

A TEST OF THE CRITICAL ASSUMPTION OF THE SENSORY BIAS MODEL FOR THE EVOLUTION OF FEMALE MATING PREFERENCE USING NEURAL NETWORKS

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The sensory bias model for the evolution of mating preferences states that mating preferences evolve as correlated responses to selection on nonmating behaviors sharing a common sensory system. The critical assumption is that pleiotropy creates genetic correlations that affect the response to selection. I simulated selection on populations of neural networks to test this. First, I selected for various combinations of foraging and mating preferences. Sensory bias predicts that populations with preferences for like-colored objects (red food and red mates) should evolve more readily than preferences for differently colored objects (red food and blue mates). Here, I found no evidence for sensory bias. The responses to selection on foraging and mating preferences were independent of one another. Second, I selected on foraging preferences alone and asked whether there were correlated responses for increased mating preferences for like-colored mates. Here, I found modest evidence for sensory bias. Selection for a particular foraging preference resulted in increased mating preference for similarly colored mates. However, the correlated responses were small and inconsistent. Selection on foraging preferences alone may affect initial levels of mating preferences, but these correlations did not constrain the joint evolution of foraging and mating preferences in these simulations.

KEY WORDS: Genetic constraints, mate choice, pleiotropy, preexisting bias, sexual selection.

The term “sensory bias” is used in two distinct ways in evolutionary biology. First, sensory bias is used to denote which types of secondary sex traits males should evolve. The prediction is that males should evolve traits that maximally stimulate the sensory systems of females (Endler 1992; Ryan and Keddy-Hector 1992; Endler 1993; Vorobyev et al. 1998; Endler et al. 2005; Cummings 2007; Cummings et al. 2008). The second way in which “sensory bias” is used is as an explanation for the evolution of female mating preferences (West-Eberhard 1984; Basolo 1990; Ryan 1990, 1998; Kirkpatrick and Ryan 1991; Fuller et al. 2005a). The prediction here is that female mating preferences evolve as a by-product of natural selection on sensory systems in other nonmating contexts such as foraging and/or predator avoidance (Kirkpatrick and

Ryan 1991; Fuller et al. 2005a; Kokko et al. 2006). It is this second use of sensory bias that is the focus of this article.

Historically, the sensory bias hypothesis has been tested using the comparative method. A pattern in which female mating preferences evolve prior to the evolution of male secondary sex traits has been taken as evidence for sensory bias (Basolo 1990; Ryan 1990; Ryan et al. 1990; Basolo 1995; Shaw 1995; Basolo 1996; Endler and Basolo 1998; Ryan 1998; Smith et al. 2004; Macias-Garcia and Ramirez 2005; Fernandez and Morris 2007). Although there are a variety of issues with the interpretation of such data (Fuller et al. 2005a), the basic concept is relatively simple. A pattern in which female mating preferences evolve to appreciable levels within populations in the absence of the male

Table 1. Models for the evolution of female mating preference and the critical assumptions concerning genetic correlations.

Model	Critical correlations
Direct benefits	No correlation required
Fisher process	Gametic disequilibrium between mate preference and male signal trait
Good genes	Gametic disequilibrium between mate preference and viability
Sensory bias	Pleiotropic genes affect mate preference and other behaviors under natural selection

secondary sex trait is inconsistent with other models for the evolution of female mating preference that rely on the build-up of gametic disequilibria either between the female preference and the male secondary sex trait (in the case of the Fisherian model) or between the female preference and viability as indicated through the male secondary sex trait (in the case of the good genes model) (O'Donald 1962; Lande 1981; Kirkpatrick 1982; Pomiankowski et al. 1991). Because the male secondary sex traits were absent during the establishment of the female preference, neither type of covariance could have existed and, thus, neither model can explain the evolution of the female mating preferences.

However, the sensory bias model also relies on the presence of a genetic correlation (Ryan 1998; Fuller et al. 2005a). Table 1 lists the critical assumptions of the direct benefits, Fisherian, good-genes and sensory bias models in regard to genetic correlations and their underlying causes. The critical assumption of the sensory bias model is that pleiotropy creates strong genetic correlations between behaviors that share a common sensory system (Kirkpatrick and Ryan 1991). The prediction of pleiotropy has never been tested and for good reason. Demonstrating pleiotropy between multiple behaviors is notoriously difficult. Pleiotropy can be demonstrated in one of two main ways. First, pleiotropy can be demonstrated through a series of crosses involving multiple generations in which one examines the extent to which correlations remain in the face of random breeding. Strong correlations that persist over many generations are interpreted as being due to pleiotropy and not the result of gametic disequilibria (Davies 1971; Conner 2002). Second, pleiotropy can be demonstrated through selection experiments that attempt to tease apart mating preferences from other nonmating behaviors such as foraging behavior to determine the extent to which each can evolve independently (Brakefield 2003). Ideally, one would test the sensory bias hypothesis by exerting various forms of selection on mating preferences and on other nonmating behaviors (e.g., foraging preferences) that share a common sensory system and determining the extent to which selection on one behavior affects selection on another (Fuller et al. 2005a,b). In reality, selec-

tion experiments—particularly selection experiments on multiple behaviors—are very difficult.

The best evidence for strong genetic correlations between behaviors sharing a common sensory system comes from studies of guppies. Rodd et al. (2002) have shown strong among population correlations between preferences for inanimate orange objects (which are interpreted as an indicator of foraging preference) and female mating preferences for orange males, which is consistent with pleiotropy. Variation among populations in selection for orange foraging preference would result in a pattern in which the strength of foraging and mating preferences for orange covary across populations provided that there is pleiotropy between foraging and mating preferences. However, an alternate interpretation is that orange foraging preferences and orange female mating preferences have evolved separately. Many authors have suggested that female choice for males with orange spots is adaptive because males must ingest carotenoids to produce these colors (Houde 1997). Carotenoid coloration could be an honest indicator of male quality (Kodric-Brown and Brown 1984; Kennedy et al. 1987; Grether et al. 2005; but see Grether et al. 2001). Thus, sexual selection for orange-colored males and natural selection for animals to prefer orange-colored fruits may have occurred independently.

Again, the critical assumption of sensory bias is that pleiotropy generates genetic correlations between behaviors that share a common sensory system. In this study, I tested this assumption by exerting various forms of selection on populations of artificial neural networks. Neural networks provide a tractable way to simulate evolution on sensory systems (Enquist and Ghirlanda 2005; Phelps 2007). Their utility does not lie in the fact that they accurately represent sensory systems. On the contrary, they are typically quite artificial in comparison to the complexity of real sensory systems. Rather, their strength comes from the fact that, despite their simplicity, they can make meaningful predictions about animal behavior (see Phelps 2007 for a review). Neural networks have been used to test a variety of hypotheses in evolutionary biology. Phelps and colleagues have used neural networks to examine the effects of species recognition on general mate choice and have verified their results by comparing the predicted behavior with that of real animals (Phelps and Ryan 1998). They have also found that the past history of selection on neural networks has strong effects in predicting present day behaviors (Phelps and Ryan 2000; Phelps et al. 2001). Pfennig and Ryan (2006, 2007) have used neural networks to examine the extent to which reproductive character displacement among species promotes behavioral isolation among populations within species. Neural networks have also been used to study the evolution of hidden preferences (Enquist and Arak 1993, 1994), female mating preferences and search strategies (Bjorklund 2002, 2006), the evolution of crypsis (Merilaita 2003, 2007), and

the evolution of aposematic coloration (Merilaita and Tullberg 2005).

Here, I created populations of neural networks that respond to simulated food objects and mate objects. I specifically designed the networks so that foraging and mating behaviors shared a common sensory system and subsequent pathways which should be capable of generating pleiotropy. However, the networks also had the potential to evolve somewhat independently because there were separate outputs for foraging and mating behaviors. I performed two sets of simulations that examined the extent to which a shared common sensory system influences the outcome of selection. These simulations were based loosely on the biology of the bluefin killifish, *Lucania goodei*. Male *L. goodei* are polymorphic in coloration (Foster 1967; Fuller 2002). The three most common color patterns are males with solid blue anal fins, solid yellow anal fins, and solid red anal fins (Fuller 2002; Fuller and Travis 2004). I also used known values on *L. goodei* cone sensitivities to build the neural network (Fuller et al. 2003). I measured the responses of the neural networks to blue, yellow, and red mates as well as blue, yellow, and red food items and determined the extent to which selection on one affected selection on the other.

In the first set of simulations, I used bivariate selection to address the question of whether there are some combinations of preferences for mates and food objects that are unattainable. This simulation tested the idea that natural selection on nonmating behaviors alters the adaptive landscape on which mating preferences can evolve thereby constraining the evolution of mating preferences. Specifically, I tested the extent to which the response to selection on mating preferences was independent of the evolutionary response to selection on foraging preferences. I did this by selecting on populations of neural networks for various combinations of foraging preferences (e.g., preferences for red-, yellow-, or blue-colored food objects) and mating preferences (e.g., preference for red, yellow, or blue mates). The prediction of the sensory bias model was that selection for similarly colored foraging and mating preferences (e.g., red food and red mates) should more quickly reach an equilibrium in which the entire population could exert the proper preferences in comparison to selection for differently colored foraging and mating preferences (e.g., red food and blue mates).

In this simulation, the populations started with random preferences for foraging or mating items, and then were selected for various combinations of preference. This scenario may seem unlikely because it simulates a situation in which there was previously no selection on either foraging or mating preferences, and then selection arises on both behaviors. However, this scenario is not as unlikely as it may seem. Fernandez and Morris (2007) have shown that the transition from two cones to three cones in primates (which allowed for color vision) was associated with the emergence of novel mating preferences in primates. The evolution

of color vision is also thought to be linked to foraging preferences (Osorio and Vorobyev 1996; Regan et al. 2001). More important, bivariate selection tests whether there are some combinations of preferences that are unattainable—or at least more difficult—to attain. By starting with random preferences and selecting for all possible combinations, this simulation examines a large area of phenotypic space.

In the second set of simulations, I exerted univariate selection on foraging preferences (i.e., selection for networks that prefer red, yellow, or blue food items) and examined the extent to which there were correlated responses in mating preferences (i.e., increases in mating preferences for red, yellow, or blue mates). This simulation tested the idea that previous selection in a nonmating context creates biases in the sensory system which affects the evolution of subsequent mating preferences. This is the scenario typically proposed in empirical studies of sensory bias (Basolo 1990; Proctor 1991; Rodd et al. 2002; Smith et al. 2004; Macias-Garcia and Ramirez 2005).

Methods

I created populations of neural networks and exerted various forms of selection on them. Below, I describe the design of the network, the nature of the incoming visual information, how fitness was assigned to networks, how populations were created and propagated, and the two types of selection that were exerted on the populations of neural networks.

NETWORK DESIGN

The network contains several layers that represent the retina and brain. The input layer is the mosaic of photoreceptor cells (Fig. 1). There are a total of 144 photoreceptor cells embedded in a 12×12 matrix. The maximal wavelength sensitivity of cones (λ_{\max}) is based upon values found for Cyprinodontiform fishes (Archer et al. 1987; Archer and Lythgoe 1990; Flamarique and Harosi 2000; Fuller et al. 2003). There are 24 mosaic units that are each composed of two sets of double cones, plus a single violet cone (405 nm), and a single UV cone (359 nm). At the start of each simulation, one double represents a blue/yellow pair (455/538 nm) and the other represents a yellow/red pair (538/567 nm). The only significance of the “double cones” is that the two cones are always adjacent to one another. All cone cells connect to both horizontal cells and bipolar cells.

The design of the subsequent layers is based on the general pattern of retinal organization in vertebrates (for reviews see Djamgoz and Yamada 1990; Wagner 1990; Masland 2001). In vertebrates, horizontal cells receive inputs from many cones across a wide area of retina and are thought to help adjust for overall brightness and background. Six horizontal cells are used in this network (Table S1, Fig. S1). Five horizontal cells are specific to

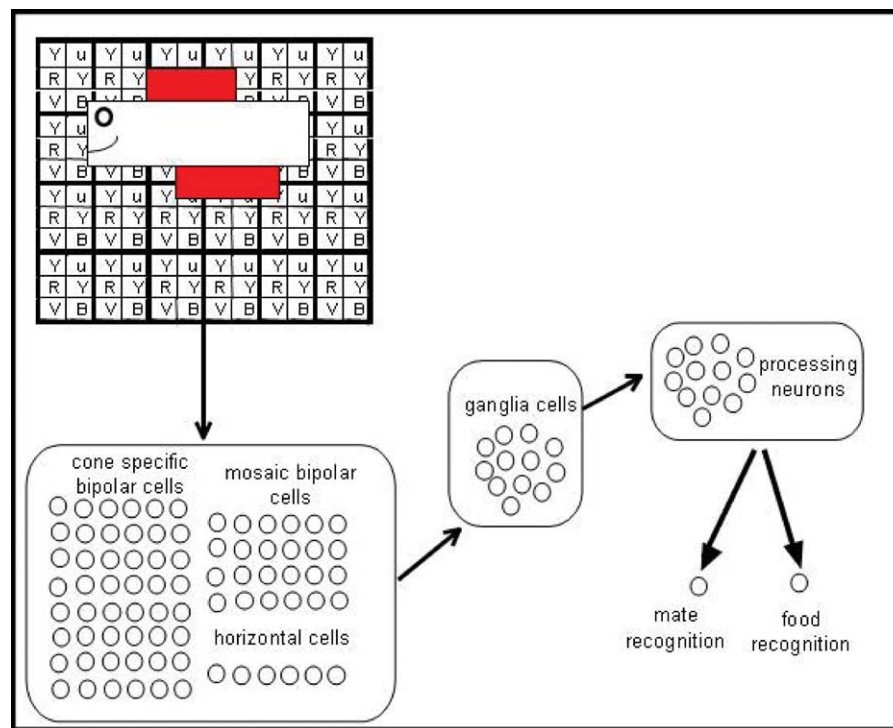


Figure 1. Schematic of a large neural network. The fish image is being projected onto the retina. Twenty-four mosaic units are shown. Each unit has a UV (u), violet (V), blue (B), red (R), and two yellow (Y) cone cells.

each cone type. The UV horizontal cell connects to all UV cones, and the violet horizontal cell connects to all violet cells, etc. There is also a sixth universal horizontal cell that connects to all 144 cone cells in the mosaic. Bipolar cells (BP) typically cover much shorter areas of the retina and convey information concerning visual input at a specific area of retina. Sixty-four bipolar cells are used here. Forty are specific to cone type (i.e., UV-BP, violet BP, etc.) (Table S1, Fig. S2). Each cone-specific bipolar cell connects to cones from nine adjacent subunits. For example, a single UV bipolar cell connects nine UV cones. Eight UV bipolar cells are necessary to cover the retina. In addition to the cone-specific bipolar cells, there are bipolar cells that are specific to one mosaic. There are 24 mosaic bipolar cells that connect to each cone in a given mosaic.

Each horizontal and bipolar cell connects to each of the ganglion cells. Each ganglion cell then connects to each neuron in the processing center (Fig. 1). In my simulations, I examined the effects of varying the number of ganglion cells and the number of neurons in the processing center (see below). Figure 1 shows the largest neural network in which there are twelve ganglion cells and twelve neurons in the processing center. Each neuron in the processing center then connects to two output neurons. One output neuron corresponds to the decision to eat, and the other corresponds to the decision to mate. This simple alteration makes this neural network distinct from previous neural network studies that have had a single output representing mate choice (Arak and

Enquist 1993; Enquist and Arak 1993; Johnstone 1994; Phelps and Ryan 1998, 2000; Phelps et al. 2001). Finally, each neuron is also connected to a single bias neuron. There is one bias neuron for each of the cells shown in Figure 1. This neuron is tonally active. By weighting the bias neuron high or low, an individual neuron can adjust its threshold for firing.

Following Phelps and Ryan (1998, 2000), the activity of each neuron (A) is determined by the input (α_j) from each of the n connecting neurons and the weight (ω_j) it assigns that neuron in the following manner

$$A \equiv \frac{1}{1 + e^{-2.5949(\sum_{j=1}^n \omega_j * \alpha_j)}}, \quad (1)$$

resulting in a sigmoidal activation function. Weights varied between -1 and 1 . Photoreceptor cells have no weights for input from the color pattern as this is determined by the wavelength of maximal sensitivity for each cone class (λ_{\max}) and the reflectance spectra.

THE INPUT OF VISUAL INFORMATION

In the simulation, I projected blue, yellow, and red food objects as well as blue, yellow, and red potential mates on the retina and measured the output of the network. Many small fish, including *L. goodei*, feed on small invertebrates and will readily consume insect larva such as chironomids (Taylor et al. 2001; R. C. Fuller pers. obs.). I therefore simulated worms as prey objects (Fig. 2).

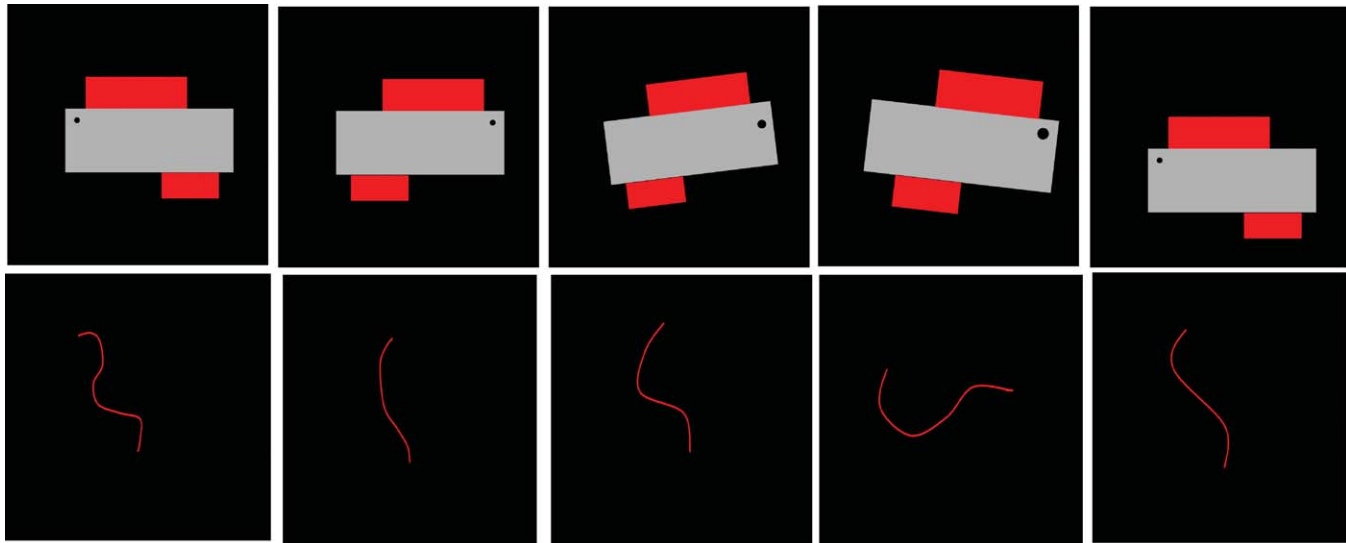


Figure 2. A subset of the mate and food images. The images are shown with the red reflectance spectrum. Neural networks were also assayed for preferences for blue and yellow mates and food items. In those cases, the fins of the fish and the entire food item were colored either blue or yellow using the reflectance spectra shown in Figure 3.

To avoid the network evolving trivial solutions to the task of recognizing the appropriate food and mate objects, I used 20 different mate images and 20 different food item images that differed slightly in the size and orientation of the item on the retina. Each time an individual network was assayed for its mating and foraging preference, the program randomly chose among the possible images and assigned the object the correct reflectance spectra to the appropriate parts. When an individual network was assayed for its mating preference, a single fish image was used with only the reflectance spectra varying between blue, yellow, and red mates. Similarly, when an individual network was assayed for its foraging preference, the program selected a single food image and measured the response of the network when the blue, yellow, or red reflectance spectrum was applied to the image. Figure 2 shows a subset of the mating and foraging objects for males with red fins and for red food items.

The output of each photoreceptor cell was a product of the reflectance spectra (R), relative irradiance (I), and cone sensitivity (S) summed across all wavelengths so that

$$\text{output}(\lambda) = \sum_{\lambda=360\text{nm}}^{\lambda=700\text{nm}} R(\lambda) * I(\lambda) * S(\lambda). \quad (2)$$

Figure 3A shows the reflectance spectra used. These spectra represent actual reflectance spectra taken from the anal fins of *L. goodei* males with an Ocean Optics spectrophotometer (R. C. Fuller, unpubl. data). Due to the peculiarities of the spectrophotometer used to take the measurements, there was an unusually high reading at 610 nm which is reflected in all three curves. I also assumed that signals were propagated over a short distance with minimal attenuation in a clear water system with high light avail-

ability of all wavelengths. Figure 3B shows the relative irradiance based on data presented in Fuller and Travis (2004). Figure 3C shows the sensitivity of each of the five cone cell types. Sensitivities were based on the templates presented by Lamb (1995) in which the sensitivity (S) of a cone cell at wavelength λ is a function of λ_{max} (the wavelength of maximum sensitivity for a given cone type) such that

$$S(\lambda) = \frac{1}{e^{70(0.88 - \frac{\lambda}{\lambda_{\text{max}}})} + e^{28.5(0.924 - \frac{\lambda}{\lambda_{\text{max}}})} + e^{-14.1(1.0104 - \frac{\lambda}{\lambda_{\text{max}}})} + 0.655}. \quad (3)$$

I allowed λ_{max} values of each cone type to evolve such that λ_{max} could take any value between 350 and 700 nm (see details below).

ASSIGNING FITNESS TO INDIVIDUAL NETWORKS

The fitness of an individual network was a function of its ability to discern between target and alternate food items and target and alternate mating items. For a given simulation, one of the colored food items was the “food target” and the other two colored food items were the food alternates. Similarly, one of the colored mates was the “mate target” and the other two were the mate alternates. The preference for the food target over the alternate color morphs was measured as $f_{\text{target}} / (f_{\text{target}} + f_{\text{alternate1}} + f_{\text{alternate2}})$ where f_{target} represents the output of the foraging neuron when the target food item was projected on the neural network, and $f_{\text{alternate1}}$ and $f_{\text{alternate2}}$ represent the output of the foraging neuron when the alternate food items were projected on the network. Similarly, I measured the mating preference for the target versus alternate-colored mates as $m_{\text{target}} / (m_{\text{target}} + m_{\text{alternate1}} + m_{\text{alternate2}})$

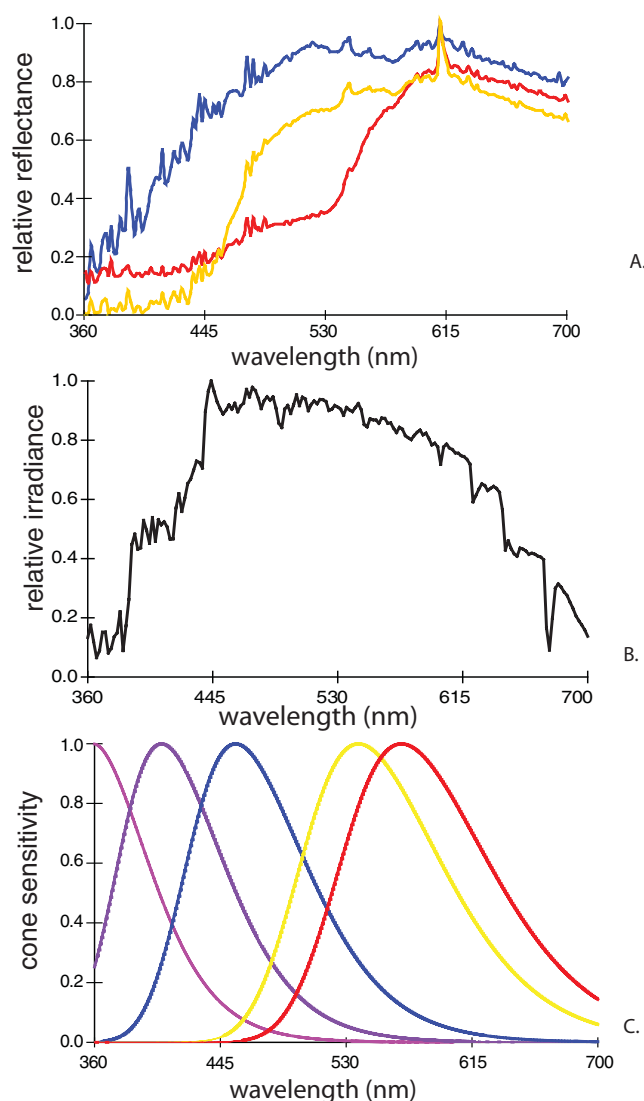


Figure 3. (A) Reflectance spectra of blue-, yellow-, and red-colored anal fins among male color morphs in bluefin killifish. These reflectance spectra were used for both mate and food objects. (B) Lighting conditions represented by relative irradiance. Data from Fuller and Travis (2004). (C) Sensitivity of cones as a function of wavelength (nm) as determined from λ_{\max} values reported for bluefin killifish (Fuller et al. 2003) and templates developed by Lamb (1995).

where m_{target} , $m_{\text{alternate1}}$, and $m_{\text{alternate2}}$ represent the response of the neural network to target and alternate mates.

The fitness of an individual network was a function of its foraging and mating preferences such that

$$W = F \left(\frac{f_{\text{target}}}{f_{\text{target}} + f_{\text{alternate1}} + f_{\text{alternate2}}} \right) + (1 - F) \left(\frac{m_{\text{target}}}{m_{\text{target}} + m_{\text{alternate1}} + m_{\text{alternate2}}} \right), \quad (4)$$

where W represents the fitness of the network, F is the index of the relative importance of foraging preference on fitness, and

$1 - F$ is the relative importance of mating preference on fitness. Networks had their highest fitness when they had high responses to target items and low responses to alternate items.

CREATING AND EVOLVING A POPULATION OF NEURAL NETWORKS

Neural networks evolved to discriminate among foraging items and among mating items due to the fact that the weights evolve. The weights were both variable and heritable. Each neuron had a series of weights that it assigned to the inputs from the connecting neurons (or photoreceptors) in the previous layer as well as the weight assigned to the bias neuron that affects overall threshold for firing. For all of the simulations, I created a population of 100 networks. In generation 0, all weights were randomly assigned a value between -1 and 1 for all 100 networks. I then determined the fitness of each network. I simulated a selection coefficient of 0.5 . The 50 networks with the highest fitness were allowed to “breed” and create the next generation of networks. The 50 networks with the lowest fitness were discarded. To create the next generation, I randomly paired two networks among the 50 “breeders” and randomly chose which weight to assign to the new network. This assumes that there is no linkage among the various weights. I also allowed random mutations to occur. For a given simulated population, mutations occurred at each weight for each individual with a probability of 10^{-3} , 10^{-4} , or 10^{-5} . For example, if the mutation rate was 10^{-3} , then each time a new network was made for the next generation, I generated a random number between 0 and 1 for each weight. If the number was less than 0.001 , then a new weight was randomly assigned for the given weight. Otherwise, the weight from one of the two parents was used (see above). Populations of neural networks were allowed to evolve until the mean fitness of the population was greater than 0.95 or until 10,000 generations had passed.

I also allowed λ_{\max} values to evolve. λ_{\max} values were initially set as described above. However, I allowed for the input of new mutations. When a mutation occurred, I randomly generated a new value for λ_{\max} that lay between 350 and 700 nm. Changes in a given λ_{\max} value affected all of the cone cells expressing that particular type of photopigment. For example, if a mutation occurred that shifted the UV cones from $\lambda_{\max} = 359$ to $\lambda_{\max} = 500$, then all of these cones subsequently had a λ_{\max} max of 500 nm. The five types of photopigment could evolve different values for λ_{\max} , but individual cone cells in the retina could not evolve λ_{\max} independent of the other cone cells that shared the same type of photopigment.

SIMULATION #1—BIVARIATE SELECTION ON FORAGING AND MATING PREFERENCES

The goal of this set of simulations was to determine whether some combinations of foraging and mating preferences were

unattainable—or at least slower to evolve—than others. According to the sensory bias model, pleiotropy should create strong correlations between behaviors that share a common sensory system. Here, I tested whether two preferences (mating and foraging) that shared a common pathway influenced one another's response to selection. I used bivariate selection to test this hypothesis. I simulated selection on populations of networks that involved all combinations of food and mate targets. Specifically, I exerted selection on networks for (1) red foraging preference and red mating preference, (2) red foraging and yellow mate preferences, (3) red foraging and blue mate preferences, (4) yellow foraging and red mate preferences, (5) yellow foraging and yellow mate preferences, (6) yellow foraging and blue mate preferences, (7) blue foraging and red mate preferences, (8) blue foraging and yellow mate preferences, and (9) blue foraging and blue mate preferences. The sensory bias model predicts that selection for similarly colored objects (e.g., red food and red mates) should evolve more quickly and should reach the near equilibrium (mean population fitness > 0.95) faster than selection for different-colored objects (e.g., red food and blue mates). I tested this by determining (1) which simulations reached the near equilibrium before 10,000 generations and (2) how long it took for simulations to reach the near equilibrium.

To determine the robustness of the outcome, I also examined the effects of network size, mutation rate, and the relative importance of foraging and mating preferences on fitness. I altered the overall size of the networks by adjusting the number of ganglia and processing neurons in the network. Table S1 delineates the total number of weights for each of three simulations. A network with 12 ganglia and 12 processing neurons results in a total of 1,111 weights (plus 5 λ_{\max} values). A network with eight ganglia and eight processing neurons results in 735 weights (plus 5 λ_{\max} values). A network with four ganglia and four processing neurons results in 391 weights (plus 5 λ_{\max} values). I also performed simulations with three different mutation rates (10^{-3} , 10^{-4} , 10^{-5}). Together, network size and mutation rate allow an investigation into whether the overall evolvability of the network affects the outcome of selection. A large network with a high mutation rate should evolve faster than a small network with a low mutation rate. My simulations allowed me to determine whether these dynamics affect the outcome of bivariate selection.

I also examined the effect of altering F (the relative importance of foraging preference on fitness) and conversely $1 - F$ (the relative importance of mating preference on fitness). In reality, there are few measures of the relative importance of foraging versus mating preferences on fitness. I initially simulated F at values of 0.05, 0.25, 0.50, 0.75, and 0.95. However, because F values of 0.05 and 0.95 can result in populations that reach the near equilibrium via selection on a single preference, I limited the analysis to F values of 0.25, 0.50, and 0.75 (although see the supplement

for results for F at 0.05 and 0.95). I conducted three replicates for each combination of mate target, food target, network size, mutation rate, and F which resulted in a total of 729 simulations. I used a general linear model to determine the effects of mate target, food target, network size, mutation rate, and F , as well as their interactions on the natural log of the number of generations it took to reach a near equilibrium.

SIMULATION #2—CORRELATED RESPONSES TO UNIVARIATE SELECTION

Here, I simulated a scenario in which there is selection only on foraging preferences and asked whether this created a correlated response in mating behavior. I exerted selection on foraging preferences for red, yellow, or blue food items. Because there was selection solely on foraging preferences, F (the relative importance of foraging preference on fitness) was equal to 1. The simulation ran until the mean fitness of the population was greater than 0.95 or until 10,000 generations had passed. For this simulation, I report a value for the mating preference in which mating preference was measured as $m_{\text{target}} / (m_{\text{target}} + m_{\text{alternate1}} + m_{\text{alternate2}})$. I then determined the mean mating preference for the 100 neural networks in each simulated population. The sensory bias model predicts that selection for foraging preference for a specific color (e.g., red food items) should create a correlated response in mating preference (e.g., red mates). I measured the correlated response in preference for blue, yellow, and red mates as the difference between the final preference (mean population mating preference after selection on foraging preference) and the initial preference (mean population mating preference prior to selection on foraging preference). I also examined the effects of network size (small, medium, and large) and the effect of mutation rate (10^{-3} , 10^{-4} , 10^{-5}) on the outcome of selection. I conducted 27 replicates of each treatment combination which resulted in 729 simulations.

I performed these simulations using Java programming language in a Unix platform. Simulations were performed on a cluster supported by the School of Computational Science at Florida State University. I used Proc GLM in SAS version 9.1 for all subsequent analyses (SAS Institute, Cary, NC). I visually examined all residuals to ascertain that variances were not significantly heteroscedastic. Probability values for all post hoc t -tests are two tailed.

Results

BIVARIATE SELECTION ON FORAGING AND MATING PREFERENCE

All simulations reached the near equilibrium (mean population fitness > 0.95) within 10,000 generations, and most did so in a relatively short time frame (mean time to near equilibrium = 103.1 ± 239.9 SD generations), but there was a large coefficient of variation ($CV = 232.7$). Network size and mutation had by

Table 2. General linear model on \ln (time to equilibrium) for simulations where selection occurred simultaneously on mating and feeding preferences. Highly significant ($P < 0.0001$) effects are listed in bold. The critical test for the sensory bias model is food target*mate target (FT*MT).

Source	df	MS	F	P
Network size (NS)	2	36.76	129.20	<0.0001
mutation rate (MR)	2	6.96	24.45	<0.0001
NS*MR	4	5.45	19.14	<0.0001
food index (FI)	2	2.95	10.36	<0.0001
food target (FT)	2	1.24	4.37	0.0132
mate target (MT)	2	0.03	0.11	0.8972
NS*FT	4	1.24	4.37	0.0018
MR*FT	4	0.62	2.19	0.069
MR*FT*FI	8	0.57	2.00	0.0445
NS*MR*MT*FI	16	0.55	1.93	0.0159
<u>FT*MT</u>	<u>4</u>	<u>0.53</u>	<u>1.85</u>	<u>0.1189</u>
NS*FI	4	0.51	1.81	0.1259
NS*MR*FT	8	0.50	1.76	0.0835
MR*FT*MT	8	0.46	1.61	0.1188
NS*MR*FT*FI	16	0.45	1.60	0.065
FT*MT*FI	8	0.37	1.29	0.2487
NS*FT*MT*FI	16	0.35	1.22	0.2448
MR*MT*FI	8	0.29	1.02	0.4234
NS*FT*MT	8	0.27	0.96	0.4688
MR*FT*MT*FI	16	0.26	0.92	0.5412
NS*FT*FI	8	0.23	0.80	0.6037
NS*MT*FI	8	0.21	0.72	0.6726
NS*MR*FT*MT	32	0.20	0.72	0.8725
NS*MR*FT*MT	16	0.20	0.71	0.789
FT*FI	4	0.19	0.68	0.6046
MT*FI	4	0.14	0.48	0.7478
MR*FI	4	0.11	0.37	0.8284
NS*MT	4	0.08	0.30	0.8788
NS*MR*FI	8	0.08	0.28	0.9719
MR*MT	4	0.07	0.23	0.9205
NS*MR*MT	8	0.07	0.23	0.985
Error	486	0.28		

far the largest effect on the time to near equilibrium (Table 2, Fig. 4: network size: $F_{2,486} = 129.2$; mutation rate: $F_{2,486} = 24.5$; network size * mutation rate: $F_{4,486} = 19.1$). Smaller networks resulted in longer times to near equilibrium presumably because they resulted in populations with less genetic variation and lower probabilities of harboring combinations of weights that could correctly solve the task. Additionally, smaller networks provided fewer targets for incoming mutations. Lower mutation rates led to longer times to the near equilibrium particularly in smaller networks.

The sensory bias model was not supported. First, selection always resulted in populations that could correctly perform the task indicating that correlations that arise due to a shared sensory sys-

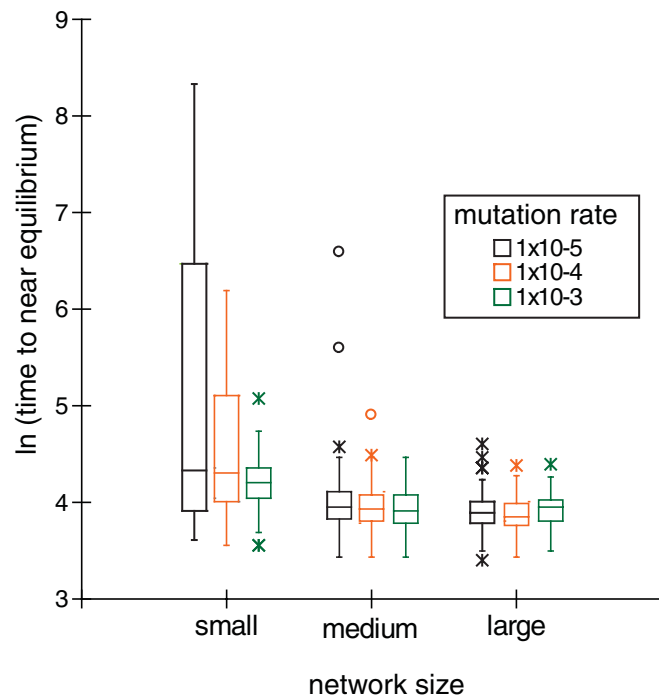


Figure 4. \ln (time to near equilibrium) in generations as a function of network size and mutation rate as a result of bivariate selection on mating and foraging preferences. Box plots denote the median (midline), 25th and 75th percentiles (edges of box), and ± 1.5 * interquartile range (whiskers). Minor outliers are denoted by x, and major outliers are denoted by o. Each treatment combination represents $N = 81$.

tem do not result in constraints on the final outcome of selection. Second, there was no evidence that the time to near equilibrium was differentially affected by the various combinations of mate targets and food targets (food target * mate target: $F_{4,486} = 1.85$, $P = 0.1189$). The initial food preferences were random (mean = 0.33 for red, yellow, and blue foraging preferences) as were the initial mating preferences (mean = 0.33 for red, yellow, and blue mating preferences). Selection resulted in populations that had strong relative responses to the appropriate target food and mate items and minimal responses to the two alternate items. Raw data with the initial and final preferences for red, yellow, and blue mate and food items as well as the time to reach the near equilibrium are listed in supplemental Table 2.

The relative importance of foraging preference on fitness (F) also affected the time to near equilibrium ($F_{2,486} = 10.36$, $P < 0.0001$). Average time to near equilibrium was highest when F was 0.5 (mean = 126.8 generations), lowest when F was 0.75 (mean = 85.1 generations), and intermediate when F was 0.25 (mean = 97.3 generations) (Fig. S3). In another group of simulations, I considered more extreme values for F including 0.95 and 0.05. The general finding was that the time to near equilibrium was greatest when F was intermediate indicating that bivariate

selection increases the time to near equilibrium (Fig. S3). Food target also had a slight effect where blue food targets were associated with longer times to near equilibrium (average time to near equilibrium: blue food target—119 generations; yellow food target—98.9 generations; red food target—91.2 generations).

CORRELATED RESPONSES TO UNIVARIATE SELECTION ON FORAGING PREFERENCE

All simulations reached the near equilibrium within 10,000 generations, and most reached the near equilibrium quite rapidly (time to near equilibrium mean = 35.4 ± 21.2 SD generations). Selection on a single trait resulted in a much faster time to equilibrium than in the previous scenario in which there was selection on two traits. The time to the near equilibrium was also less variable than in the previous simulation ($CV = 59.9$). Foraging preferences for red, yellow, and blue food items were random at the beginning of the simulations (preferences = 0.333). Selection resulted in populations that had strong preferences (> 0.95) for the appropriate food items (see Table S3).

There was modest support for sensory bias. Selection on foraging preferences resulted in small, but statistically significant correlated responses for increased mating preferences for similarly colored mates (Figs. 5 and 6), which are consistent with sensory bias. Specifically, the analysis of variance indicated a significant effect of food target on the change in preference for blue, yellow, and red mates (Table S4, effects of food target— Δ blue mate preference, $F_{2,702} = 25.57$, $P < 0.0001$; Δ yellow mate preference, $F_{2,702} = 17.58$, $P < 0.0001$; Δ red mate preference, $F_{2,702} = 17.98$, $P < 0.0001$). Further, the response to selection on a particular food target generated a positive correlated response to selection for similarly colored mates (and negative responses for differently colored mates) that differed significantly from zero.

However, although the correlated responses differed significantly from zero, there was also a good deal of variance. At generation 0, the mating preferences did not differ from the null expectation of 0.333. The range in preference prior to selection was approximately 0.14 for all three types of mates. After selection on foraging preferences, the ranges in mating preferences increased by 5–7 times (Figs. 5 and 6). Furthermore, negative correlated responses to selection were observed even in treatments in which the sensory bias model predicted positive correlated responses (Figs. 5 and 6). For example, selection for increased preferences for red foraging items did result in a small overall increase in mating preference for red mates. Prior to selection, mean preference for red mates was 0.33. After selection for red foraging preferences, mean preference for red mates was 0.35. However, a sizable number of simulations had negative correlated responses (106 simulations with negative responses, 137 with positive responses). Hence, there is considerable variation in the correlated responses to selection.

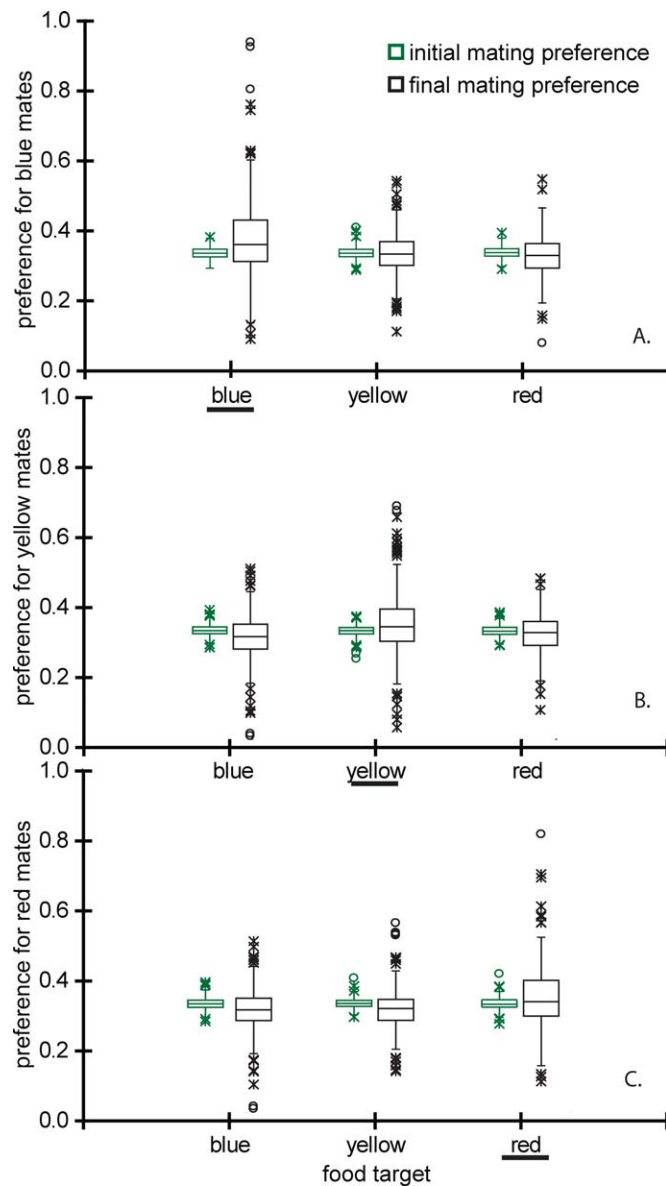


Figure 5. Initial and final mating preferences for blue (A), yellow (B), and red (C) mates as a function of univariate selection on foraging preferences. Initial preferences denote mating preferences at generation 0 prior to selection. Final preferences denote mating preferences after selection on foraging preference to reach the near equilibrium (fitness > 0.95). In each graph, the underlined food target denotes the treatment in which sensory bias predicts an increase in female mating preference. Box plot symbols are the same as in Figure 3. $N = 81$ for each treatment combination.

There were no overall effects of mutation rate or network size on the correlated responses. There was a two-way interaction between network size and mutation rate and a three-way interaction between network size, mutation rate, and food target for the correlated response in preference for yellow mates (Table S4, $F_{2,702} = 2.69$, $P = 0.0304$; $F_{8,702} = 2.04$, $P = 0.0398$). However, there were no compelling patterns

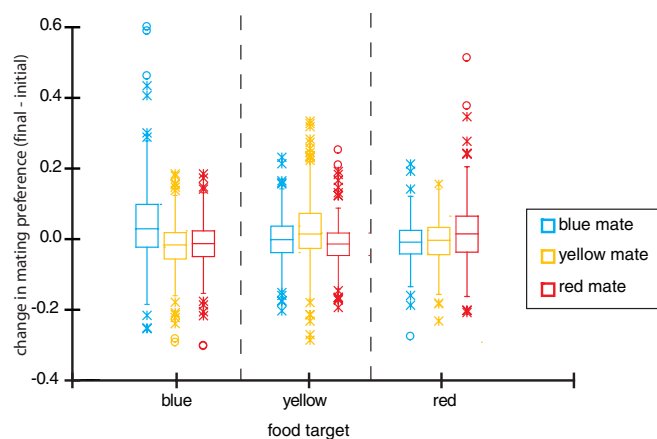


Figure 6. Change in population level mating preferences (final preference—initial preference) as a function of univariate selection on foraging preference. Box plots denote the same statistics as in Figure 3. $N = 81$ for each treatment combination.

emerging from these results (see Table S5 for means and standard deviations).

Discussion

This study provides modest support for the sensory bias model. Selection on foraging preferences for a particular colored object resulted in correlated responses for increased mating preferences for like-colored mates. However, the responses were not very large and not extremely consistent. Although the responses were significantly positive and differed from zero, there were many negative responses some of which were large in magnitude. The results from bivariate selection also indicated that the responses to selection on foraging and mating behavior were independent from one another even when selection favored preferences for differently colored objects. This indicates that natural selection on nonmating behaviors should not unduly constrain the evolution of mating preferences. Assuming that these phenomena are representative of what happens in nature, the critical question is whether the small correlated responses to univariate selection have meaningful effects on the evolution of female mating preferences and male secondary sex characters.

Many authors have proposed a scenario in which sensory bias occurs in conjunction with other models such as the Fisherian model (Ryan and Rand 1993; Phelps and Ryan 2000; Jennions and Brook 2001; Ryan et al. 2001; Arnqvist 2006). One feature of the Fisherian model is that female mating preferences must already be present in the population when males with secondary sex traits matching the preference first invade the population (Lande 1981; Kirkpatrick 1982). Some versions of the good-gene models also are sensitive to the initial levels of female mating preferences (Pomiankowski 1987; Payne and Pagel 2001). Correlated

responses on mating preferences as a function of selection on foraging preferences could lead to the initial increase in female mating preference. However, in order for male ornaments to invade the population via the Fisher process, the mating advantage conferred to males possessing the secondary sex trait must exceed the costs of the trait (Lande 1981; Kirkpatrick 1982). In this study, the sensory bias model caused small increases in female mating preferences. This suggests that only male ornaments with low costs to male viability could initially invade a given population.

On the other hand, one could argue that the correlated responses to selection on foraging behavior were somewhat large. Most females in nature will respond and mate with multiple types of males and may even mate with closely related species under certain circumstances (Jennions and Petrie 2000; Veen et al. 2001; Gow et al. 2006). Houle and Kondrashov (2002) have also shown that modest levels of mating preference can generate very strong selection on male traits. Hence, small correlated effects on mating preferences may actually result in a sizable change in the preference function. However, the ease with which selection could tease apart mating and foraging preferences indicates that selection on nonmating behaviors does not preclude the evolution of mating preferences for any particular color morph. Instead, the results suggest that the evolution of mating preferences via sensory bias is most likely to occur when mating preferences are neutral with respect to fitness.

Despite that foraging and mating preferences evolved independently of one another, there was some evidence to indicate that the response to bivariate selection was somewhat constrained. The time to reach the near equilibrium was longer when there was bivariate selection than when there was univariate selection. The time to the near equilibrium was longer when both foraging and mating preferences affected fitness as opposed to when one was more important than the other (Fig. S4). This suggests that the response to selection is more constrained when there is selection on two types of behaviors. This may seem somewhat paradoxical. There was no evidence to suggest that a common sensory system biased the outcome of selection on various foraging and mating preferences, yet selection on two behaviors resulted in a longer time to equilibrium than selection on a single behavior. This is most likely attributable to the Hill–Robertson effect which is simply that selection on one trait effectively reduces the amount of genetic variation in another trait and therefore reduces the response to selection (Hill and Robertson 1966).

As with any simulation study, the results depend on the details of the model. The neural network employed in this study did not capture all aspects of vision. In nature, animals have to recognize multiple objects in their environment, deal with changing light levels, recognize motion patterns, etc. The critical question is whether other aspects of the network design had important effects

on the outcome of this study. There are three critical aspects of the network design and selection regime that deserve mention.

STRENGTH OF SELECTION

I exerted strong selection on the population of neural networks. At each generation, half of the population was selected to create the subsequent generation. Theory predicts that differences in pleiotropic systems should be detectable when the effective population size, intensity of selection, and heritability are high, and when selection is exerted for many generations (Lascoux 1997). Large selection differentials result in large initial responses to selection, but also result in a rapid reduction of effective population size and genetic variation simply due to the fact that a smaller fraction of the population is being used to create the subsequent generations (Robertson 1960, 1961). The consequence is that rare alleles with small, but beneficial effects on fitness can be lost. In my simulations, alleles with small, beneficial effects would have had their highest probability of being lost in the early generations of selection when there was substantial genetic variation in the population. In real selection experiments, the loss of small, beneficial alleles can be substantial particularly if heritability is low (see Fuller et al. 2005b for a discussion). However, this study, like most neural network studies, had high heritability because there was no environmental variation.

The pertinent question is whether the large selection differential affected the correlated response to selection. The correlated response to selection may have been underestimated as a result of the strength of selection *if* alleles of small effect were more likely to be pleiotropic than alleles of large effect. Further simulations that alter the strength of selection as well as population size are warranted and may provide useful insight into the joint evolution of foraging and mating preferences.

OUTPUT NEURONS

The fact that this network had two output neurons (one for mating and the other for foraging) is critical for this study. I assumed a large degree of overlap between the physiological pathways underlying foraging and mating preferences, but that the overlap was not 100%. This meant that foraging and mating preferences had the potential to evolve independently despite the fact that the two behaviors shared a common sensory system. Different verbal renditions of the sensory bias model (and the closely related sensory trap and sensory drive models) make different assumptions about the degree to which multiple behaviors can evolve independently. The sensory trap hypothesis is the most extreme in this regard and states that males evolve secondary sex traits that cause females to perform some type of nonmating behavior which allows males to mate with them, thereby increasing male fertilization success (Proctor 1991; Christy 1995; Cordoba-Aguilar 2002). Under this scenario, there is complete overlap between the mating behavior

and the nonmating behavior which means that the two behaviors cannot be decoupled. Other authors have suggested that males initially evolve secondary sex traits that act as mimics (and fool females), but that females respond over time by evolving the ability to subsequently discriminate between male secondary sex traits that act as mimics versus the original item they were modeling (Greenfield 2002; Macias-Garcia and Ramirez 2005). This implies an initially high genetic correlation that decreases as a function of selection.

Most studies in sensory bias suggest that past natural selection on sensory systems (as manifested by selection on nonmating behaviors) has predisposed females to be sensitive to certain types of male cues (Basolo 1990; Rodd et al. 2002; Smith et al. 2004; Herzner et al. 2005; Macias-Garcia and Ramirez 2005). Also, sensory drive clearly implies that sensory systems have strong effects on mating and foraging behavior, but that the two traits are somewhat independent of one another (Endler 1992, 1993). The implication is that a genetic correlation is present but is less than 1.

To the best of my knowledge, there are no published estimates for genetic correlations between foraging and mating preferences. The extent to which shared common sensory systems constrain the evolution of multiple behaviors in natural populations is unknown. Theory indicates that genetic correlations only create true evolutionary constraints (where some combinations of trait values can never be attained) when pleiotropy results in genetic correlations equal to 1 (Via and Lande 1985). However, others have argued that high genetic correlations that are less than 1 can effectively create a constraint because the extended time it takes for populations to reach the evolutionary optimum (plus the fact that optima most likely change over time) means that populations will lag behind their phenotypic optima (Schluter 1996; Houle 2001).

MALE ORNAMENTS AS MIMICS

Male ornaments that more closely mimic food items may be more difficult for females to discern and may result in a larger correlated response to selection. In this study, food items and male ornaments were only similar in hue. One might argue that this task was too easy. For example, males with anal fins shaped like worms would pose a more difficult recognition task for females. In fact, Basolo (1990) initially suggested that the swords found on male swordtails may have evolved to mimic food items. This scenario could easily be investigated using neural networks. A large number of studies have suggested that male ornaments have evolved to mimic various items such as food (Proctor 1991; Rodd et al. 2002; Smith et al. 2004; Macias-Garcia and Ramirez 2005), predators (Greenfield and Weber 2000; Greenfield 2002), and eggs (Wickler 1962; Hert 1989; Porter et al. 2002). The issue is whether these female mating preferences evolve due to correlated responses to natural selection, due to direct or indirect sexual

selection, or some combination of the two (Kokko et al. 2003, 2006; Arnqvist and Rowe 2005; Arnqvist 2006).

FITNESS CRITERIA

Alternate fitness criteria are potential avenues for future investigations into sensory bias. In this study, a network achieved high fitness by identifying the target food or mate item. When a network was assayed for its foraging preference, I only considered the output at the foraging neuron and ignored the output at the mating neuron (and vice versa for assaying mating preference). A more challenging task would be to select for networks that correctly chose the correct colored food item and had no output at the mating neuron (and vice versa for the foraging output neuron when presented with a mate). These behaviors are more challenging and may be more difficult to evolve. Whether a pattern of sensory bias would be generated by such a fitness criterion warrants further investigation.

Another possibility is that animals need to do more than simply identify the correct colored food item. Animals may also need to be highly responsive to proper food items. In this study, networks achieved high fitness by having a large response to the correct food item and no response to the alternates. However, I made the fitness criterion relative (output to target/sum of outputs to all three food items) so that I could measure the ability of the network to respond to the correct item without confounding the measure with the absolute magnitude of response. One can easily imagine a scenario in nature in which food is limiting and animals must respond quickly to available food. In this case, the absolute response (output to target–output to alternates) may be a more appropriate measure of fitness because it incorporates both the ability of the network to differentiate between the two items plus the overall excitation produced by the food item. Whether different preferences are evolutionarily independent of one another under these alternate fitness criteria remains to be determined.

Finally, I do not mean to imply that hidden preferences do not exist, nor do I mean to imply that the history of past selection is unimportant in shaping the sensory system. Animals can clearly harbor hidden preferences and can respond to supernormal stimuli (McClintock and Uetz 1996; Burley and Symanski 1998; Draganoiu et al. 2002; Ghirlanda and Enquist 2003; Jansson 2004; Elias et al. 2006). A large number of empirical studies as well as simulated neural network studies have shown that selection for a given task can create preferences that extend beyond the original task (Ryan and Rand 1990; Enquist and Arak 1993; Johnstone 1994; Enquist and Johnstone 1997; Phelps and Ryan 1998, 2000; Phelps et al. 2001). However, these studies typically focus on the mismatch between preference levels and male display traits rather than on the evolution of the preference itself.

In conclusion, this study found modest evidence to support the sensory bias model for the evolution of female mating prefer-

ences. Univariate selection on foraging preferences did produce a correlated response where there were increased levels of mating preference for like-colored objects (e.g., red food and red mates). Yet, these responses were not exceedingly large and were not extremely consistent. Furthermore, the responses in foraging and mating preferences under bivariate selection were independent of one another. Hence, selection on foraging preferences did not constrain the evolution of mating preferences. If these patterns are representative of those in nature, then this study suggests that sensory bias alone is unlikely to result in the evolution of female mating preferences to substantial levels within populations—at least for visually oriented behaviors. However, neural networks are simplistic representations of sensory systems. Alternate network designs or alternate fitness rubrics may, of course, produce a stronger pattern that is consistent with sensory bias. The unique contribution of this study is that it shows that the conditions under which mating preferences evolve as a correlated response to natural selection on nonmating behaviors may be more restrictive than previously thought. Future studies adopting a neural network framework should include a minimum of two outputs so that the evolution of multiple behaviors and their genetic associations can be examined.

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Supporting Information

The following supporting information is available for this article:

Table S1. Derivation for the number of evolvable units in small, medium, and large networks.

Table S2. Raw data from the bivariate selection simulations.

Table S3. Raw data from the univariate selection simulations.

Table S4. Results from univariate selection simulations.

Table S5. Means and standard deviations for the change in preference for (A) blue mates, (B) yellow mates, and (C) red mates as a function of food target, network size, and mutation rate from the univariate selection simulations.

Figure S1. Connections between cone cells and horizontal cells.

Figure S2. Connections between the bipolar cells and the cone cells.

Figure S3. Time to near equilibrium as a function of relative importance of foraging preferences on fitness.

Supporting Information may be found in the online version of this article.

(This link will take you to the article abstract).

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