. Do surfperch with luminance-biased visual systems have color pattern properties that have diverged to favor luminance detection in their habitats? Similarly, do surfperch with chromatic-biased visual systems have color patterns that have diverged in a direction favoring chromatic detection? Here I use a target detection modeling approach to test two major predictions of the sensory drive hypothesis (1) whether environmentally

driven sensory divergence leads to divergent biases (chromatic or luminance) and (2) whether detectional biases in the visual system predict the direction of signal divergence across surfperch color patterns.

Methods

The objective of this study is to examine whether the evolutionary pattern of detectional biases is the same for sensory and signaling traits across five species of surfperch. To address this objective, color pattern reflectance measurements from the five surfperch species were combined with previous measurements of visual pigment sensitivities and optical habitat use (Cummings and Partridge 2001) to identify sensory and signal biases using a previously described target detection model (Cummings 2004). To identify sensory biases independent of communication events, visual performance estimates were evaluated in terms of surfperch ability to detect an important foraging target within their specific optical habitat. Signal biases were evaluated in terms of color pattern detectability within species-specific habitats. To comprehensively characterize habitat differences, target detection was evaluated across the entire set of each species' optical measurements. Sensory and signal biases were defined as the estimated gain in luminance or chromatic detection relative to a standard point of divergence for photoreceptor sensitivities and reflectance properties. Two different reference points are used to evaluate the estimated evolutionary divergence: the maximum likelihood estimate of the ancestral state (a phylogenetic estimate) and the simple mean of each trait (a nonphylogenetic estimate).

COLOR PATTERN MEASUREMENTS

In an ideal world, measurements of color pattern radiance (light emanating from the surface of a fish) would be measured directly and used in estimating target detection; however, such measurements are difficult to obtain underwater. In the absence of these measurements, researchers measure the inherent color pattern properties (the spectral reflectance) and estimate the radiance as a product of the reflectance and illumination spectra; and some have even attempted to correct for the difference between wet and submerged reflectance measurements (Johnsen 2005). In the underwater light field of the kelp forest, light is impinging on these fish from all directions—the stronger or more intense downwelling illumination from above, as well as scattered light that impinges on the fish from the side. Paired downwelling and sidewelling irradiance measurements ($I_D(\lambda)$ and $I_S(\lambda)$, respectively) in each species' habitat show that the downwelling irradiance is significantly more intense than sidewelling light for all five surfperch (species' habitat mean $\sum_{\lambda=350}^{700} I_D(\lambda) / \sum_{\lambda=350}^{700} I_S(\lambda)$ values ranged from 18 to 235). Although the true illumination field is some combination of both the downwelling and sidewelling radiance fields,

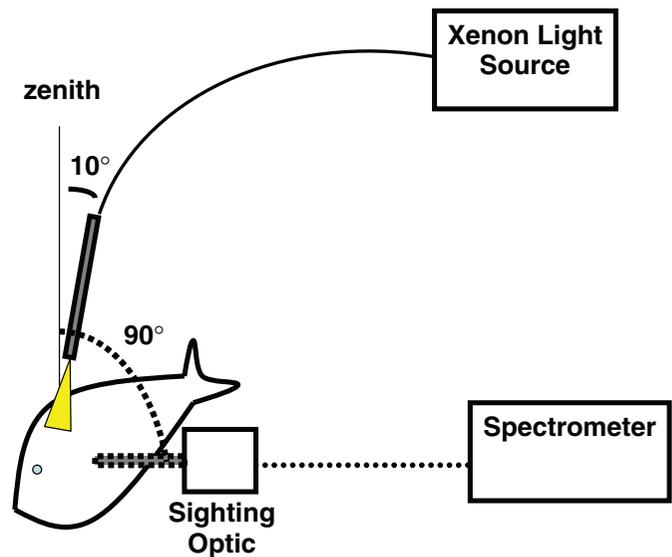


Figure 1. Apparatus for measuring fish reflectance. Illumination fiber (solid lines) and receiving apparatus (dashed lines) were positioned to mimic a fish's color pattern illuminated with downwelling irradiance and viewed from the side.

here I estimated the color pattern radiance based on the downwelling field only. To this end, all reflectance measurements were collected to mimic downwelling illumination—for example, the light probe was positioned to illuminate the fish from above (10° zenith angle), whereas the receiving fiber (mimicking a female viewer) was positioned directly to the side of the fish (90° zenith angle; Fig. 1).

All reflectance measurements were made on live, wild-caught male surfperch within 24 h of capture. Spectral reflectances were collected for each species in accordance with the UCSB Animal Care Guidelines (IACUC protocol #11-97-464-1). All surfperch were captured using handnets on nighttime SCUBA dives while temporarily stunning the fish with a bright dive light. Once captured, the fish were transferred to a water-filled plastic bag to avoid unnecessary damage to scales. The fish were housed in outdoor aquaria at Hopkins Marine Station (Pacific Grove, CA) with flow-through seawater until reflectance measurements were made. Wild caught marine fish are known to blanch during captivity (J. O'Sullivan, Monterey Bay Aquarium Fish collector, pers. comm. 1998), and to avoid such deterioration of color patterns, live fish were measured with spectral reflectance within 24 h of their capture, and made acquiescent during the measurement procedure by using an ice-packed towel soaked in seawater. The fish were released back into the same vicinity of their capture within 6 h of measurements.

Male surfperch body reflectances were measured using an Ocean Optics PS1000 spectrometer and illuminated by an Oriel 150W Xenon lamp (model 6255) with an unfocused illumination

light guide (Oriel waterlight guide model #77800) held stationary at a 10° angle incident to the fish's dorsal area, and the receiving apparatus (focusing assembly feeding into the spectrometer) was positioned normal (90°) to the side of the fish (see Fig. 1). The fish were immobilized for spectral measurements using a chilling method (hand-held towel soaked in saltwater with crushed ice). While immobilized, reflectance spectra were collected from live fish at various locations on the body, while maintaining a constant angle and distance between incident illumination and collection devices. The fish were dorsally illuminated with a diffuse light attached to a protractor to maintain a fixed angle of illumination to mimic a downwelling lightfield. The reflected illumination was collected by a focusing assembly (fused silica biconvex lens within a sighting scope) stationed normal to the side of the fish, hence the reflectance measurements mimic a female viewing a male conspecific from the side while his color patterns are illuminated from above through Snell's window. The reflected illumination was collected by a focusing assembly consisting of a 25.4 mm fused silica biconvex lens (Edmund Scientific UV DCX L08-016) fitted in an Orion (#5264) camera adapter and attached with a T-ring adapter to a 35 mm camera body. A 400-micron UV-VIS (Ocean Optics, Inc) fiber optic was fixed with an SMA connection to the back of the camera body and received the focused reflectance when the shutter release was pressed thereby removing the mirror from the path of light. The focusing assembly focuses the surface reflectance from a $1\text{--}2\text{ mm}^2$ diameter area of the fish onto the 400-micron fibre optic that feeds directly into an Ocean Optics PS1000 (UV-VIS grating) spectrophotometer. All reflectance values are relative to a 99% (300–700 nm) reflectance standard (SpectralonTM). Replicate spectral reflectance measurements were taken from at least two different areas within a body region (e.g., under eye facial area; or flank), and two to nine males were measured per species.

Surfperch exhibit a number of distinct forms of coloration including structural (silvers), carotenoid or pteridine-based (oranges), melanophore-based (browns and blacks), and a combination of structural and pigmented coloration (blues). Three of these major color classes (orange, silver, or blue) are exhibited by two different surfperch species allowing for an examination of signal divergence. For example, both *H. caryi* and *E. lateralis* display prominent blue facial markings during courtship; both *M. aurora* and *E. lateralis* display orange flank regions; and both *M. aurora* and *D. vacca* have silver flanked regions that are sexually dimorphic (e.g., *M. aurora* halfmoon silver flank region is only present above the gonopodium). For each of these pairs of species that exhibit similar color types, reflectance measurements were collected in the same body location to compare site-specific reflectance properties between species. Species mean reflectance spectra for each color element were used in the target detection modeling described below to identify chromatic and luminance

detectability properties. To identify divergent properties among surfperch color patterns, each reflectance spectrum was identified by a wavelength that characterized the spectral region with reflectance properties of interest. Color elements such as "blue" that have a single wavelength of peak reflectance were described by the wavelength of maximum reflectance, R_{peak} ; whereas the wavelength at 50% of the maximum reflectance or the midpoint between the peak and baseline reflectance termed the "cut-on" wavelength, $R_{\text{cut-on}}$, was used to characterize color elements that have broad sloping rises in reflectance (e.g., orange). Differences in luminance and chromatic detectability due to divergence in these spectral properties were then evaluated with the target detection model (see Estimating Intraspecific Signal Bias below). Color elements that are unique to one species, such as the brown flanks in *E. jacksoni* and dusky flanks in *D. vacca*, were also evaluated in terms of their relative chromatic and luminance detectability properties; however, no estimation of divergence was possible.

PREVIOUS MEASUREMENTS AND MODELING

Over 2000 habitat light measurements were collected in the presence of surfperch in more than 250 SCUBA dives across all seasons and optical conditions over a three year period in a manner that characterized the illumination field and the visual background in the nearshore California kelp forest environment (Cummings and Partridge 2001). Measurements were collected with a cosine-corrected underwater spectroradiometer built with an Ocean Optics PS1000-UV-VIS grating spectrometer (described in Cummings and Partridge 2001) in pairs of downwelling and sidewelling spectral irradiance while noting the presence of surfperch species. Downwelling irradiance, $I_D(\lambda)$, was collected by orienting the spectroradiometer upward and represents the illumination available for target reflection, whereas sidewelling irradiance, $I_S(\lambda)$, estimates the horizontal visual field or visual background and was measured by orienting the spectroradiometer horizontally. Sidewelling irradiance, which collects light from a hemisphere in the horizontal direction, was used as an estimate of the fish's visual background to account for the extremely wide field of view that fish eyes afford. The spherical lenses of most teleosts protrude from the body with a pupil that is nearly the same size as the lens (Jagger 1992) providing nearly 180° field of view (Sivak et al. 1999). The irradiance collector on the spectroradiometer approximates a cosine function over a hemisphere, and therefore these sidewelling irradiances include features of the downwelling and upwelling irradiance fields but are mostly a measure of the highly colored radiance of the horizontally viewed open water. Although sidewelling irradiance measurements may be appropriate estimates for the visual background for organisms with a wide field of view such as fish, they may not be appropriate for animals with more restricted viewing angles.

On each SCUBA dive, paired optical measurements were collected in a stratified random design across various nearshore environments in Hopkins Marine Life Refuge (Pacific Grove, CA) including surfgrass zone, canopied and noncanopied kelp forest areas, and sand channels as different surfperch species occupy different combinations of nearshore microhabitats (Holbrook and Schmitt 1989, 1992). The entire set of paired irradiance data collected in the presence of each surfperch species was used to characterize each species' optical habitat.

Along with habitat irradiance measurements, surfperch whole lens transmittance and photoreceptor absorbances were previously measured (Cummings and Partridge 2001). Visual pigment divergence was characterized in a similar manner as reflectance by identifying peak sensitivities or wavelength of maximum absorbance, λ_{\max} , of different cone classes (SWS, short-wavelength sensitive, and LWS, long-wavelength sensitive). Surfperch exhibit great divergence in peak sensitivities within each cone class (455–482 nm range of species' mean SWS cones λ_{\max} values; 525–545 nm range of species' mean LWS cones λ_{\max} values, Cummings and Partridge 2001). The model outlined below (see Estimating Intraspecific Sensory Bias) examines how divergence in visual pigment λ_{\max} affects target detection in both the luminance and chromatic pathways.

To estimate how surfperch use photoreceptor input to detect targets (foraging or conspecifics) using color and brightness contrast, a simple model of dichromatic vision was developed for the nearshore environment (for more details, see Cummings 2004). The first step of this model is photoreceptor photon capture (cone quantum catch), Q_c , which represents the level of excitation for cone class c (either SWS or LWS cones) while viewing target, t , and background b radiances under specific optical conditions:

$$Q_{t,c} = \sum_{\lambda=350}^{700} L_t(\lambda) A_c(\lambda), \quad (1)$$

$$Q_{b,c} = \sum_{\lambda=350}^{700} L_b(\lambda) A_c(\lambda), \quad (2)$$

where cone quantum catch of target and background radiance, Q_c , is summed at 2-nm intervals over 350 to 700 nm. The spectrum of light entering the eye from the target, known as radiance, $L(\lambda)$, has quantal units of photons $\text{s}^{-1} \text{cm}^{-2} \text{sr}^{-1} \text{nm}^{-1}$ and is estimated as the product of measured downwelling irradiance, $I_D(\lambda)$, and target reflectance, $R_t(\lambda)$, per solid angle. The estimated fish target radiance was calculated as the average radiance from a cylindrical fish body viewed horizontally in a light field dominated by downwelling irradiance ($L_t(\lambda) = \frac{I_D(\lambda)R_t(\lambda)}{2\pi}$) as in Cummings and Johnsen (2007). Cone quantum catch of background radiance, $Q_{b,c}$, represents the quantal absorption of light entering the eye from the visual background, or the horizontal

light field in this underwater environment. Background radiances, $L_b(\lambda)$, were evaluated as the sidewelling irradiance converted to radiance using the same quantal units and restricted viewing field as $L_t(\lambda)$, ($L_b(\lambda) = \frac{I_S(\lambda)}{2\pi}$). Cone absorbance, $A_c(\lambda)$, represents the fraction of light incident to the eye that is absorbed by each cone class and is calculated using species-specific microspectrophotometric (MSP) absorbance, lens-transmittance, and optical density (OD) measurements from Cummings and Partridge (2001). Although the absolute LWS cone OD measurements were used (where $LWS(OD) = MSP\text{-measured LWS cone optical density}$), SWS cone optical density values were standardized to LWS values to account for high measurement variation (presumably due to small sample sizes) such that $SWS(OD) = LWS(OD) \times 0.8$ (see Cummings 2004, fig. 6). Cone quantum catch estimates were calculated for each pair of irradiance measurements collected in the presence of a given surfperch species.

The model then assumes that photoreceptors undergo physiological adaptation to background light in a cone-specific manner (von Kries transformation). Assuming this type of chromatic adaptation, the cone quantum catches, Q_c , are adjusted for both background and target radiances with the following:

$$a_c = k_c Q_c, \quad (3)$$

where $k_c = 1/\sqrt{Q_{b,c}}$ represents the von Kries transformation coefficient that follows the De Vries–Rose law for low-light environments (Rose 1942; De Vries 1943; Barlow 1964).

Photoreceptors send information of quantum catch to higher order neurons that have quantitatively distinct processes to extract qualitatively different visual features. The chromatic pathway evaluates the spectral properties of visual stimuli and the luminance pathway is sensitive to the total intensity of stimuli. Among fish taxa, the number and relative weightings of cone classes that contribute to the luminance channel varies across species, with some marine and freshwater species showing multiple cone inputs (Svaetichin and MacNichol 1958; Saszik et al. 2002), particularly at low light levels (e.g., goldfish, Neumeyer et al. 1991). Without electrophysiological information on these specific pathways in surfperch, the model makes the simplest assumption of SWS and LWS cone inputs with equal weightings. To represent these different pathways, the model assumes that the adjusted cone signals, a_c , are then processed by opponency (C , chromatic) and nonopponency (L , luminance) channels (Vorobyev and Osorio 1998) for both background, b , and target, t , radiances:

$$C = a_{c1} - a_{c2}, \quad (4)$$

$$L = a_{c1} + a_{c2}, \quad (5)$$

where $c1$ and $c2$ represent SWS and LWS cones, respectively. Target detection was estimated by computing the signal-to-noise

ratios in each pathway and assuming that performance is limited by receptor noise in a low light environment (Vorobyev and Osorio 1998; Vorobyev et al. 2001):

$$C_{s:n} = \frac{|C_t - C_b|}{e_C}, \tag{6}$$

$$L_{s:n} = \frac{|L_t - L_b|}{e_L}, \tag{7}$$

where e_C and e_L represent the total noise in the respective chromatic and luminance channels. For the chromatic channel, noise was evaluated as the summation of target and background signal variances by individual receptor cells weighted by the cone class ratio within the receptive field (e.g., Chiao et al. 2000),

$$(e_C)^2 = \left(\frac{1}{\sqrt{Q_{t,SWS}}} \right)^2 + \left(\frac{1}{\sqrt{R * Q_{t,LWS}}} \right)^2 + \left(\frac{1}{\sqrt{Q_{b,SWS}}} \right)^2 + \left(\frac{1}{\sqrt{R * Q_{b,LWS}}} \right)^2, \tag{8}$$

where R represents the relative ratio of LWS to SWS in the receptive field of signal response. Surfperch cone mosaic structure has not yet been identified; however, a common cone mosaic in fish dichromats has a SWS surrounded by four LWS cones (Ali and Ancia 1976), and this model applies a conservative estimate of $R = 4$ representing a 4:1 (LWS: SWS) cone ratio.

Unlike the chromatic signal, the luminance signal and noise estimates were assumed to be pooled responses. The total noise in the luminance channel was estimated as the additive variance in both target and background radiances:

$$(e_L)^2 = \left[\frac{1}{\sqrt{(Q_{t,SWS}) + R * Q_{t,LWS}}} \right]^2 + \left[\frac{1}{\sqrt{(Q_{b,SWS}) + R * Q_{b,LWS}}} \right]^2. \tag{9}$$

ESTIMATING INTRASPECIFIC SENSORY BIAS

To evaluate sensory biases, I examined how photoreceptor sensitivity divergence provides each species with gains or losses in chromatic or luminance target detection within their specific habitat. Divergence in visual pigment sensitivity was evaluated as the change in peak sensitivity relative to the estimate of the ancestral surfperch visual pigments, as well as to the average surfperch visual pigment peak sensitivities. A previous examination of surfperch visual detection performance identified a detection trade-off in luminance and chromaticity based on photoreceptor spectral tuning (Cummings 2004). Here, I examined the likely evolutionary direction that species have taken in this

trade-off by comparing estimated performance between surfperch measured visual pigment relative to a standard pair of surfperch visual pigments. The estimated detection performance of each species' measured visual pigments were compared to two different "benchmarks" of divergence: the arithmetic mean of each photoreceptor class (e.g., mean SWS $\lambda_{max} = \frac{1}{N} \sum_{i=1}^N SWS_i$) across all five surfperch, and the maximum likelihood estimate of the ancestral surfperch visual pigment properties. The ancestral visual pigment estimates were calculated based on phylogenetic branch lengths using a maximum likelihood estimate that assumes a conservative, random walk process of evolution (Brownian motion), which is a standard practice for examining character transformations relative to a molecular phylogeny (Felsenstein 1985).

The ancestral SWS and LWS cone λ_{max} values were estimated using the maximum likelihood program ANCML ver.1.0 (Ludwig and Schluter 1997; Schluter et al. 1998) with Embiotocidae molecular sequence divergence data (Bernardi and Bucciarelli 1999). The ANCML program estimates the state of a continuous trait (e.g., λ_{max}) at each node in a phylogeny and provides a standard error for this estimate, by assuming a Brownian motion model for evolution. The maximum likelihood calculation finds the set of continuous trait estimates at each node that minimizes the difference between ancestor and descendent traits across all branches (Schluter et al. 1998). An evaluation of continuous change, rather than a punctuated model, was employed to account for the near continuous gradations in visual pigment sensitivity in many photoreceptor classes in teleosts afforded by chromophore mixing (rhodopsins and porphyropsins, A_1 and A_2 , respectively), differential opsin expression, and potential changes in opsin sequences. The ancestral estimates of the SWS and LWS cone peak sensitivities were calculated by providing the ANCML program with a phylogenetic treefile along with the measured SWS and LWS λ_{max} values of the five species in this study. The phylogenetic treefile was calculated from the molecular sequence divergence data between extant taxa (supplied by G. Bernardi, pers. comm. 2000). The molecular phylogeny was based on mitochondrial cytochrome b and 16S ribosomal gene regions (Bernardi and Bucciarelli 1999). The maximum likelihood estimate of the ancestral surfperch visual pigments was calculated for the most basal node for the five surfperch species examined in this study and does not represent an ancestral visual pigment estimate for the entire Embiotocidae family.

The visual task used to identify sensory biases was the ability of surfperch to detect a major foraging target (the red algae, Rhodophyta) against the background light (sidewelling irradiance) as species rove through their specific habitats. Surfperch are microcarnivores and forage by roving through the kelp forest understory, in search of patches of suitable macroalgae (Schmitt

and Coyer 1982). Once a patch is found, surfperch ingest the turf algae along with the cryptic and encrusting prey that live upon this algae. Dietary studies have shown that various Rhodophyta can be the most abundant item in their diet accounting for up to 30% of their stomach contents (Laur and Ebeling 1983). Rhodophyta are members of a division of mostly multicellular algae possessing a specific set of accessory pigments (e.g., phycobilins) resulting in uniform dark red coloration, and represent one of the two main divisions of macrophytes found in the nearshore environment of the California kelp forests (Rhodophyta and Phaeophyta). Reflectance measurements on a number of noncoralline species of Rhodophyta exhibited identical reflectance spectra, and a mean reflectance spectrum from 36 reflectance measurements from a number of different species including *Neogardiella sp.*, *Gigartina corymbifera* was used to represent the “red turf algal” target. In this study, I examined visual detection of this major surfperch foraging target (Rhodophyta), as well as another major macrophyte (Phaeophyta) in the nearshore environment (the giant kelp, *Macrocystis pyrifera*).

To estimate relative visual detection performance across photoreceptors with different peak sensitivities, 100 LWS and 100 SWS model absorbance curves were calculated for each species using species-appropriate A_1 or A_2 Govardovskii et al. (2000) templates and varying the λ_{\max} at 1-nm intervals. The model absorbances were converted to absorptance curves (as in Cummings 2004, fig. 6) and represent a range of SWS visual pigments varying in peak absorptance from 400 to 500 nm, as well as a 100 nm range of LWS cones varying in λ_{\max} from 500 to 600 nm. All possible pairs of model LWS and SWS absorptance curves were evaluated in the surfperch target detection model described above (eqs. 1–9) using the mean Rhodophyta and *M. pyrifera* reflectance spectra from Cummings (2004).

Each possible pair of visual pigments was evaluated for target detection performance in chromatic and luminance pathways for all optical measurements in each species’ habitat. The median chromatic and luminance signal-to-noise value was calculated for each pair of pigments to compare target detection performance across photoreceptor pairs within a habitat. The median, rather than the mean, was selected to characterize performance to avoid the influence of extremely high-intensity measurements and to emphasize the lower signal-to-noise conditions where visual detection is limited. The visual pigment pair with the greatest median value for target detection in each species-specific habitat was defined as the best performing pair, and all model photopigment performances were reported as a proportion of this value (pC or pL). Sensory bias was quantified as the difference in performance between ancestor and extant (or average and extant) performance in each detection channel within each species-specific habitat: (chromatic gain: $pC_{\text{extant}} - pC_{\text{ancestor}}$ and $pC_{\text{extant}} - pC_{\text{average}}$; luminance gain: $pL_{\text{extant}} - pL_{\text{anc}}$ and $pC_{\text{extant}} - pC_{\text{avg}}$).

ESTIMATING INTRASPECIFIC SIGNAL BIAS

The visual tasks used to identify sensory and signaling biases differ in that one examines the ability to “see” foraging targets, whereas the other examines the ability to be “seen” by conspecifics. Each task was used to examine how divergence in sensory or signaling traits favors chromatic or luminance detection, with the sensory examination focusing on how variation in photoreceptor λ_{\max} values affects target detection, and the signal examination focusing on how variation in color pattern reflectance properties (R_{peak} or $R_{\text{cut-on}}$) affects conspecific detectability. Sensory bias was evaluated by estimating the difference in measured trait detection performance relative to a standard reference point (average or ancestral estimate) within each distinct photoreceptor class (SWS and LWS). Similarly with reflectance spectra, signal bias was evaluated by comparing divergence in reflectance detectability within distinct classes of color elements (orange, blue, and silver). An important difference in estimating divergence between sensory and signaling traits is that for sensory traits ancestral estimates can be made for the most basal node across all five species, whereas for signal traits ancestral estimates can be made for discrete pairs only. All five surfperch have SWS and LWS cones, whereas all five surfperch do not share the same color elements (orange, blue, or silver), and therefore signal divergence estimations are made specific to the pairs of species exhibiting each color trait.

To examine how continuous variation within a color type affects signal detection, each species measured reflectance spectrum was compared to a reflectance spectrum with an R_{peak} or $R_{\text{cut-on}}$ representing the arithmetic mean or the ancestral estimate for that color class (orange, silver, or blue). The ancestral estimate of each color element’s R_{peak} or $R_{\text{cut-on}}$ was computed using ANCMML ver.1.0 and surfperch molecular sequence data and represents the character state at the ancestral node between the two species displaying that color element. The arithmetic mean, or midpoint, of R_{peak} or $R_{\text{cut-on}}$ was also calculated for each pair of species displaying specific color elements.

Color pattern detectability was examined with the same detection model described above by exchanging the target, $R_t(\lambda)$, from Rhodophyta to male color pattern reflectances. To evaluate signal detectability across reflectances with different spectral shapes (R_{peak} or $R_{\text{cut-on}}$), model reflectance curves were created by displacing each species’ average reflectance spectrum toward shorter or longer (R_{peak} or $R_{\text{cut-on}}$) wavelengths at 2-nm intervals across an appropriate range for each color element (e.g., “blues” [350 to 450nm]; “silvers” [500 to 650 nm]; “oranges” [500 to 610 nm]; “brown” [610 to 710 nm]; and “dusky” [450 to 550 nm]). Total reflectance was kept constant while varying only the spectral properties of the reflectance (R_{peak} or $R_{\text{cut-on}}$). For example, the average R_{peak} of *H. caryi* under-eye blue reflectance spectrum was 418 nm. The 50 model reflectance spectra created from this species’ average blue reflectance have the same total intensity

properties as the measured reflectance, but vary in their R_{peak} values from 350 to 450 nm at 2 nm intervals. This method isolates the effect of spectral reflectance properties on signal detection (e.g., Osorio et al. 1997) and is a first step in determining features of signal properties that influence detection.

Species-specific model reflectances were evaluated in terms of their luminance and chromatic detectability in each habitat with the signal-to-noise detection model and species-specific visual pigment measurements described above (eqs. 1–9). The median performance of each reflectance spectrum across all optical measurements in each species' habitat was used to estimate the best signal design for each species. Ideal signal design was identified as the model reflectance that produced the greatest median chromatic or luminance signal-to-noise ratio across all optical measurements in each habitat, and the performance of all model reflectance spectra are reported as a proportion of this value in each detection channel (e.g., pC , pL). Signal design bias was then quantified as the difference in detectability between ancestor and extant (or average and extant) reflectances in each detection channel within each species-specific habitat: (chromatic gain: $pC_{\text{extant}} - pC_{\text{anc}}$ and $pC_{\text{extant}} - pC_{\text{avg}}$; luminance gain: $pL_{\text{extant}} - pL_{\text{anc}}$ and $pL_{\text{extant}} - pL_{\text{avg}}$).

STATISTICAL ANALYSES

To examine whether the evolutionary pattern of sensory and signal biases was statistically significant across species, I used two methods to quantify the inferred correlation between surfperch sensory and signal characters. The first method examined the relationship between evolutionary gains in specific sensory detection channels and gains in signal detectability using Pearson correlation coefficients. Correlations on the sensory and signal gains (extant – ancestral estimates; $N = 5$) within each pathway were evaluated (e.g., sensory chromatic gain and signal chromatic gain). I also examined the statistical relationship between visual detection and reflectance detectability performances with independent contrast estimates ($\text{extant}_a - \text{extant}_b / \text{variance}$; $N = 4$; where variance was a function of branchlengths) using the CONTRAST program from the PHYLIP package (Felsenstein 1995) and branch length information from Bernardi and Bucciarelli (1999). Both methods use phylogenetic information to assess correlation, yet both are restricted in power to determine statistical significance given the small number of taxa.

Results

The maximum likelihood estimate of the peak absorbance of the ancestral surfperch SWS cone λ_{max} was 468.7 ± 12.5 nm (standard error) and 537.9 ± 12.5 nm for the LWS cone λ_{max} . Note that the maximum likelihood estimates for ancestral surfperch visual pigments were within 2 nm of the arithmetic average across

these five species (SWS $\lambda_{\text{max}} = 470.48 \pm 4.68$ nm, LWS $\lambda_{\text{max}} = 536.64 \pm 2.22$ nm). Given the similar values between ancestral and average visual estimates, the estimates of divergence patterns were similar with either point of reference and graphical results are shown only for the ancestral estimates in Figures. 2, 5. The high error values associated with the ancestral estimate suggests that the variation in interspecific visual pigments is not largely explained by phylogeny: closely related species, such as the congeners *E. jacksoni* and *E. lateralis*, exhibit as much divergence in visual pigment as non-congeners across this species' group. Such divergence implies that something other than phylogenetic history is driving the variation across species' visual pigments.

Figure 2 shows the detectional trade-off for the surfperch's most important foraging patch, Rhodophyta, and also emerges when estimating performance for another common foraging target, *M. pyrifera* (data not shown). Although detectional performance is a function of the spectral tuning of both cone classes, it is the tuning of the SWS cone that has a more pronounced effect on the sensory trade-off. For many of the surfperch species, the same spectral placement of the LWS cone that maximizes chromatic detection will also maximize luminance detection (e.g., *E. lateralis*: LWS of 525–530 nm will maximize both luminance and chromatic detection). However, maximizing detection in each of these channels calls for very different spectral placement of the SWS cones. In general, a longer SWS λ_{max} is estimated to favor a higher luminance detection performance (Fig. 2; right column) but hampers chromatic capabilities (Fig. 2; left column); whereas a shorter SWS λ_{max} favors a high chromatic with low luminance detection performance. For example, the divergence of the SWS cone of *H. caryi* to shorter peak λ_{max} values from the estimated ancestor results in a chromatically biased visual system with an estimated 12.0% gain in performance in the chromatic channel (or 12.9% gain in performance if comparing to the average surfperch visual pigments: 470.48, 536.64 nm) and a 4.3% (or 4.7% relative to average) estimated loss in luminance detection (Fig. 5A). Meanwhile the divergence of *E. lateralis* SWS cones to longer λ_{max} values results in an estimated gain in luminance performance (4.7% compared to ancestral estimate; or 4.3% compared to average), and a 7.2% (or 5.8% relative to average) loss in chromatic detection performance. Species that diverged from the ancestor in a direction that provides estimated gains in chromatic detection (*H. caryi*, *M. aurora*) also exhibit estimated losses in the luminance channel (Figs. 2, 5A). Meanwhile species that gain in luminance detection (*E. jacksoni*, *E. lateralis*, and *D. vacca*) exhibit losses in chromatic detection.

Male color elements that are sexually dimorphic and prominently displayed during surfperch courtship events have diverged among species (Fig. 3; Table 1) in the total amount of reflected light, wavelength of maximum reflectance (R_{peak} ; e.g., silver and blue), or wavelength of midrise ($R_{\text{cut-on}}$; e.g., orange). Although

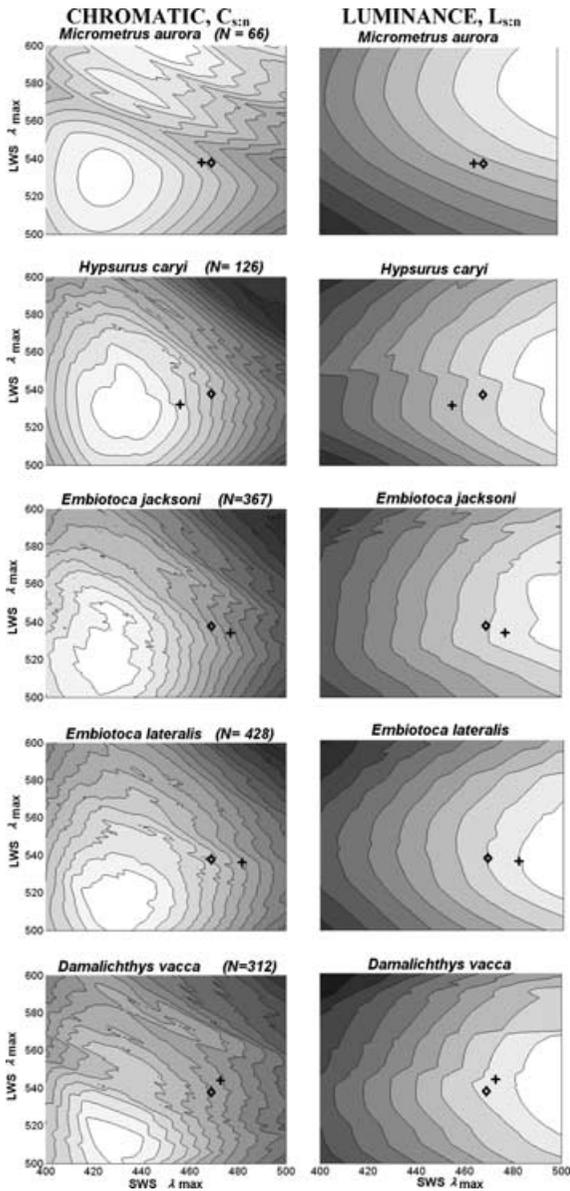


Figure 2. Estimated performance for detecting Rhodophyta against all sidewalling radiance measurements (N) collected in each species' habitat as in Cummings (2004; Fig. 6). All possible paired combinations of model SWS (the x-axis) and LWS (the y-axis) visual pigment absorptance curves are evaluated in terms of chromatic ($C_{s,n}$, Left column) and luminance ($L_{s,n}$, Right column) target detection estimations, with high values (lighter shades) indicating better performance. Contour levels represent 5% performance levels as a function of different photopigment pairs relative to the pair with the maximum median signal-to-noise ratio in each environment. Highest performance ($>95\%$) is marked in white with progressively darker contours exhibiting poorer performance. Both measured visual pigments (+) and the estimate of the ancestor's visual pigments (\diamond) are shown. These diagrams could be regarded as 2D maps of the multivariate adaptive topography. The direction of divergence (from \diamond to +) shows the reconstructed trajectory to the present position on the adaptive landscape, as projected into two different 2D planes.

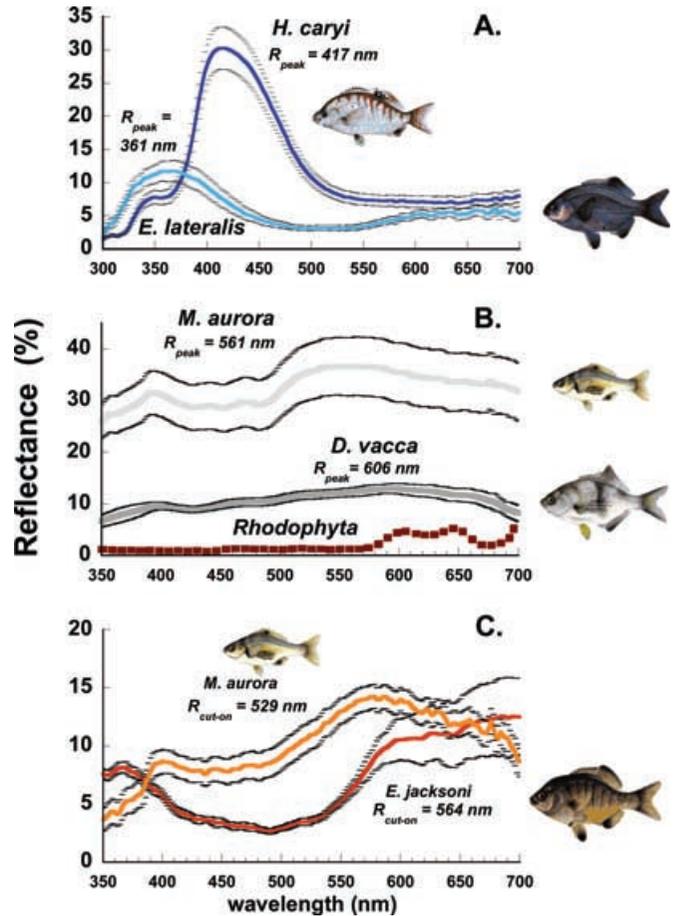


Figure 3. Mean reflectance spectra (± 1 SE) of male surfperch color elements that are sexually dimorphic or prominently displayed during courtship events. Reflectances are paired by species exhibiting similar colors. All reflectance measurements were taken on live fish illuminated from above and collected perpendicular to the side mimicking female viewing conditions. (A) "Blue" spectral reflectance from under the eye of *H. caryi* and *E. lateralis*. (B) "Silver" spectral reflectance from flank areas for *D. vacca* and above the male gonopodium of *M. aurora*. Mean Rhodophyta reflectance spectrum is from Cummings (2004). (C) "Orange" spectral reflectance from flank regions of *E. jacksoni* and *M. aurora*.

some species may exhibit the same class of color, the specific reflectance features of these colors have divergent spectral properties. Not surprisingly, estimations of the point of divergence between pairs of species were very similar whether calculating the maximum likelihood estimate of the ancestral state or the midpoint (Table 1); resulting in similar patterns of signal design bias for either estimate (data shown for the midpoint only in Figs. 4, 5). Changing reflectance design properties (i.e., shifting to longer or shorter R_{peak} or $R_{\text{cut-on}}$) is likely to change the abilities of surfperch to see these color patterns via luminance or chromatic channels (Fig. 4). In general, species with luminance-biased visual systems have color patterns that yield higher estimates of luminance detectability (*E. lateralis*, *E. jacksoni*, and *D. vacca*

Table 1. Species-specific mean color element reflectance properties, and average (midpoint) and ancestral estimate for species with similar colors.

Species	Color element <i>N</i> spectra (<i>N</i> males)	Mean ± SE $P = R_{\text{peak}}, C = R_{\text{cut-on}}$	Midpoint	Ancestral estimate
<i>H. caryi</i>	under eye blue <i>N</i> =33 (9)	$P=417.5\pm 2.2$	389.3	390.2
<i>E. lateralis</i>	under eye blue 12 (4)	$P=361.0\pm 3.7$	389.3	390.2
<i>M. aurora</i>	flank orange 22 (4)	$C=529.2\pm 4.0$	546.7	549.9
<i>E. jacksoni</i>	flank orange 10 (2)	$C=564.2\pm 5.0$	546.7	549.9
<i>M. aurora</i>	halfmoon silver 22 (4)	$P=560.6\pm 7.5$	583.45	586.11
<i>D. vacca</i>	flank silver 6 (2)	$P=606.3\pm 7.9$	583.45	586.11

mean luminance performance $pL = 97.7\%$) than chromatic detectability (mean $pC = 77.5\%$). Meanwhile chromatically biased species have reflectances with higher detectabilities in the chromatic channel while maintaining high estimated performance in both channels (*H. caryi* and *M. aurora* mean $pC = 97.5\%$, mean $pL = 92.1\%$).

Damulichthys vacca and *M. aurora*, species with divergent sensory biases, have “silver” color elements that have diverged in reflectance properties (Fig. 3) to favor luminance for *D. vacca* and chromatic detection for *M. aurora* (Fig. 4). The relative gain in luminance or chromatic divergence from average reflectance parallels the divergence shown in the visual system (Fig. 5). For example, “blue” color elements for *H. caryi* have diverged from the average blue peak reflectance in a direction that offers them 25.5% increase in chromatic detection, paralleling a gain in visual detection of foraging patches (12.2% increase in chromatic detection from the ancestral estimated performance). Meanwhile, another species that uses blue as a dominant display element, *E. lateralis*, has measured blue reflectance that exhibits a 2.0% increase in luminance detectability relative to the average blue reflectance peak—mirroring its visual system gain in foraging detection relative to the ancestor (4.7% gain in luminance).

The inherent trade-off in visual detection performance between luminance and chromatic detection (Fig. 5A) was confirmed with a significant negative correlation between luminance and chromatic sensory gains among surfperch (Pearson’s $r = 0.964$, Bartlett $\chi^2 = 6.628$, $N = 5$, $P = 0.010$). Examining the co-evolutionary relationship between sensory and signal detectability performance shows a tight link between gains in the visual system’s chromatic channel with signal design gains in chromatic detectability (Pearson’s $r = 0.918$, Bartlett $\chi^2 = 4.623$, $N = 5$, $P = 0.032$). This relationship was not significant when examining gains in the luminance channel; most likely due to the small gains in signal luminance detectability by *H. caryi* (see Fig. 5B; Pearson’s $r = 0.439$, Bartlett $\chi^2 = 0.536$, $N = 5$, $P = 0.464$). Note that all the reflectance comparisons (signal gains) were between pairs of species with divergent visual biases: one species with a luminance sensory bias and the other

with a chromatically biased sensory system. Thus, signal gain estimates in effect evaluate the node between the apparent switch between luminance and chromatic visual systems (Fig. 5C). Relatively large correlation coefficients emerged when examining the independent contrast estimates for visual and signal performances, although nonsignificant with only four contrasts (luminance sensory and signal contrasts: Pearson’s $r = 0.888$, Bartlett $\chi^2 = 2.335$, $N = 4$, $P = 0.126$; chromatic sensory and signal contrasts: Pearson’s $r = 0.781$, Bartlett $\chi^2 = 1.414$, $N = 4$, $P = 0.234$).

Discussion

SENSORY DRIVE IN SURFPERCH

The many receiver bias models predict that sensory biases arise through natural selection to shape signal design. When environments and/or sensory systems are biased by physical constraints on information extraction, the constraint on sensory system design produces testable predictions for signal properties favored by intraspecific communication. The sensory bias described in this study is based on an inherent trade-off in color and brightness detection due to differences in the spectral tuning of photoreceptors within dichromatic fish. Divergence in surfperch habitats and sensory properties provides gains in either luminance or chromatic detection but never both, producing quantifiable predictions for color pattern evolution. When trade-offs dominate the sensory system of species living in divergent habitats, this presents an excellent test of the receiver bias model that highlights the environmental influence on sensory and signal evolution—the sensory drive hypothesis.

Sensory drive predicts that the direction of sensory and signal evolution is set by the environment, in a process where traits coevolve simultaneously or where signal properties evolve in response to environmentally induced receiver biases (Endler and Basolo 1998). According to the sensory drive model, the environment provides directional selection on signal evolution—directly by visibility on the signals and indirectly by selection on the viewer’s eyes. The three main predictions of the sensory

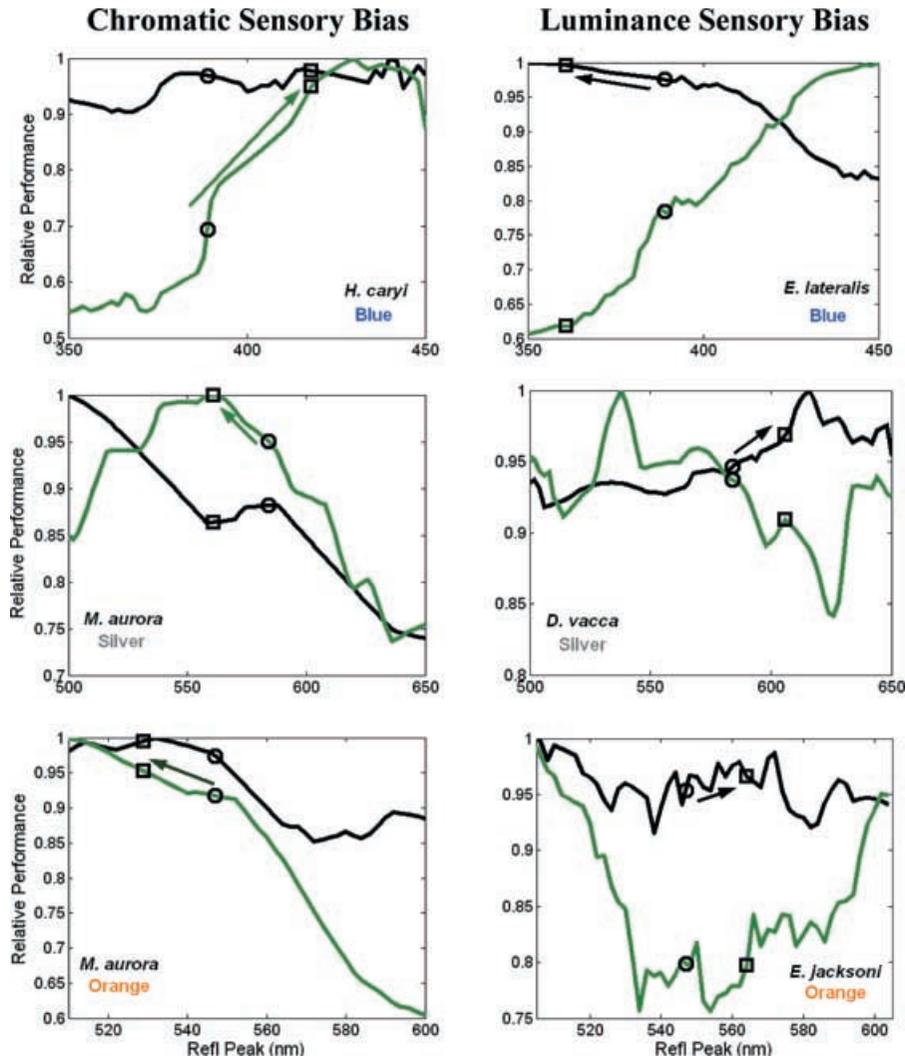


Figure 4. Detectability performance estimates of shared color elements. Left column: Reflectance detectability estimates for species with sensory systems favoring chromatic detection. Right column: Reflectance detectability estimates for species with sensory systems favoring luminance detection. Model reflectances are identified by their characteristic wavelength (R_{peak} or $R_{\text{cut-on}}$; the x axis), with the relative performance of each model reflectance in both the luminance (black) and chromatic (green) channels (the y axis). Species that share the same general color element (e.g., “blue”) are paired across from each other, and the between-species average (\circ) and species-specific measured (\square) values for R_{peak} (blue and silver) or $R_{\text{cut-on}}$ (orange) are plotted. Arrows indicate the direction of greatest positive change (signal bias) in color pattern design relative to the average. Display elements that are unique to one species were evaluated with this model, but not shown graphically (*E. jacksoni* brown flank: $pL = 92.61\%$, $pC = 86.13\%$; and *D. vacca* dusky flank: $pL = 97.91\%$, $pC = 95.71\%$).

drive model (Endler 1992): (1) environmental variation leads to changes in sensory systems, (2) these changes produce different receiver biases, and (3) signaling traits that stimulate these biases will be favored—are well supported with surfperch. First, variation in optical habitat use significantly predicts divergence in surfperch visual pigments (phylogenetically corrected linear regressions: SWS cones $r^2 = 0.83$, $P = 0.002$; LWS cones $r^2 = 0.63$, $P = 0.012$, from Cummings and Partridge 2001). Second, these changes in receptor properties produce estimated divergent biases in the detectability on the basis of different visual environments (Figs. 2, 5A). And, third, the surfperch exhibit a nonrandom

pattern of signal evolution predicted by variation in receiver biases (Fig. 5; sensory and signal chromatic gain $r = 0.91$, $P = 0.032$).

In general, divergence of estimated performance relative to the ancestor is predicted by species-specific habitat characteristics—deeper dwelling surfperch (*E. jacksoni*, *E. lateralis*, *D. vacca*) have diverged toward luminance biased visual systems; whereas species occupying habitats with higher intensities and higher luminance variability have diverged to favor chromatic detection (*M. aurora*, *H. caryi*). Interestingly, the divergence in visual pigments and sensory biases is not a simple matter of depth. Although *M. aurora* inhabits the shallowest of all near-shore

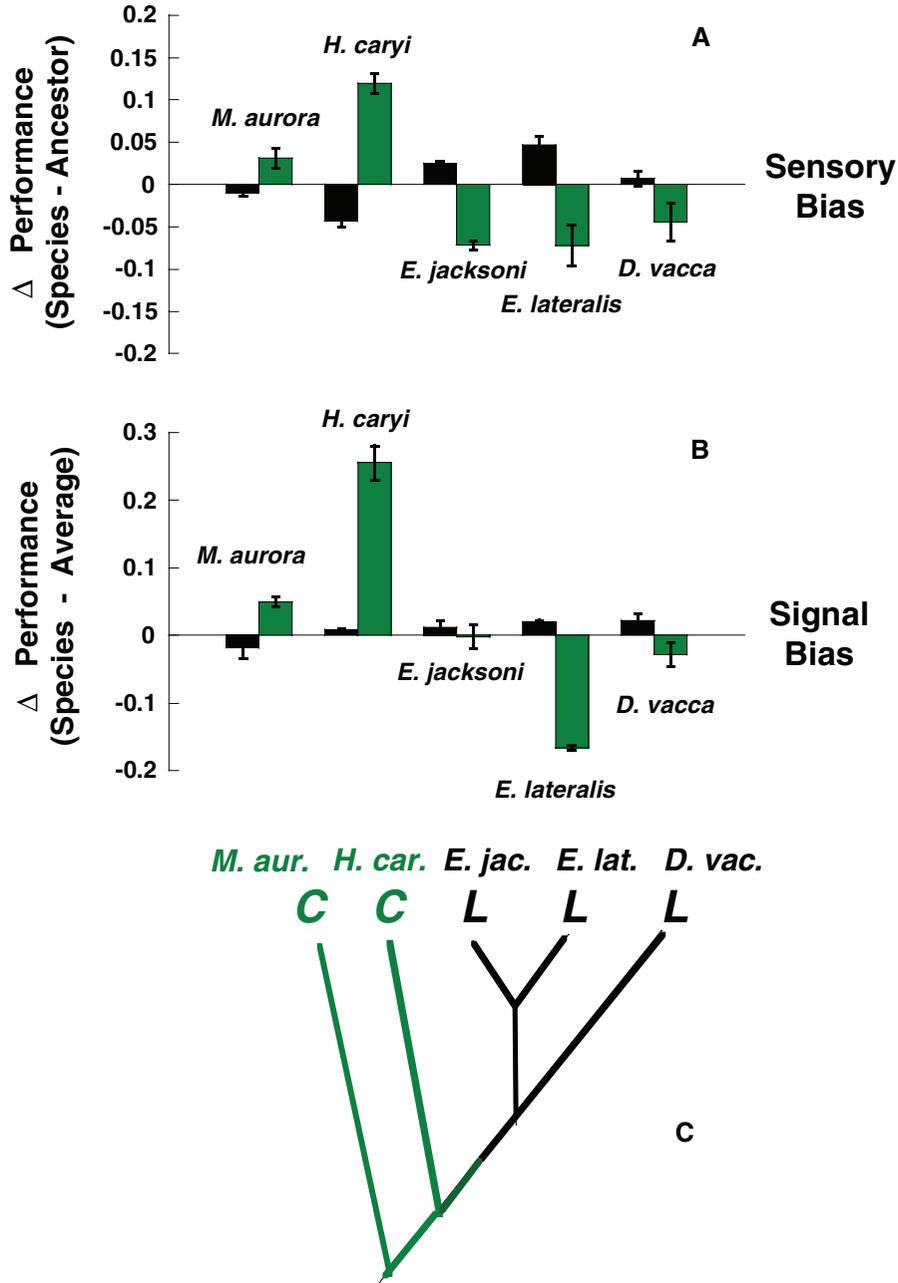


Figure 5. (A) Proportional change in Rhodophyta estimated detection performance between measured and ancestral surfperch visual pigments in the luminance (black) and chromatic (green) channels. Proportional change values calculated from signal-to-noise performance estimated in Figure 2, with standard error bars representing performance based on one standard error in SWS cone λ_{max} measurements (Cummings and Partridge 2001). This same pattern emerges if calculating performance gains relative to average surfperch SWS and LWS cone λ_{max} values (470.48, 536.64). (B) Proportional change in color pattern detectability from performances estimated in Figure 4 for species' measured reflectance spectra relative to average reflectance for shared color elements from Figure 3. Detection performance relative to the average performance is plotted for "silvers" (*M. aurora*, *D. vacca*), "blues" (*H. caryi*, *E. lateralis*), and "orange" (*E. jacksoni*), with the standard error bars representing the range in performance based on one standard error in reflectance R_{peak} or R_{cut-on} measurements. This same pattern emerges if calculating performance gains relative to the ancestral estimates of each color element (from Table 1). (C) Surfperch phylogenetic tree modified from Bernardi and Bucciarelli (1999), with branch color indicating chromatic (green) or luminance (black) visual detection performance estimates determined by visual modeling (Figs. 2, 5A). Surfperch male color pattern signal properties are mapped onto the extant tips of the tree: reflectance property signal bias for chromatic (green C) and luminance (black L) from Figure 5B.

environments (0.5–1.5 m depth range), *H. caryi* inhabits the deepest habitat depth across all five of these surfperch species (depth range 1–20 m, mean depth 7.9 m; Cummings and Partridge 2001). The driving force for the chromatic bias for this species appears to be the great variation in background luminance observed in its habitat (four log units) which is even greater than that measured in the terrestrial forest (three log units; Sumner and Mollon 2000) where background luminance dappling is thought to be the selective force driving advances in color vision (trichromacy over dichromacy). Also of note is that the general trade-off in luminance versus chromatic detection mediated by SWS cone tuning is found only in the deeper dwelling species that have a more spectrally constrained environment in which a single region is defined for maximizing luminance and chromatic detection that places the SWS at very different positions (Fig. 2). Meanwhile, the one shallow-dwelling species (*M. aurora*) has multiple maximization hotspots (> 95%) where photoreceptor tuning could achieve high chromatic discrimination, and consequently the trade-off in this spectrally broader environment is less pronounced.

As predicted by the sensory drive model, surfperch color patterns exhibit biases in detectability that match the visual detection biases of each species. Species that have photoreceptor peak sensitivities favoring luminance detection (*E. lateralis*, *E. jacksoni*, and *D. vacca*) have color patterns with reflectance properties providing greater estimated detectability within the luminance channel and greater gains relative to the average reflectance design (Figs. 4, 5). Meanwhile, surfperch with photoreceptor sensitivities favoring chromatic detection (*H. caryi*, *M. aurora*) have color properties that have diverged to provide greater gains in the chromatic channel. Sensory drive predicts that sexual selection can drive the divergence in reflectance in opposing directions for species with opposing sensory biases. Males with color elements that are more easily detected by conspecific females are likely to gain more attention from females for courtship assessment. According to this argument, female *E. lateralis* are equipped with a sensory system that will be more stimulated by blues that produce higher luminance contrast against the background than blues with greater chromatic contrast properties; whereas the females of *H. caryi* should be more attentive (via increased sensory stimulation) to male display features that exhibit a high chromatic contrast against the background light. This may allow females to better attend courtship displays or to assess male size which has been suggested to play a role in female mate choice decisions in the surfperch system (Warner and Harlan 1982).

The idea that diversification of animal communication traits is driven by the need to maintain conspicuousness in different environments has been suggested for some time (Endler 1978, 1991, 1992; Lythgoe 1979). Several studies have been able to show a strong correlation between the variation in color pattern and habitat background between closely related species or pop-

ulations based on physical differences between color pattern and background radiances (Reimchen 1989; Marchetti 1993; Endler and Théry 1996; Seehausen et al. 1997; Marshall et al. 2003). Studies that have incorporated sensory information to evaluate detectability of color patterns also lend support to the idea that signal diversification is driven by changes in the sensory system or environment (Lall et al. 1980; Endler 1991; Boughman 2001; Maan et al. 2006). With the surfperch system, we are able to expand the level of sensory drive predictions from asking whether contrast is increased or maintained by signal diversification, to determining the specific direction in which signals should increase favoring luminance or chromatic detectability.

SENSORY AND SIGNAL COEVOLUTION

The parallel evolution between sensory and signaling traits in surfperch supports the sensory drive hypothesis; however, it does not indicate a specific evolutionary order of events. Sensory and signaling traits could coevolve simultaneously, sensory biases could predate signaling traits (e.g., Basolo 1990; Ryan et al. 1990; Proctor 1992), or it is possible for signals to drive sensory biases in instances with fierce intrasexual competition for mating targets (e.g., Hornstein et al. 2000). Although all three alternatives are possible, the ecological specialization that surfperch show to particular foraging habitats (Holbrook and Schmidt 1989, 1992) and habitat use driven by foraging patch competition (Schmitt and Holbrook 1990) suggest that the environment places a direct selective force on sensory systems for foraging, and may be a possible initiator of this parallel evolutionary pattern. Furthermore, the selective pressure for foraging success in surfperch where female fecundity increases with body size (Warner and Harlan 1982; Schultz et al. 1991) suggests that the need to detect suitable foraging patches may have a more direct impact on a female's reproductive success than finding suitable mates.

A phylogenetic glimpse at the pattern of sensory and signal evolution is suggestive of a single shift in sensory bias (Fig 5C); however, a consideration of the lability of the surfperch sensory system should warrant considerable caution in drawing definitive conclusions. Visual pigments in lower vertebrates are often highly plastic, either through differential expression of opsin proteins (Carleton and Kocher 2001), or through variation in chromophore moieties attached to the same opsin (Bridges 1972; Loew and Dartnall 1976). Although opsin sequence variation is still unknown in surfperch, they are known to have retinas with mixed chromophore composition (mixtures of vitamins A₁ and A₂, Cummings and Partridge 2001). A₁: A₂ mixtures can shift the spectral tuning of the same photoreceptor class 20–60 nm in a matter of weeks with changes in optical conditions (Dartnall et al. 1961; Beatty 1966; Bridges and Yoshikami 1970). Hence, although the phylogeny suggests a single shift in sensory biases given the ecological niches of these surfperch species in Monterey Bay, California,

a further test would examine sensory bias and signal evolution for this group under different environmental conditions that promote different sensory biases (e.g., southern California).

SIGNAL DESIGN VERSUS SIGNAL CONTENT

Divergence in surfperch signal design across three different types of coloration (orange, blue, silver) are coincident with divergence in the visual systems' detectional biases. These three colors likely represent very different developmental pathways with distinct genetic controls from carotenoid deposition (orange), to structural formation (silvers), to a combination of noncarotenoid pigmentation and structural coloration (blue). Hence, the shift in three signaling traits represents three separate tests of signal divergence predicted by sensory bias. The diversity of signals used in the surfperch system differs from other systems where receiver biases are considered to influence signal evolution by mimicking prey. None of the diverse surfperch color elements resembles the dark red algae (Rhodophyta) that is the main foraging item in the surfperch diet (Fig. 3B), demonstrating that surfperch signals have not converged to mimic foraging targets as has been suggested in water mites (Proctor 1992), guppies (Rodd et al. 2002), and good-inid fish (Garcia and Ramirez 2005). Rather it is the detectional properties, not prey mimicry, that appears to drive color pattern divergence.

The bidirectionality of signal design evolution across color elements in five surfperch species differs from other studies that exhibit unidirectional patterns of evolution on a single trait (e.g., for swords and size in swordtails, Basolo 1990; Rosenthal and Evans 1998), or redness in sticklebacks (Boughman 2001; Smith et al. 2004). Here carotenoid, noncarotenoid, and structural coloration are diverging in directions that are predicted by the species-specific sensory divergence. These three independent examinations of signal design matching sensory bias across five species are a strong indication that receiver biases influence the evolution of signal design independent of the possible signal content. Isolating signal design from signal content is often difficult. For instance, female preferences for orange or red coloration in some fish systems is predicted by sensory drive models from a visual foraging bias for carotenoid-rich food (Boughman 2001; Rodd et al. 2002). Meanwhile, this preference is also predicted by indirect or direct benefit models if these colors serve as indicators of male carotenoid-foraging ability or condition (Endler and Houde 1995; Smith et al. 2004). Hence, a bidirectional bias of signal design across three coloration types helps dissociate these results from other models of sexual selection.

Although signal evolution is a function of both signal design and content, it is important to isolate each component to evaluate their evolutionary contributions. Sensory related models of signal evolution emphasize that signal efficacy and receiver biases alone may direct trait evolution. In this surfperch system, the

inter-specific pattern of signal divergence is predicted by species-specific gains in sensory detection trade-offs independent of signal content. Whether a male's "blue" or "silver" reflectance spectrum has a peak that is shifted to longer or shorter wavelengths is not likely to affect this trait's ability to serve as an indicator for foraging ability or parasite load. It is, however, likely to catch a female's eye more or less depending on how her visual system is tuned for luminance or chromatic detection in her environment. The power of investigating sensory systems that diverge in this dichotomous fashion is the power to more clearly identify the role of signal efficacy and the environment in directing signal evolution.

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LITERATURE CITED

- Ali, M. A., and M. Anctil. 1976. *Retinas of fishes: an atlas*. Springer, Berlin.
- Barlow, H. B. 1964. The physical limits of visual discrimination. Pp. 163–202 in A. C. Giese, ed. *Photophysiology*. Vol II. Academic Press, New York.
- Basolo, A. L. 1990. Female preference for male sword length in the green swordtail (*Pisces: Poeciliidae*). *Science* 250:808–810.
- Bernardi, G., and G. Bucciarelli. 1999. Molecular phylogeny and speciation of the surfperches (Embiotocidae, Perciformes). *Mol. Phylo. Evol.* 13:77–81.
- Boughman, J. W. 2001. Divergent sexual selection enhances reproductive isolation in sticklebacks. *Nature* 411:944–948.
- Beatty, D. D. 1966. A study of the succession of visual pigments in pacific salmon (oncorhynchus). *Can. J. Zool.* 44:429–455.
- Bridges, C. D. B. 1972. The rhodopsin-porphyrpsin visual system. Pp. 417–480 in H. J. A. Dartnall, ed. *Handbook of sensory physiology*. Vol. VII. Springer, Berlin.
- Bridges, C. D. B., and S. Yoshikami. 1970. The rhodopsin-porphyrpsin system in freshwater fishes I. Effects of age and photic environment. *Vis. Res.* 10:1315–1332.
- Carleton, K. L., and T. D. Kocher. 2001. Cone opsin genes of African cichlid fishes: tuning spectral sensitivity by differential gene expression. *Mol. Biol. Evol.* 18:1540–1550.
- Chiao, C.-C., M. Vorobyev, T. W. Cronin, and D. Osorio. 2000. Spectral tuning of dichromats to natural scenes. *Vis. Res.* 40:3257–3271.
- Christy, J. H. 1995. Mimicry, mate choice, and the sensory trap hypothesis. *Am. Nat.* 146:171–181.
- Cummings, M. E. 2004. Modelling divergence in luminance and chromatic detection performance across measured divergence in surfperch (Embiotocidae) habitats. *Vis. Res.* 44:1127–1145.
- Cummings, M. E., and J. C. Partridge. 2001. Visual pigments and optical habitats of surfperch (Embiotocidae) in the California kelp forest. *J. Comput. Phys. A* 187:875–889.

- Cummings, M. E., and S. Johnsen. 2007. Light in the Rocky Shores. *in* M. Denny and S. Gaines, eds. *Encyclopedia of tidepools*. Univ. of California Press, Berkeley, CA.
- Dartnall, H. J. A., M. R. Lander, and F. W. Muntz. 1961. Periodic changes in the visual pigment of fish. Pp. 203–213 *in* C. Christensen and B. Buchmann, eds. *Progress in Photobiology*. Elsevier, Amsterdam.
- De Martini, E. E. 1969. A correlative study of the ecology and comparative feeding mechanisms morphology of the Embiotocidae (surf-fishes) as evidence of the family's adaptive radiation into available ecological niches. *Wasmann J. Biol.* 27:177–245.
- De Valois, R. L., and G. H. Jacobs. 1984. Neural mechanisms of color vision. Pp. 425–456 *in* I. Darian-Smith, ed. *Handbook of physiology The nervous system*. Vol. III. Williams and Wilkins, Baltimore, MD.
- De Vries, H. 1943. The quantum character of light and its bearing upon the threshold of vision, the differential sensitivity, and visual acuity of the eye. *Physika* 10:553–564.
- Endler, J. A. 1978. A predator's view of animal color patterns in *Poecilia reticulata*. *Evol. Biol.* 11:319–364.
- . 1991. Variation in the appearance of guppy color patterns to guppies and their predators under different visual conditions. *Vis. Res.* 31:587–608.
- . 1992. Signals, signal conditions, and the direction of evolution. *Am. Nat.* 139:S125–S153.
- Endler, J. A., and A. E. Houde. 1995. Geographic variation in female preferences for male traits in *Poecilia reticulata*. *Evolution* 49:456–468.
- Endler, J. A., and A. L. Basolo. 1998. Sensory ecology, receiver biases and sexual selection. *Trends Ecol. Evol.* 13:415–420.
- Endler, J. A., and M. Théry. 1996. Interacting effects of lek placement, display behavior, ambient light and color patterns in three neotropical forest-dwelling birds. *Am. Nat.* 148:421–452.
- Felsenstein, J. 1985. Phylogenies and the comparative method. *Am. Nat.* 125:1–15.
- . 1995. PHYLIP: phylogeny inference package. Vers. 3.6c. Distributed by author, University of Washington, Seattle.
- Garcia, C. M. and E. Ramirez. 2005. Evidence that sensory traps can evolve into honest signals. *Nature* 434: 501–505.
- Govardovskii, V. I., N. Fyhrquist, T. Reuter, D. G. Kuzmin, and K. Donner. 2000. In search of the visual pigment template. *Vis. Neurosci.* 17:509–528.
- Hixon, M. A. 1980. Competitive interactions between California reef fishes of the genus *Embiotoca*. *Ecology* 61:918–931.
- Holbrook, S. J., and R. J. Schmitt. 1989. Resource overlap, prey dynamics, and the strength of competition. *Ecology* 70:1943–1953.
- . 1992. Causes and consequences of dietary specialization in surfperches: patch choice and intraspecific competition. *Ecology* 73:402–412.
- Hornstein, E. P., D. C. O'Carroll, J. C. Anderson, and S. B. Laughlin. 2000. Sexual dimorphism matches photoreceptor performance to behavioral requirements. *Proc. R. Soc. Lond. B* 267:2111–2117.
- Jagger, W. S. 1992. The optics of spherical fish lens. *Vis. Res.* 32: 1271–1284.
- Johnsen, S. 2005. The red and the black: bioluminescence and the color of animals in the deep sea. *Integr. Comp. Biol.* 45:234–246.
- Lall, A. B., H. H. Seliger, and W. H. Biggley. 1980. Ecology of colors of firefly bioluminescence. *Science* 210:560–562.
- Laur, D. R., and A. W. Ebeling. 1983. Predator-prey relationships in surfperches. *Environ. Biol. Fish.* 8:217–229.
- Loew, E. R., and H. J. A. Dartnall. 1976. Vitamin A₁/A₂-based visual pigment mixtures in the cones of the Rudd. *Vis. Res.* 16: 891–896.
- Ludwig, D., and D. Schluter. 1997. ANCMML ver 1.0. Available at <http://www.zoology.ubc.ca/schluter/ancmml.html>
- Lythgoe, J. N. 1979. *The ecology of vision*. Clarendon Press, Oxford, U.K.
- Lythgoe, J. N., and J. C. Partridge. 1991. The modeling of optimal visual pigments of dichromatic teleosts in green coastal waters. *Vis. Res.* 31:361–371.
- Maan, M. E., K. D. Hofker, J. J. M. Alphen, and O. Seehausen. 2006. Sensory drive in cichlid speciation. *Am. Nat.* 167:947–954.
- Marchetti, K. 1993. Dark habitats and bright birds illustrate the role of the environment in species divergence. *Nature* 362:149–152.
- Marshall, N. J., K. Jennings, W. N. McFarland, E. R. Loew, and G. S. Losey. 2003. Visual biology of Hawaiian coral reef fishes. II. Colors of Hawaiian coral reef fish. *Copeia* 2003:455–466.
- Maynard Smith, J., and D. Harper. 2005. *Animal Signals*. Oxford Univ. Press, Oxford, U.K.
- Maximov, V. 2000. Environmental factors which may have led to the appearance of colour vision. *Phil. Trans. R. Soc. Lond. B.* 355: 1239–1242.
- McFarland, W. N., and F. W. Munz. 1975. Part III: The evolution of photopic visual pigments in fishes. *Vis. Res.* 15:1071–1080.
- McFarland, W. N., and E. R. Loew. 1983. Wave produced changes in underwater light and their relations to vision. *Environ. Biol. Fish.* 8:173–184.
- Mollon, J. D. 1989. Tho she kneel'd in that place where they grew. . . *J. Exp. Biol.* 146:21–38.
- Neumeier, C., J. J. Weitsma, and H. Spekrijse. 1991. Separate processing of "color" and "brightness" in goldfish. *Vis. Res.* 31:537–549.
- Osorio, D., N. J. Marshall, and T. W. Cronin. 1997. Stomatopod photoreceptor spectral tuning as an adaptation for colour constancy in water. *Vis. Res.* 37:3299–3309.
- Proctor, H. C. 1992. Sensory exploitation and the evolution of male mating behaviour: a cladistics test using water mites (Acari: Parasitengona). *Anim. Behav.* 44:745–752.
- Reed, D. C., and M. S. Foster. 1984. The effects of canopy shading on algal recruitment and growth in a giant kelp forest. *Ecology* 65:937–948.
- Reimchen, T. E. 1989. Loss of nuptial color in threespine sticklebacks (*Gasterosteus aculeatus*). *Evolution* 43:450–460.
- Rodd, F. H., K. A. Hughes, G. F. Grether, and C. T. Baril. 2002. A possible non-sexual origin of mate preference: are male guppies mimicking fruit? *Proc. R. Soc. Lond. B* 269:475–481.
- Rose, A. 1942. The relative sensitivities of television pickup tubes, photographic film, and the human eye. *Proc. Inst. Rad. Eng.* 30:293–300.
- Rosenthal, G. G., and C. S. Evans. 1998. Female preference for swords in *Xiphophorus helleri* reflects a bias for large apparent size. *Proc. Natl. Acad. Sci. U.S.A.* 95:4431–4436.
- Ryan, M. J. 1990. Sexual selection, sensory systems, and sensory exploitation. Pp. 156–195 *in* D. Futuyma and J. Antonovics, eds. *Oxford surveys in evolutionary biology*. Oxford Univ. Press, Oxford, U.K.
- Ryan, M. J., J. H. Fox, W. Wilczynski, and A. S. Rand. 1990. Sexual selection for sensory exploitation in the frog *Physalaemus pustulosus*. *Nature* 343:66–67.
- Ryan, M. J. and M. E. Cummings. 2005. Animal signals and the overlooked costs of efficacy. *Evolution* 59:1160–1161.
- Saszik, S., A. Alexander, T. Lawrence, and J. Bilotta. 2002. APB differentially affects the cone contributions to the zebrafish ERG. *Vis. Neurosci.* 19:521–529.
- Schluter, D., T. Price, A. Ø. Mooers, and D. Ludwig. 1998. Likelihood of ancestor states in adaptive radiation. *Evolution* 51:1699–1711.
- Schmitt, R. J., and J. A. Coyer. 1982. The foraging ecology of sympatric marine fish in the genus *Embiotoca* (Embiotocidae): importance of foraging behavior in prey size selection. *Oecologia* 55:369–378.
- Schmitt, R. J., and S. J. Holbrook. 1990. Population responses of surfperch released from competition. *Ecology* 7: 1653–1665.

- Schultz, E. T., L. M. Clifton, and R. R. Warner. 1991. Energetic constraints and size-based tactics: the adaptive significance of breeding-schedule variation in a marine fish (Embiotocidae: *Micrometrus minimus*). *Am. Nat.* 138:1408–1430.
- Seehausen, O., J. J. M. van Alphen, and F. Witte. 1997. Cichlid fish diversity threatened by eutrophication that curbs sexual selection. *Science* 277:1808–1811.
- Sivak, J. G., M. E. Andison, and M. T. Pardue. 1999. Vertebrate optical structure. Adaptation of visual pigments to the aquatic environment. Pp. 73–94 in S. N. Archer, M. B. A. Djamgoz, E. R. Loew, J. C. Partridge, and S. Valerga, eds. *Adaptive mechanisms in the ecology of vision*. Chapman and Hall, London.
- Smith, C., I. Barber, R. J. Wootton, and L. Chittka. 2004. A receiver bias in the origin of the three-spined stickleback mate choice. *Proc. R. Soc. Lond. B* 271:949–955.
- Sumner, P., and J. D. Mollon. 2000. Catarrhine photopigments are optimized for detecting targets against a foliage background. *J. Exp. Biol.* 203:1963–1986.
- Svaetichin, G., and E. F. MacNichol. 1958. Retinal mechanisms for chromatic and achromatic vision. *NY Acad. Sci. Ann.* 74:385–404.
- Tarp, F. H. 1952. A revision of the family Embiotocidae (the surfperches). *Cal. Div. Fish Game Fish. Bull.* 88:1–99.
- Vorobyev, M., and D. Osorio. 1998. Receptor noise as a determinant of colour thresholds. *Proc. R. Soc. Lond. B* 265:351–358.
- Vorobyev, M., R. Brandt, D. Peitsch, S. B. Laughlin, and R. Menzel. 2001. Colour thresholds and receptor noise: behavior and physiology compared. *Vis. Res.* 41:639–653.
- Warner, R. R., and R. K. Harlan. 1982. Sperm competition and sperm storage as determinants of sexual dimorphism in the dwarf surfperch, *Micrometrus minimus*. *Evolution* 36:44–55.
- Wing, S. R., J. L. Leichter, and M. W. Denny. 1993. A dynamic model for wave-induced light fluctuations in a kelp forest. *Limnol. Ocean.* 38:396–407.

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