Perceptual Biases and Mate Choice

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Abstract

Our view of the evolution of sexually selected traits and preferences was influenced radically in the 1990s by studies that emphasized how signals interact with sensory properties of receivers. Here, twenty-five years later, we review evidence that has accumulated in support of this idea. We replace the term sensory biases with perceptual biases to emphasize the growing knowledge of how cognitive processes generate selection on sexual traits. We show that mating preferences among conspecifics (e.g., sexual selection by mate choice) often are influenced by perceptual adaptations and constraints that have evolved in other contexts besides mate choice among conspecifics. We suggest that these perceptual biases need not be costly to females when they influence mate choice because in many cases they generate direct benefits. Although we do not reject a role for indirect benefits in mate choice, such as good genes, exclusive focus on eugenic mate choice limits our understanding of the evolution of the remarkable diversity of sexually selected traits.

1. INTRODUCTION

Sexual selection:
variance in
reproductive success
that results from
variance in access to
mates

Interacting forces:
any combination of
female choice, male
choice, male
competition, and/or
female competition

Sensory traps: traits
that attract females
because they resemble
stimuli that are salient
in other contexts

Sensory drive:
sensory and signaling
trait evolution driven
by ecological
determinants

Sensory exploitation:
occurs when males
evolve traits that
increase their
attractiveness to
females due to
preexisting biases of
females

When male animals utter sounds in order to please the females, they would naturally employ those which are sweet to the ears of the species; and it appears that the same sounds are often pleasing to widely different animals, owing to the similarity of their nervous systems (Darwin 1872, p. 91).

Sexual selection by female mate choice was a controversial thesis when Darwin first suggested it (Cronin 1991). Now it is one of the most active areas of research in evolutionary biology (Andersson & Simmons 2006; Kuijper et al. 2012). Sexual selection was proposed by Darwin to explain the evolution of elaborate male courtship traits that seemed to reduce rather than enhance survivorship (Darwin 1871). Darwin's preoccupation with this problem is illustrated by an early letter to Asa Gray: "The sight of a feather in a peacock's tail, whenever I gaze at it, makes me sick!" (Darwin 1860).

Darwin's thesis was elegant. He proposed that males evolved weapons and adornments because they enhanced their ability to gain access to females. Darwin's suggestion of direct male combat for females was accepted by his peers, but the notion of females choosing males was not. One reason might have been that the Victorian social mores of the time made it difficult to grant females such an important role in the mating decision. Another was the fact that Darwin did not posit an adaptive explanation for female mating preferences (Cronin 1991). Instead, he proposed that females are attracted to the sexual adornments of males because females have an aesthetic sense. Some have suggested Darwin's proposal was merely a redefinition of the problem of female mate choice and not a solution to it (Cronin 1991). But the quotation above shows that Darwin considered that the manner by which courtship signals interact with the sensory biology of the female (constituting interacting forces) is a part of the puzzle of understanding sexual preferences. This, like many of Darwin's suggestions, was prescient.

The perceptual biology of sexual selection has its deep roots in research traditions that emphasize how an animal's internal biology influences its perception of the external world, perhaps best exemplified by Jakob von Uexküll's concept of the *Umwelt* (reviewed by Ryan 2011). In addition to Darwin's quotation above, the importance of the animal's sensory world in mate choice was emphasized in the contexts of sensory traps (West-Eberhard 1979, Christy 1995), sensory drive (Endler & McLellan 1988; Endler & Basolo 1998), latent preferences (Burley & Symanski 1998), and sensory exploitation (Ryan 1990; also see Basolo 1990, Prum 2010). We expand the concept of sensory biases to the animal's perceptual biology, as it is now clear that various cognitive processes also introduce biases into mate choice. We review evidence that has accumulated in the past decades supporting an important role for how the sensory, neural, and cognitive systems of females influence the types of traits that males evolve in response to sexual selection by mate choice to exploit the female's perceptual proclivities.

Our goal in exploring the relationship between perceptual biases and mate choice is to understand how adaptations and general processing principles of sensory and perceptual systems that evolved in other contexts influence intraspecific mating preferences and thus drives the evolution of male sexual traits. There is no doubt that perceptual adaptations can evolve in the service of mate choice; Andersson (1994), for example, provides many examples in which a female's choice among conspecific males results in enhanced reproductive success. In many other cases, as we also know, intraspecific mating preferences can be influenced by perceptual biases that did not evolve for fitness benefits generated by preferring one conspecific male over another. Such biases can have their origins in how sensory end organs respond to the environment. For example, prey detection can favor certain photopigment sensitivities, which incidentally influence female preferences for male courtship colors (e.g., Cummings 2007). Biases can also derive from cognitive processes. For example, species recognition can favor processes, such as peak shift displacement, to avoid

mismatings with heterospecifics, which incidentally influence mate preference among conspecific males (Grant & Grant 2010). Our underlying theme is that the brain and its associated structures and processes evolve to accomplish many tasks, and how the brain responds during any one of them is influenced to some degree by how it has evolved under selection in other contexts.

Studying courtship traits through the brain of the female forces a broader consideration of adaptive mate choice as it takes into account how perceptual adaptations in other domains might influence trait preferences. Central to our argument is the fact that elaborate courtship traits are communication signals, and they are salient only if they are detected and perceived (Shannon 1948, Bradbury & Vehrencamp 1998). There is strong selection for signals to stand out against environmental noise (Morton 1975, Endler 1978), to match the parameters to which the receiver's sensory system is most sensitive (Capranica 1983, Cummings 2007), to avoid detection of unwanted targets (Cummings et al. 2003), to circumvent perceptual masking by neural phenomena such as habituation (Dong & Clayton 2009), and to stand out against competitors in the social group (Ryan & Cummings 2005). All of these tasks influence how sexual signals and receivers interact.

In this review, we first examine the mechanisms that shape perceptual biases. We discuss nonlinearities in the end receptors (Section 2.1) of the three main sensory modalities used in communication and the cognitive processes (Section 2.2) that contribute to perceptual biases. We then review the evidence (Section 3.1) (**Supplemental Table 1**; follow the **Supplemental Material link** from the Annual Reviews home page at **http://www.annualreviews.org**) for pleiotropic interactions between female sensory systems, mate choice biases, and the evolution of male traits that exploit such biases. From there we explore the costs (Section 3.2) and benefits (Section 3.3) of exploiting such biases. And last, we discuss these processes in a context outside of mate choice (Section 4).

Weber's Law:
predicts $\Delta I/I = k$, where ΔI is the minimum difference required to discriminate from a stimulus of magnitude I, and k is a constant

2. MECHANISMS

No animals have an unbiased sense of the world around them. There are no sensory modalities that exhibit a linear response to stimulus variation. To understand how and why animals respond to sexual signals the way they do, we must first understand how they detect and perceive them. In Section 2.1, we present a brief review of how individuals process stimuli in the main sensory modalities (audition, olfaction, and vision) via receptor cells in the periphery. We then describe how researchers can map a species-specific sensory response onto a perceptual space with uni- or multivariate dimensions. Perceptual spaces allow researchers to quantitatively test whether signals are conspicuous relative to background to specific viewers, as well as determine whether male signal properties mimic a sensory target important to females for survival tasks. Perceptual spaces can also uncover hidden or latent preferences and thus generate quantifiable predictions as to the specific direction of male trait evolution driven by a perceptual bias process. In Section 2.2, we describe a number of cognitive processes (generalization, peak shift displacement, signal complexity, and Weber's Law) that can work synergistically with end-receptor biases to influence female responses to male stimuli.

2.1. Perceptual Biases Resulting from Filters at the Periphery

Animals' initial sensory contact with their environments is through specialized sensory receptors that transduce specific forms of energy into the currency of the nervous system (electrical impulses). Mechanoreceptors (hair cells) in the basilar membrane of our human ear respond to sound pressure waves ranging over three orders of magnitude (20 to 20,000 Hz). Photoreceptors in our retinas are sensitive to a smaller bandwidth of the electromagnetic energy spectrum that we call light (400 to 700 nm); and chemoreceptor cells in our olfactory epithelium respond uniquely
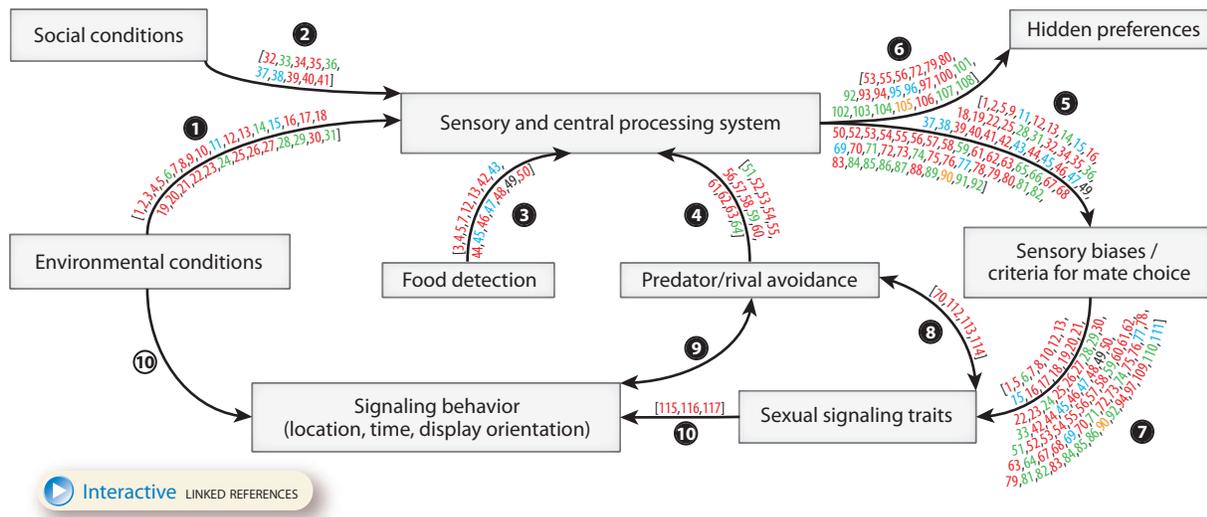
Figure 1

Stages and evidence of signal elaboration via perceptual bias mode of sexual selection. A flowchart modified from the sensory drive model by Endler & Basolo (1998). Species-specific habitats have unique environmental properties imposing selective constraints on sensory systems (*step 1*). Social conditions (often early in development) may influence perceptual processes or responses of females toward specific stimuli (e.g., peak shift phenomena, *step 2*). Sensory systems undergo further selection for detection of specific targets necessary for survival, such as prey (*step 3*) and predators (*step 4*). Sensory, cognitive, and social mechanisms combine to influence the target properties to which females are likely most attentive as well as determine the level of elaboration necessary to generate a response in a mate choice context (via receptor biases, Weber's Law, release from habituation, stimulus generalization, complexity advantages, and peak shift processes, *step 5*). These perceptual biases influence preferences by way of increased detectability, stimulation, or attention of target for particular stimulus features. Some of these features are absent in conspecific male phenotypes, and the preference for such features are uncovered only through experimentation (hidden preferences, *step 6*). Female perceptual biases influence the evolution of male sexual signaling traits (*step 7*) via the communication advantage males may gain with signaling features that are more detectable, memorable, or stimulating for the female observer. Male signaling features may also be shaped by the need to avoid detection by the perceptual biases of predators (*step 8*) or rivals due to intrasexual competition. Predator avoidance may impose a selective constraint on the time and place of signaling display (*step 9*). Furthermore, male selection of display location, timing, and specific behavioral features may be influenced by the perceptual biases of the female viewer (*step 10*). Colored numbers at each step refer to the reference number (see **Supplemental Table 1**; follow the **Supplemental Material link** from the Annual Reviews home page at **http://www.annualreviews.org**) of a research study that presented evidence for that particular stage of the perceptual bias model. References are color coded by sensory modality: visual in red, auditory in green, olfaction in blue, gustatory in yellow, tactile in black.

to nearly 1,000 different airborne molecules. Other animals have sensitivities that range beyond our own human window into these energy fields extending to ultrasonic and subsonic sound frequencies; UV, IR, and polarized light; olfactory stimuli to which we are anosmic; and even magnetic and electrical fields.

Perceptual biases arise at the initial stage of sensory transduction due to variation in receptor cell response properties. Natural selection should favor animals with sensory systems biased toward target detection against the dominant energies found in their habitats (Endler & McLellan 1988, Dusenbery 1992), and there are numerous examples of this across different modalities (see **Figure 1**, *step 1*). Receptor cells maximize contrast detection in specific environments by one of two strategies-having receptor cell sensitivities matched to background properties or having receptor cells offset to the background in a consistent direction (McFarland & Munz 1975). In the visual system, species often exhibit both strategies simultaneously; one set of photoreceptors are highly tuned to the dominant spectral bandwidth, allowing targets that are darker than

background to be detected, whereas other photoreceptor classes exhibit maximum sensitivity offset to the dominant bandwidth, allowing targets that reflect beyond the background spectrum to be detected. Evidence for covariation of visual pigment sensitivities with optical habitat properties is abundant in marine (Lythgoe & Partridge 1989, Lythgoe et al. 1994, Cummings & Partridge 2001, Carleton et al. 2005) and freshwater systems (Boughman 2001) and has been demonstrated experimentally (Fuller et al. 2005). Environmental tuning of the auditory system to changes in the environment has also been observed both at peripheral (Wilczynski & Ryan 1999, Witte et al. 2005) and central (e.g., Langemann et al. 1998) processing stages. Studies of auditory tuning in the basilar papilla membrane or auditory midbrain of amphibians have demonstrated shifting sensitivities to frequencies outside the range of the dominant background frequency in populations (Witte et al. 2005) or species (Feng et al. 2006) in divergent habitats. Research into the environmental correlates of the olfactory system has also found correlations between habitat differences and olfactory receptor genes across 50 mammalian genomes (Hayden et al. 2010). Overall, these environmentally correlated changes in receptor propertiesbe they visual, auditory, or olfactoryserve as an initial filter or lens that constrains mate choice processes.

After transduction by sensory end organs, the next stage of sensory processing involves feature extraction. It is at this stage that outputs from several different sensory receptor types are pooled and compared. Feature extraction is modality specific. However, with sufficient information about the postreceptor processing, sensory biologists have been able to estimate how similar and dissimilar stimuli may be perceived by an animal. For instance, olfactory cues are processed first by the receptor cells in the periphery and then by olfactory centers that extract features such as the carbon chain length and functional group signatures of the olfactory stimulus (**Figure 2**). For acoustic signals, intensity, frequency, and temporal features are initially coded by hair cells in the inner ear and further processed by auditory centers in the brain. In the visual system, signals from photoreceptors are sent on to higher-order neurons that extract information about the brightness, color, and pattern of light stimuli. Initial stages of visual feature extraction occur in the retina (e.g., color and brightness), with subsequent pattern extraction occurring in higher visual centers in the brain.

Perceptual biases may emerge as a consequence of end-receptor tuning to environmental conditions. As sensory systems tune to environmental conditions, either as a consequence of change in receptor sensitivity or subsequent higher order processing, specific target features may be more detectable to an observer than others. The specific stimulus features that are more easily extracted are predictable based on targets necessary for survival (e.g., carbon chain length of food source, frequency of a calling prey item, color of a foraging target; **Figure 1**, *steps 1, 3, and 4*), and these features then provide a sensory filter for mate choice and male trait evolution (**Figure 1**, *steps 5* **and** 7). A good example of this process occurs with the California surfperch, Embiotocidae, a family of fishes living in the underwater kelp forest. Surfperch species occupy unique optical habitats that vary in terms of background brightness and color properties, and species' visual pigment sensitivities covary with the dominant wavelength of each species' background radiance (**Figure 3**). Specifically, one class of photoreceptors (long-wavelength-sensitive or LWS cones) are spectrally tuned to maximize photon capture of the background light field, whereas the other class of photoreceptors (short-wavelength-sensitive or SWS cones) are offset from the background dominant wavelength in a direction that provides high target contrast (Cummings & Partridge 2001). This tuning of the end receptor to the background light has consequences for feature extraction. The visual tuning of some species provides an advantage for detecting food items using color contrast detection, whereas other species have a visual system biased toward brightness contrast detection (Cummings 2004, 2007). This peripheral sensory tuning, which happens in response to environmental parameters, results in sensory biases for foraging that predict specific male signaling features (Cummings 2007). Surfperch species have divergent
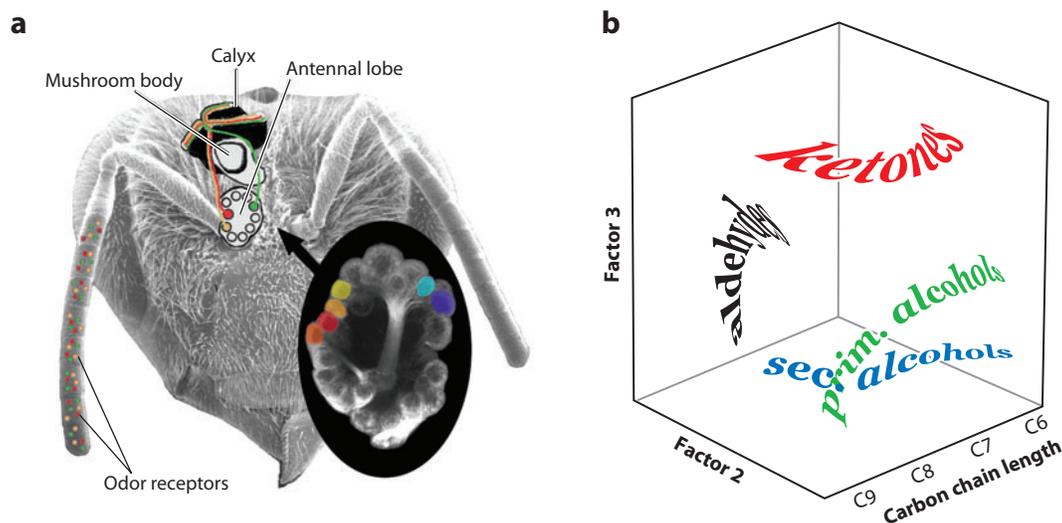
Figure 2

Perceptual odor space in honeybees (with permission from Chittka & Brockmann 2005). (*a*) Schematic view of the odor receptors and olfactory processing centers in the honeybee brain. Approximately 60,000 odorant receptor cells are distributed along the antenna (different colors represent receptors with different affinities to different molecular structures). Axons from these receptors project onto glomeruli in the antennal lobe, with glomeruli sensitive to similar odors physically located closer together than glomeruli processing more dissimilar odors (e.g., *red* and *yellow* are near each other, and farther away from *blue*; see enlarged antennal lobe image). Axons from the glomeruli in the antennal lobe project onto higher processing centers such as the calyces of the mushroom bodies. (*b*) A putative 3D odor space for honeybees. The distances between substances in the odor space was estimated based on behavioral trials with honeybees (Guerrieri et al. 2005). The most important axis corresponds to the substances' carbon chain length, whereas the other two dimensions separate substances according to functional group (aldehydes, primary and secondary alcohols).

nuptial coloration, and the direction of evolutionary change in reflectance properties (e.g., shorter or longer reflectance peaks) is predicted by each species' sensory bias (**Figure 3**). Surfperch therefore provide a quantitative example where environmentally predictive changes in the peripheral sensory system predict evolutionary change in male traits (**Figure 1**, *steps 1*, *3*, *5*, **and** *7*).

In sexual selection by mate choice, the receiver is one source of selection and the signal is the target of selection. One of the most important findings in the field of sexual selection in the past several decades is that there are preexisting or hidden preferences ready to generate selection on new signal variants as they arise. Researchers can study preexisting biases by mapping receptor tuning and postreceptor processes into a univariate or multivariate perceptual space, which allows quantitative predictions about responses to stimuli and predicts the type of male signals that might evolve to exploit biases (**Figure 1**, *steps 5* **and** 7). In acoustic systems, for example, studies have shown how mate choice varies as a function of call syllable number in a katydid (Ritchie 1996), frequency and pulse rate (separately) in a Hawaiian cricket (Shaw & Herlihy 2000), pulse duration in a treefrog (Gerhardt et al. 2000), and chuck number in the túngara frog (Akre et al. 2011). Experimental documentation of multidimensional preference space includes studies of an Australian field cricket (Brooks et al. 2005), treefrogs (Castellano & Rosso 2007, Gerhardt & Brooks 2009), and the túngara frog (Ryan et al. 2003).

The perceptual space of visual systems varies by the number of photoreceptor cone classes in the retina, as this limits the number of possible opponency channels available for color processing. For monochromats, perceptual space is a univariate dimension of intensity (as a single cone class

Changes may still occur before final publication online and in print.

cannot process color). For dichromats, perceptual space can be bivariate with luminance (intensity or brightness) on one axis and chromatic/opponency processing (e.g., color) on the other (e.g., Cummings 2004). The dimensionality of the perceptual space increases as species develop more complex interactions between multiple cone classes to extract color information. Researchers working with tri- and tetra-chromatic systems often remove the intensity/brightness feature of the perceptual space as a means to isolate differences in color (Endler & Mielke 2005; Stoddard & Prum 2008). By employing a species-specific perceptual color space, researchers have successfully predicted differences in pollination behavior between honeybees and hummingbirds (Chittka 1992, Lunau et al. 2011), evolution of plumage and bower decorations in bowerbirds (Endler et al. 2005), and sexual selection on signaling displays in chameleons (Stuart-Fox & Moussalli 2008) and tropical forest birds (Gomez & Théry 2007).

Quantifying olfactory perceptual space is one of the most recent developments in sensory biology (Chittka & Raine 2006). Guerrieri and coworkers (Guerrieri et al. 2005) mapped the olfactory space of a honeybee. Their findings show that despite having over 100 different olfactory receptor types, the postreceptor processing can be collapsed onto a few perceptual axes that distinguish key features of the olfactory signature, such as carbon chain length, and primary and secondary functional groups (alcohols, aldehydes, and ketones; **Figure 2**). The researchers were able to show that the distinguishability of odors was related to the distances between these odors in the olfactory perceptual space.

The studies of perceptual space parallel those of nonlinearities of sensory systems. Within the univariate and multivariate perceptual space that characterizes sexual signals, there is substantial variation in how attractive signals are to females and areas of the perceptual space that do not encompass any current signal variants. Thus, perceptual spaces provide insights into how traits should evolve in response to sexual selection by mate choice.

2.2. Perceptual Biases Resulting from Cognitive Processes

A hallmark of many sexually selected traits, such as the peacock's tail, is the extreme degree to which they have evolved. Ryan & Keddy-Hector (1992) and Andersson (1994) reviewed hundreds of examples in several sensory modalities in which females preferred traits that were of greater magnitude than the mean, including numerous cases in which females preferred traits that were larger, louder, or brighter than the extant range of that trait. For example, in Andersson's (1982) classic study of widowbirds, he showed that females preferred males with tails that were artificially lengthened beyond the normal size of tails in the population. Thus, it appears that some of the most elaborate sexually selected traits have evolved as supernormal stimuli.

2.2.1. Preferences for supernormal stimuli are often referred to as open-ended preferences. Different mechanisms can underlie open-ended preferences for supernormal stimuli. The simplest mechanism is described above, where species' receptor processing predicts a behavioral response in a species' perceptual space. For example, male fritillary butterflies are attracted to females with a faster wing-beat frequency, which range from 8 to 10 Hz. Magnus (1958) (**Figure 1**, *steps 5*, *6*, and 7) showed that this preference extends up to 140 Hz, far beyond that of a normal range of wing-beat frequency; 140 Hz is also the flicker fusion frequency of the butterfly's eye.

Other physiological and cognitive mechanisms also contribute to the elaboration of male sexual traits. The precise placement of decorations in a male bowerbird's arena, for example, exploits how animals perceive relative size of objects at different distances (Endler et al. 2010, Kelley & Endler 2012). Processes such as stimulus generalization, a well-known phenomenon in comparative psychology (Ghirlanda & Enquist 2003), may lead to trait elaboration as females may generalize a

response to a novel stimulus. Here we review a number of processing mechanisms that may lead to the elaboration of male secondary sexual traits including peak shift displacement, Weber's Law, and cognitive biases for complexity.

Peak shift displacement: a response whose peak is shifted from a positive stimulus in a direction further from a negative stimulus

2.2.2. Peak shift displacement.

Peak shift displacement is similar to preference for supernormal stimuli (Staddon 1975); it was first reported by Hanson (1959). As with responses to supernormal stimuli, peak shift displacement could result as an adaptive and generalized response to avoid negative and respond to positive stimuli. Enquist & Arak (1993) illustrated this point beautifully when they trained artificial neural networks (ANN) to prefer stimuli resembling long-tailed birds over those resembling short-tailed birds. After they were trained, the ANN exhibited a preference for images with tails of supernormal length. Jansson & Enquist (2005) used a virtual evolution paradigm to show a similar result when domestic chickens were trained to peck stimuli on screens and the stimuli then evolved in response to the chickens' selections. There was no reward to prefer larger stimuli, but the chickens' perceptual biases drove stimulus evolution in this direction. ten Cate & Rowe (2007) review numerous examples of peak shift in naturalistic tasks, such as face

Environment selects on receptors

b Visual pigment sensitivity

c Sensory tuning changes sensory bias

a Surfperch visual backgrounds

d Sensory bias influences signal design

Signals more detectable against background

f

e

Micrometrus aurora   *Hypsurus caryi*   *Embiotoca jacksoni*   *Embiotoca lateralis*   *Damalichthys vacca*

REVIEWS IN ADVANCE
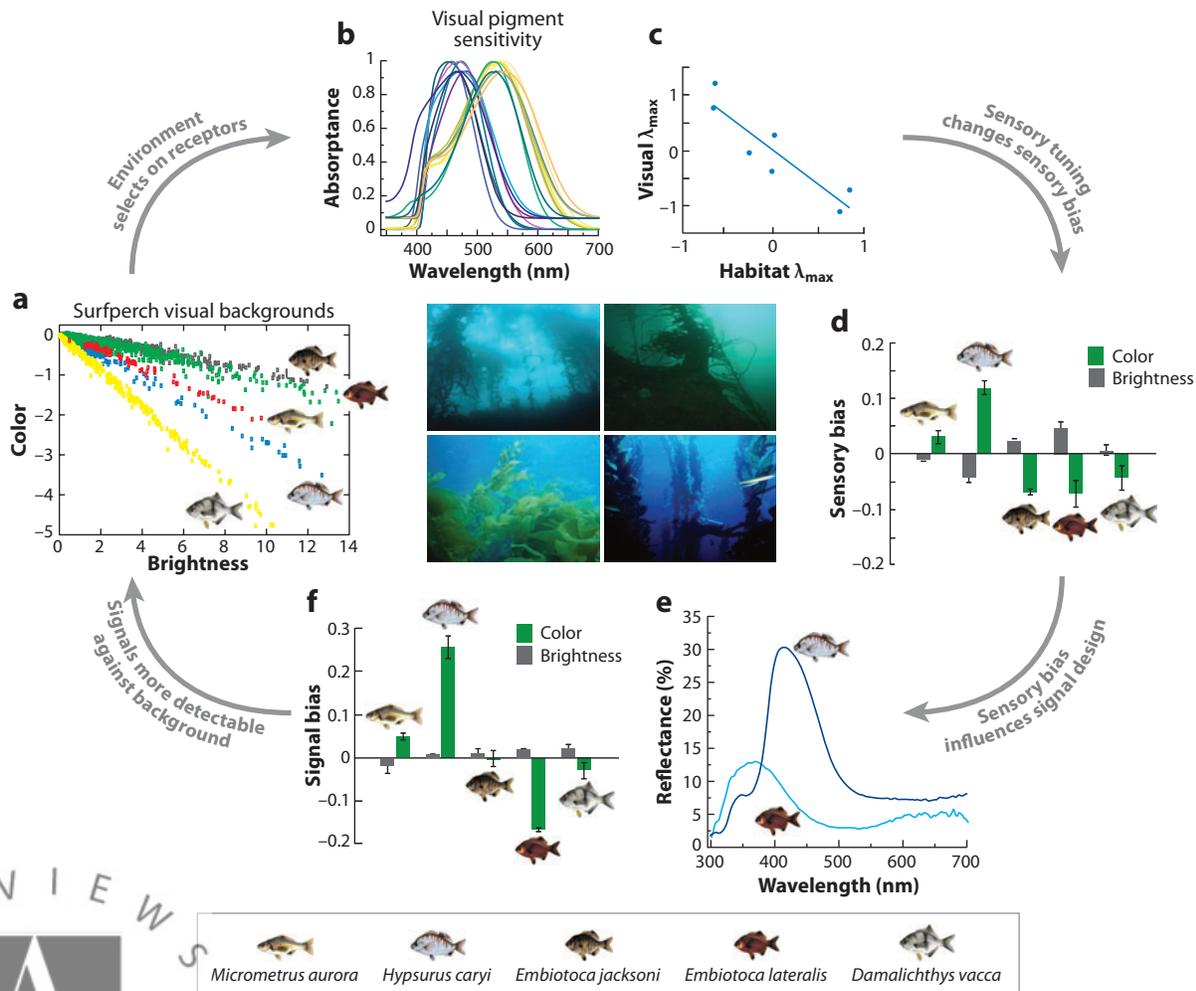
recognition in humans, spatial orientation in pigeons and honeybees, and response to aposematic coloration in chickens and to floral colors by bees.

Peak shift displacement is an important force in signal evolution (Weary et al. 1993, Lynn et al. 2005). The hallmark of sexual selection is the evolution of sexually dimorphic traits. Many animals are first exposed to these traits in their parents and it is at this time, when they are young, that they may learn to use these traits to discriminate the sexes. We know, for example, that zebra finch imprint on the beak color of males and females and later use this trait to discriminate between the sexes (Weisman et al. 1994) (**Figure 1**, *step 2*). ten Cate et al. (2006) showed that males exhibit "beak" shift displacement (Scott MacDougal-Shackleton, personal communication); they prefer females with beak colors more extreme than their mothers. Female zebra finches also show peak shift in preferring songs with more notes than those of their fathers (Verzijden et al. 2007), and Darwin's finches show peak shift displacement away from the songs of a new species that enters the community (Grant & Grant 2010).

One of the most critical decisions an animal can make is choosing a mating partner of the correct species. These decisions are often based on species-specific courtship signals. Selection to discriminate between conspecifics and heterospecifics, whether the discrimination is acquired through learning or genes, can incidentally influence mate choice among conspecifics. If a female has a choice between two conspecific males whose courtship signals are more or less like heterospecifics, she should be under selection to prefer the latter to reduce errors in species recognition. This is what túngara frogs do (Ryan et al. 2003) (**Figure 1**, *step 6*), and this is one of the arguments that Lynn et al. (2005) proposed for the importance of peak shift displacement in signal evolution. Thus we see that adaptive preferences in the context of mate choice in one context (species recognition)

←───

Figure 3

Environmentally driven sensory and signal bias evolution in surfperch. Surfperch (Embiotocidae) occupy optically divergent habitats along the near-shore environment of the California kelp forest as shown by underwater photographs collected in Monterey Bay, CA (*center*, photo credit: Giacomo Bernardi and Molly Cummings) and (*a*) underwater spectral irradiance measurements. Measurements of background light (side-welling irradiance) collected in the presence of each surfperch species: *Embiotoca jacksoni* (*gray*), *Embiotoca lateralis* (*green*), *Micrometrus aurora* (*red*), *Hypsurus caryi* (*blue*), and *Damalichthys vacca* (*yellow*). Habitat measurements are represented in a surfperch-specific perceptual color space; each side-welling irradiance is evaluated in terms of estimated brightness (*x* axis) and color (*y* axis) of background light. Brightness is estimated as a summation of quantum catch among photoreceptor classes, and color is estimated as the difference in quantum catch between photoreceptor classes. Data from Cummings 2004. (*b*) Mean visual pigment sensitivities (normalized absorptance) of the two different cone classes [short-wavelength-sensitive (SWS) cones in shades of *blue/purple*; long-wavelength-sensitive (LWS) cones in shades of *green/yellow*] for nine different surfperch species (from Cummings & Partridge 2001). (*c*) Significant covariation between environmental properties (wavelength of maximum flux in the background light, habitat λ_{max}) and surfperch visual pigment sensitivities (wavelength of maximum absorption, visual λ_{max}). Phylogenetically corrected residuals of each surfperch species' mean background wavelength (habitat λ_{max}) and SWS peak sensitivities (visual λ_{max}); regression line ($y = -1.23x$, $r^2 = 0.83$, $p = 0.0019$; Cummings & Partridge 2001). Negative relationship suggests photoreceptor sensitivities are offset to background for target detection. (*d*) Sensory bias in surfperch measured as the change in estimated foraging detection performance (signal-to-noise difference between target and background for the most common surfperch foraging item, *Rhodophyta* or red macroalgae) of each surfperch species relative to the estimated ancestral surfperch visual pigments in each species' optical habitat for color detection (in *green*) and brightness detection (in *gray*) visual pathways (Cummings 2007). Two species (*M. aurora*, *H. caryi*) exhibit gains in color detection processes relative to the maximum-likelihood estimate of the ancestral surfperch visual sensitivities; and three species (*E. jacksoni*, *E. lateralis*, *D. vacca*) exhibit gains in brightness detection abilities. (*e*) Divergence in surfperch male nuptial coloration. Mean male spectral reflectance measurements of the same body region (under eye) from two different surfperch species (*H. caryi*, *E. lateralis*) (Cummings 2007). (*f*) Surfperch male signal biases match sensory biases. Signal bias in surfperch measured as the change in estimated detectability of male reflectance relative to the average reflectance between species with changes in color detectability shown in green and changes in brightness detectability in gray. Species with a color-biased visual system exhibit reflectance properties that increase their detectability in the color channel (*M. aurora*, *H. caryi*), whereas species with a brightness-biased visual system (*E. jacksoni*, *E. lateralis*, *D. vacca*) exhibit reflectance properties that have diverged in a direction providing them with greater brightness detectability (Cummings 2007).

can lead to incidental biases in mate choice in another context (choice among conspecific males) that is unrelated to any variation in the survival quality of the males being compared.

Peak shift could result in the evolution of more extreme sexually dimorphic characters and also be favored by selection because it reduces errors in sexual discrimination. The latter issue was investigated by Lynn et al. (2005), who used a signal detection model to argue that peak shift displacement is an adaptive strategy for identifying signals in a variable world. Darwin (1872) also seemed to have some notion of the adaptive significance of peak shift displacement in the context of signal detection. Hurd et al. (1995) used ANN to confirm Darwin's principle of antithesis by demonstrating that signals of different valence evolve toward converse forms. These results show that the receivers' biases by themselves, unrelated to any strategic aspects of communication and uncorrelated with any inherent quality of the sender, can fuel the evolution of signal divergence. When this occurs, this aspect of a female's mating preference among conspecifics did not evolve for mate choice in that particular context (among conspecifics), but is an incidental consequence of discriminating mates in other contests, such as male versus females and conspecific versus heterospecific.

Peak shift phenomena may also enhance divergence between conspecific males with alternative mating strategies. Females in many systems need to learn the difference between positive male phenotypes (courters who may provide direct or indirect benefits) relative to those who provide a negative interaction (coercive phenotypes such as sneakers or force copulators). Peak shift displacement could favor the elaboration of traits of the positive male phenotype in a direction that provides greater discrimination against coercive phenotypes (Cummings 2012). For instance, in many fishes, courting and coercive phenotypes differ in size, and females prefer the larger (noncoercive) phenotype. Peak shift learning processes in these systems would favor exaggeration of the differences between these male types, particularly at early stages when the morphological differences between the two phenotypes are minimal. Hence, in these species, female biases for larger males (based on perceptual bias for easy detection or some other direct benefit) may be augmented by processes such as peak shift displacement.

2.2.3. Weber's law.

Animals compare signals when making choices. Studies of psychophysics have shown that actual stimulus value does not always vary linearly with perceived stimulus value. An example of this is Weber's Law, which predicts that comparisons of stimulus magnitudes are based on proportional and not absolute differences (Stevens 1975). As Cohen (1984) noted, if females employ Weber's Law in mate choice, the absolute size difference between traits necessary for them to be perceived as different (i.e., the just noticeable difference) increases with the absolute size of the traits. This predicts more rapid trait evolution when traits are smaller and predicts a slower rate of evolution as these same traits evolved to be larger.

Weber's Law can generate patterns of preferences that are indistinguishable from the hypothesized female resistance that should evolve under chase-away selection (Holland & Rice 1998). Chase-away selection predicts that females incur costs when mating with males having exaggerated traits and thus should evolve resistance, resulting in female response thresholds requiring higher stimulation levels from traits of even greater magnitude. Weber's Law predicts similar increases in female response thresholds without invoking resistance, resulting in the same pattern of preference predicted by chase-away selection.

A recent study of túngara frogs illustrates how Weber's Law could exert an important influence on sexual selection. The basic component of the male's call is the whine, which is sufficient to attract females for mating. Males can also add up to seven chucks to their calls and females prefer whines with chucks to whines without chucks (Ryan 1985, Bernal et al. 2009). Akre et al. (2011) (**Figure 1**, *step 5*) showed that variation in preferences among stimulus pairs was not predicted by the absolute difference in chuck number between them, but by the ratio of the chuck numbers

Antithesis: the hypothesis that signals that differ in valence should evolve different forms

Chase-away selection: predicts a coevolutionary cycle in which females evolve resistance to male courtship and, in response, males evolve more stimulating courtship

of the two calls as is predicted by Weber's Law. This response to chuck number occurs in other animals in other contexts. Frog-eating bats listen to túngara frog calls to find a meal and not a mate; they also prefer calls with more chucks and exhibit a Weber function indistinguishable from that of the female frogs.

2.2.4. Signal complexity. Sexual selection often favors increased signal complexity. An animal's attention to a repeated stimulus often wanes with time, as does the response of a neuron to repeated stimulation. Habituation is an adaptive process because it functions to inform the receiver when something in the environment has changed, as the receiver is then released from habituation (dishabituation). Animals are less interested in the constant noise in the forest than in the branch that breaks under the foot of a predator. More than half-a-century ago, Hartshorne (1956) suggested the antimonotony hypothesis to explain the evolution of complex repertoires in song birds. He suggested that in territorial interactions it is important that a male's neighbor not habituate to his song. Release from habituation, he hypothesized, could be achieved by transition between different syllables. Searcy (1992) presented some evidence for this in grackles. Males with artificially enhanced repertoires with variable syllables were more attractive to females compared to males with repertoires with the same syllable type. The enhanced attractiveness resulted from the release of females from habituation with the transition from one syllable type to the next (**Figure 1**, *steps 5 and 6*).

We know the attractiveness of complex song is widespread among oscines (Andersson 1994). There is some hint as to the underlying neural mechanisms that might modulate this attractiveness. In zebra finch, both electrophysiological and gene expression responses habituate to stimulation by same-song notes but are restored with transition to different notes (Clayton 1997, Dong & Clayton 2009). Eda-Fujiwara et al. (2006) specifically tested the hypothesis that sensory biases favor the evolution of complex song and showed that when exposed to male song, female song birds and parrots show increased immediate early gene expression in the auditory system. We do not know of studies that have examined the potential role of habituation to visual pattern and suggest that this might be a fruitful avenue of research.

An important point we make in this section is that there are numerous explanations for biases in mate choice, and not all of them initially evolved in the service of choosing among conspecific partners. To understand the mechanisms of mate choice, we need to understand the perceptual biases that influence mate choice and acknowledge that some of these mechanisms are not specific to mate choice and might subserve other functions.

3. THE EVIDENCE, BENEFITS, AND COSTS OF PERCEPTUAL BIASES

Eyes, ears, noses, and toes, and the neural centers processing the information they gather play important roles in mate choice. But these sensory systems did not originally evolve for mate choice, and they almost always serve multiple functions. If these perceptual biases are related to other functions in addition to mate choice, we need to quantify their fitness consequences in these other contexts. For example, in surfperch (**Figure 3**), we can understand how photopigment sensitivities drive the evolution of male courtship patterns, but we cannot understand the costs and benefits of this visual signal bias without considering how it influences foraging success. In this section, we review a plethora of data showing how perceptual biases that influence mate choice have evolved in other contexts. We then dispute the notion that exploitation of female perceptual biases is always costly to the female.

The evidence that perceptual biases influence the evolution of male signals has accumulated rapidly over the past 25 years. **Figure 1** (see also **Supplemental Table 1**), which we modified from Endler & Basolo (1998), shows the various influences shaping perceptual biases and male

signal evolution and provides documented accounts for each stage in the evolution of male sexual signaling traits via a perceptual bias paradigm. In our literature review, we only included research providing paired evidence for perceptual biases (**Figure 1**, *steps 1–6*) in connection to male signaling traits (**Figure 1**, *steps 7–10*). Hence, studies that only demonstrate a female preference for a male trait (without demonstrating a sensory or cognitive basis for a perceptual bias) were not included. Evidence for a perceptual bias involvement in male trait evolution does not rule out additional influences on the evolution of male traits and female choice (e.g., indirect benefits, direct benefits, Fisherian runaway); however, it does provide a sufficient and parsimonious model for the specific direction of evolution. Of the 117 studies that demonstrated a link between perceptual biases and male sexual trait evolution, 60% involved visual, 26% involved acoustic, 11% involved olfactory, 2% involved gustatory, and 1% involved tactile stimuli. We found far fewer studies that did not support the role of perceptual biases. We realize, however, that there can be strong publication bias against publishing negative results.

3.1. Evidence for Perceptual Biases Arising via Food Detection Pathways

At the level of peripheral processing of stimuli, there are several examples of how functions in other contexts can influence mate choice. One of the dominant pleiotropic effects influencing perceptual biases arises from foraging (**Figure 1**, *steps 1, 3, 5, and 7*). Rodd et al. (2002) have argued that guppies' intrinsic interest in orange objects suggests that mate preferences for orange males and the photopigment sensitivities for these wavelengths evolved originally in a foraging context, i.e., finding orange fruit, which in turn drove the evolution of orange courtship coloration in males. As mentioned earlier, changes in optical environments of the different surfperch species result in sensory biases for foraging detection. These biases in turn influence the visual signals that males use for sexual display (Cummings 2007) (**Figure 3**). Other studies have also argued that the photic environment generates selection on photopigment sensitivity, which then drives the evolution of color used in male courtship in threespined sticklebacks (Boughman 2001, McKinnon & Rundle 2002, Smith et al. 2004), bluefin killifish (Fuller 2002, Fuller et al. 2005), and *Pundamilia* cichlids (Carleton et al. 2005, Maan et al. 2006, Seehausen et al. 2008).

Hunger and sex are two of the most fundamental drives experienced by animals, and males can be quite adept at exploiting hunger in the service of sex. In a classic study of water mites, Proctor (1991) (**Figure 1**, *steps 3, 5, and 7*) showed that males vibrate their legs in the vicinity of females with a frequency that mimics the water vibration of one of their prey, copepods. Proctor argued that females turned and oriented to the male not for sex but for food. She confirmed this hypothesis by showing that female mites deprived of food were more likely to be lured by this signal and mate with a male.

Similar deception was also reported in two groups of fishes. Arnqvist & Kolm (2010; see also Kolm et al. 2012) (**Figure 1**, *steps 1, 3, 4, and 7*) showed that male swordtail characins have a flag-like structure that extends from the operculum and mimics food items. The males employ this flag to lure females into a position permitting mating. Remarkably, the flag's structure resembles food items of the local population. In goodeid fish, Garcia & Ramirez (2005) (**Figure 3, 5 and 7**) showed in a series of elegant experiments that a male's terminal yellow band (TYB) on the caudal fin is an attractive sexual trait to females of species with and without a TYB and that this trait evolved to exploit the fishes' feeding responses as the tail band mimics yellow worms these fish prey upon. It is especially interesting that once this trait becomes fixed in the population, females no longer respond to the band as a food item, only as a sexual display. These series of experiments show how a receiver can evolve out of a sensory trap but still retain the incidental influences on mate preferences.

3.2. Evidence for Biases Arising via Predator Evasion Pathways

As important as the drive to acquire food is the drive to avoid becoming food (**Figure 1**, *step 4*). In a series of elegant experiments with fiddler crabs, Christy and his coworkers (Christy 1988, Christy et al. 2002) (**Figure 1**, *steps 4, 5, and 7*) showed that males of several species construct ornaments that project vertically near their burrows, where mating takes place. The male courtship consists of a conspicuous claw-waving display, but the ornament further contributes to male mating success. This is not because the structures are related to male quality but because they are beacons that aid in finding the burrows to escape predators. The vertical structure is especially detectable given the distribution of the ommatidia in the crabs' eyes (Christy & Salmon 1991). Species without such structures will also rely on them to find burrows when experimenters place structures near them. Much as courting males can mimic food, they can also mimic predators to enhance their mating success. For example, Christy & Salmon (1991) noted an "out and back" behavior of fiddler crabs; when a female, but no predator, is in view, the male moves quickly but in low posture away from his burrow and past the female, then raises his claw and dashes back. The female startles into the burrow as she would to an approaching predator. The male then follows, the reverse of the usual sequence, and the pair may mate.

Auditory tuning can also evolve in other contexts besides mate choice and in turn influence what sounds are attractive to members of the opposite sex. Many moths have evolved both the capacity to hear the bat echolocation signals and to respond to them with their own ultrasonic calls (Roeder 1962, Fullard 1977). Some of these moths have evolved diurnal habits and thus avoid the threat of bats; they then use both the sound production and detection system for courtship (Conner 1987). This system did not evolve for getting mates but for avoiding predators.

3.3. Evidence for Biases from History

There are cases in which the precise function of sensory biases are not known, but phylogenetic evidence suggests that senders have evolved signals to exploit preexisting biases in receivers. Classic examples include the preference for swords in platyfish discussed above (e.g., Basolo 1990, Rosenthal & Evans 1998; see also **Figure 1**, *steps 5 and 7*) as well as the preference for facial ornaments in auklets (Jones & Hunter 1998) and hair tufts in spiders (McClintock & Uetz 1996).

One example that combines behavioral, phylogenetic, and neural studies involves the túngara frog (*Physalaemus pustulosus*). The high-frequency chuck that males produce stimulates one of the two inner ear organs, the basilar papilla (BP). Most of the close relatives do not produce chucks or other signal components to which their BP is sensitive, but BP tuning of close relatives is nearly identical to the túngara frog's (Wilczynski et al. 2001) (**Figure 1**, *steps 5, 6, and 7*). These data combined with phylogenetic reconstructions suggest that male túngara frogs evolved the spectral characteristics of their chucks to match a preexisting tuning bias in the BP. Why the BP tuning is conserved over this group of frogs, however, is not known.

There is some controversy as to whether the behavioral preference for the chuck, which involves neural biases in the auditory mid-brain as well as in the periphery (Hoke et al. 2004), arose prior to the evolution of preferences for it. Ryan & Rand (1993) argued that chucks arose in the clade of *P. pustulosus* (the túngara frog) and its sister species *Physalaemus petersi*. Other *Physalaemus* do not produce chucks. They then showed that *Physalaemus coloradorum* females prefer their own conspecific call, to which three chucks were added, over the normal conspecific call, which lacks chucks. Recent work by Ron (2008), which deviated from previous research by adding only one chuck and a BP-stimulating prefix to the whine portion of the call of *P. coloradorum*, showed no preference for one chuck. The results are intriguing in that they may suggest that any BP-stimulating auditory ornament (either as a prefix or a suffix to the whine) may be sufficient to elicit preferences by

females. Hence, further phylogenetic testing with clades that lack a BP-stimulating auditory signal component may help clarify the preexistence bias for BP-stimulating auditory signaling components.

If chucks and preferences for them have been lost and gained, as Ron (2008) suggests, the data still show that the widespread presence of the tuning required for the chuck preference can set the stage for exploitation of latent preferences. This type of evolutionary "come and go" can be found across a number of taxa. For instance, Gray & Hagelin (1996) argued that the simple repertoire in grackles is derived, and thus the current female preference for complex repertoires might be an ancestral trait that was adaptive in the past. If true, this is similar to the case reported in a swordtail, *Xiphophorus pygmaeus*, in which females continue to prefer large, courting males of the sister species even though both large size and courting have been lost in their own males (Ryan & Wagner 1987). Both cases suggest that even after the target sexual signal has been lost, adaptive conspecific mate choice can persist and then set the stage for exploitation of latent preferences.

A similar example comes from other studies of swordtails. Basolo (1990) showed that female swordtails, *Xiphophorus helleri*, prefer males with longer swords, and swordless platyfish are more attractive when a sword is experimentally added. Rosenthal & Evans (1998) noted that many live-bearing fishes prefer larger males, and that the sword is one way to cheaply increase a male's apparent size. Using video playbacks of two males of identical body length (measured without the sword), females preferred the male with the sword. But when the body size of the male without the sword was manipulated to be the same length of the other male's body plus the sword, the females no longer showed a preference. This appears to be another example of males evolving traits that exploit latent preferences that originally were adaptive in the context of conspecific mate choice.

3.4. Costs or Benefits for Perceptual Biases

It is sometimes assumed that receiver biases are costly in the context of mate choice because it might bias receivers away from mates of high genetic quality and deprive the receiver of obtaining these indirect benefits (e.g., Reeve & Sherman 1993, Bradbury & Vehrencamp 2000). As we argue below, however, we expect the opposite; receiver biases often deliver direct benefits to females by reducing search costs. But even if these preferences were costly in the context of mate choice, it is necessary to take into account the direct benefits accrued in other contexts (e.g., predator detection) as well as the possible costs of choosing less-than-optimal mates. This net (across-context) cost-benefit analysis is similar to the more general and controversial debate between the importance of direct and indirect benefits within the context of mate choice (e.g., Møller & Jennions 2001, Calsbeek & Sinervo 2002, Kokko et al. 2003).

Kirkpatrick & Barton (1997) and others (e.g., Kotiaho & Puurtinen 2007) have argued that everything else being equal, direct benefits will trump indirect benefits. When we evaluate the potential importance of receiver biases, we need to consider not only the costs and benefits to the receiver in the context of mate choice but the fitness consequences in other contexts served by those biases. Krakauer et al. (1995) used an ANN model to illustrate the interplay between sensory exploitation and honest signaling and concluded the two processes seem likely to operate simultaneously. There is no question that in theory the benefits of perceptual biases can override indirect mate choice benefits to females, that perceptual biases can evolve if they result in overall fitness benefits, and in some cases that indirect benefits and perceptual biases can operate hand in hand. The purpose of this review is to marshal evidence in support of the importance of perceptual biases rather than to dissect its potential interaction with good genes.

Although there is extensive evidence that male ornamentation can evolve by exploiting female perceptual biases (**Figure 1**; **Supplemental Table 1**), the evolutionary consequences of this

process are still very much debated. Much of the debate hinges on whether or not exploitation of female preferences produces fitness costs or benefits for the female and, if there are costs, understanding the evolutionary response of the preference. Much traction has been given to theoretical discussion of the costs of sensory exploitation in chase-away selection (Holland & Rice 1998, Arnqvist & Rowe 2005, Rowe et al. 2005, Arnqvist 2006), as females should evolve higher thresholds for mating to avoid being lured into mating beyond their optimal rate (Holland & Rice 1998, Arnqvist 2006). As discussed in Section 2.2, increasing thresholds are also an expected consequence of physiological constraints for stimulus processing (Weber's Law), which is analogous to predictions from other sexual selection models (e.g., Fisherian runaway, good genes, direct benefits; Rosenthal & Servedio 1999, Getty 1999). The unique prediction of chase-away selection, that female overstimulation in courtship is costly (antagonistic seduction), has yet to be demonstrated.

Studies have begun to investigate other predictions of chase-away selection, namely female resistance and fitness costs associated with sensory exploitation traits. The detailed examination of the TYB of goodeid fishes (Garcia & Ramirez 2005) (see Section 3.1) has addressed both of these predictions. Garcia & Ramirez (2005) found no evidence for female resistance to elaborate male traits in their behavioral experiments of species with and without a TYB; females of the most elaborately tailed species spent just as much or more time with TYB males than females of species lacking these ornaments. However, the loss of a false foraging response to the TYB by females of species with elaborate TYBs suggests that TYBs might incur a foraging cost when it first evolves, but that females evolve the ability to disassociate nonmating from mating signals. Subsequent tests of the possible foraging costs associated with TYB males (Garcia & Lemus 2012) are consistent with the idea that TYB males may serve as a detractor of foraging efficiency, yet further evidence that the TYB ornament per se is the detractor would bolster this conclusion.

Sensory exploitation might be more likely to cause suboptimal mating owing to sexually antagonistic alarm rather than seduction. Males of quite different taxa [antelope, moths, and crabs (see above)] produce alarm calls to trigger an antipredatory response in females, which results in increased male access to females. Bro-Jørgenson & Pangle (2010; **Figure 1**, *steps 4* **and** *7*) observed that male antelope produce alarm-snorts, which usually warn of the presence of predators, in order to retain females in their territories for mating. In an amazing example, Nakano et al. (2010) (**Figure 1**, *steps 4* **and** *7*) showed that males of the Asian corn borer moth *Ostrinia furnacalis* produce an ultrasonic courtship song of extremely low intensity during copulation attempts. They suggested that this song mimics a bat's echolocation call, which then elicits a freezing response in the females and increases the male's ability to mate with her. In their experiments, the males' success in achieving copulation increased from 63% to 98% when these courtship sounds were present.

It is important to distinguish between sensory exploitation, which may impart a cost to females prior to contact with males (sensory allurement or alarm), and sensory coercion, which may take place once males and females are in contact or copula. There is ample evidence of direct physical coercion by males using claspers and other devices by which males detain females in an involuntary manner, which are assumed to have evolved by sexually antagonistic coevolution (reviewed by Arnqvist & Rowe 2005). However, there are also examples of coercion that exploits the females' physiological or sensory responses that increase her reproductive rates. Some of this coercion involves physiological manipulation of females for mating, such as evoking a suffocation response in female snakes that enables male intromission (Shine et al. 2003). Damselfly males also coerce females in copula by stimulating their vaginal sensilla, resulting in female's ejecting competitor's sperm (Córdoba-Aguilar 1999, 2002).

We counter the notion that perceptual exploitation of female preferences is always costly to the female. There are a number of possible direct-selection benefits of having perceptual biases

"exploited" by male traits. One likely benefit is that enhanced conspicuousness to the receiver will reduce search costs (Dawkins & Guilford 1996), which would be particularly beneficial under predation threats. The ornament-building fiddler crabs (discussed in Section 3.1 above) appear to provide good evidence for this as female preference for the sensory trap pillars increases with increased risk of predation (Kim et al. 2009) (**Figure 1**, *steps 4*, *5*, and 7).

Another benefit of exploiting sensory biases is the potential to enhance the memorability of the signal. As mentioned previously, the preference for complexity shared across a number of different taxa (e.g., birds, anurans) may be driven by cognitive biases. However, a less explored effect of signal complexity is its influence on memory. Túngara frogs, like many other acoustically chorusing insects and anurans, call in ephemeral bouts that are often shorter than the female's assessment time. Enhancing a female's ability to remember the calls of a male should be beneficial to the female as well as the male. Akre & Ryan (2010) (**Figure 1**, *step 5*) showed that calls of túngara frogs that had three chucks were remembered for up to 45 s, which is substantially longer than the average time of 25 s between chorus bouts, but there was no evidence for memory of calls with 0, 1, or 2 chucks.

4. PERCEPTUAL BIASES OUTSIDE OF INTERSEXUAL COMMUNICATION

Most of the vast amount of research in perceptual biases and signal evolution in mate choice interactions has focused on female sensory biases. However, there are a number of other viewers that may contribute to the diversification of male traits. Here we review how perceptual biases of other viewers, specifically males and other species, may interact with female perceptual biases to direct the evolution of communication traits. We further suggest that these areas may be a particularly enriching area of future research.

4.1. Intersexual Competition

As noted in the introduction, Darwin's suggestion of male competition for females was accepted during Victorian times, and it has received much attention by evolutionary biologists ever since (e.g., Emlen 2008). In fact, one theory regarding the origins of ornamentation used for female mate choice decisions posits that they first arise as armaments in male-male combat and are then co-opted by females for mate assessment (armaments to ornaments theory; Berglund et al. 2008). If armaments give rise to ornaments, the perceptual biases of conspecific male viewers could initially shape the detectability of these traits. The same suite of factors discussed in previous sections regarding female perceptual biases such as receptor tuning, cognitive processing, and pleiotropic effects are applicable to male perceptual biases influencing the signal properties that arise from male-male interactions (e.g., Ryan & Rand 1998). For instance, any male that has a badge or display that advertises his fighting ability is likely to gain a fitness advantage if his signal is better detected, perceived, and remembered by rivals. However, there are situations in which intrasexual selection is likely to impose different perceptual constraints than female mate choice, leading to unique predictions for signal evolution driven by male perceptual biases. We propose that cases where intrasexual and intersexual selection impose different perceptual constraints may provide possible test cases for the armaments to ornaments theory.

One major behavioral difference between the sexes is that males, more often than females, establish and defend territories. If the signaling environment remains relatively constant between territorial establishment (male-male communication) and territorial use (male-female communication), then intrasexual competition is unlikely to impose any differential demands on signal design

than intersexual selection. However, if males initially establish territories prior to the breeding season, then any ecological differences between the seasons could lead to different signal features being favored for detectability. For instance, temperate species that begin establishing territories in winter but acquire mates in spring contend with seasonal differences in acoustic and visual backgrounds and acoustic transmission properties. Although territorial demands may impose different ecological constraints on signal design driven by intrasexual selection, any sexual dimorphism in habitat use, diet, or sensory target may further promote divergent perceptual biases between the sexes. An excellent example of the latter exists in the housefly, *Musca domestica*, where a sexually dimorphic region of their retina provides males with the ability to track females while in pursuit of them. Males are able to chase females "on the fly" via a region of their retina termed "the love spot" that provides higher acuity and faster visual processing than equivalent regions in the female retina (Hornstein et al. 2000). In this system, intense male competition for access to mates appears to have driven sexually dimorphic sensory tuning.

4.2. Interspecific Biases: Synergistic or Constraining Effects?

Although most of the biases we have discussed in this review so far have been those of conspecifics, there are also biases of heterospecifics that may influence the design of signal evolution. One of the earliest proposed examples of signaling trait evolution as a consequence of perceptual bias focused on the biases of conspecifics and their predators (**Figure 1, *step 8***). Endler (1978) suggested that variation in guppy orange coloration was driven in part owing to variation in the presence of predators that could see orange. Similarly, in swordtails, variation in the degree of male UV ornamentation (and female preference for this trait) is predicted by the abundance of UV-blind predators (Cummings et al. 2003).

Another example of signals influenced by heterospecific biases is that of aposematic signal design (Guilford & Dawkins 1991). Here, defended organisms communicate their unpalatability to potential predators with conspicuous signals (odors, acoustics, or visuals). The design of an aposematic signal is not straightforward, particularly if the defended prey have an array of predators with different sensory biases (Endler & Mappes 2004). Recent research employed a perceptual bias approach to identify likely predators of a locally varying aposematic group of strawberry poison frogs, *Oophaga pumilio*, in western Panama. Maan & Cummings (2012) examined the relationship between morph toxicity and visual conspicuousness as perceived by four different visual systems (conspecifics and three potential predators). The relationship was nearly perfect for the avian visual system, more so than all others, suggesting that the specific aposematic design was in part influenced by bird predators.

Perhaps one of the most complicated multiviewer, multibias signal evolution scenarios occurs when signals attend to both heterospecific and conspecific biases. The polytypic strawberry poison frog is subjected to selection generated by multiple viewers, as predators along with male and female conspecifics all attend to the same aposematic signaling trait (Cummings & Crothers 2013). As noted above, predators appear to impose reliability on the aposematic signal (conspicuousness scales with toxicity), whereas females prefer brighter males (even in populations where males are not particularly toxic). The forces may be interacting in ways that promote signal diversity due to nonlinearities in sensory processing between viewers. Recent modeling suggests that the brightness variation that is salient to male and female *O. pumilio* in one population is not detectable by the visual system of birds (Crothers & Cummings 2013) (**Figure 1**, *step 8*). Hence, sensory constraints of the predator may allow sexual selection to drive smaller scale variation at the within population level while natural selection shapes the variation at larger scales (between populations).

SUMMARY POINTS

1. Mate choice is an important factor in driving the evolution of elaborate courtship traits.

2. A critical determinant of mating preferences is how the sexual trait interacts with the sensory and cognitive systems of the receiver.

3. Biases in perception can arise from selection in contexts outside of conspecific mate choice; some of the biases are particular to specific functions (e.g., species recognition, sex recognition, predator avoidance), whereas others result from more general processing phenomena (e.g., habituation, Weber's Law, peak shift displacement).

4. Our review of the literature reveals abundant evidence that perceptual biases arising in contexts outside of mate choice influence the evolution of sexually selected traits.

5. To understand the fitness effects of a perceptual bias, we must consider not only how it influences benefits derived from mate choice but the costs and benefits of the bias in other contexts (e.g., visual sensitivity and foraging success).

6. Perceptual biases need not be costly in terms of mate choice, and in many instances they are advantageous as they deliver direct benefits to the chooser (e.g., lower search costs and predation risks).

7. Our emphasis on perceptual biases does not reject a role for "good genes" selection, but exclusive focus on eugenic mate choice limits our understanding of the evolution of the remarkable diversity of sexually selected traits.

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