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Review

Taking the sensory approach: how individual differences in sensory perception can influence mate choice

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Many male signallers convey information to female receivers in multimodal courtship displays. While much is known about how males vary in terms of signalling, variation in female detection of these multimodal signals is relatively unexplored. We suggest that there is a critical, albeit underdeveloped, link between multimodal sensory reception and individual variation in mate choice. This review addresses the potential effects of developmental and conditional factors (e.g. nutrient availability, hormone profiles and age) on female multimodal processing, and illustrates that differences in the (1) source of individual variation and (2) the number of sensory processing modes affected by this variation can influence the receiver's mate choice patterns. Based on these two factors, we outline novel predictions of preference functions and choosiness in a redundant multimodal signalling context. Moreover, we explore the theoretical implications of individual variation in multimodal signal perception in relation to sensory drive, honest signalling, assortative mating and intrasexual selection. We propose that understanding the role of variation in sensory processing and its relation to mate choice can help us better identify the factors that influence sender and receiver fitness, and subsequently the rate and direction of signal evolution.

The study of multimodal signals in mate choice has shed light on the complexity of intersexual selection (Candolin 2003; Partan & Marler 2005). Multimodal research often focuses on signal content (Hebets 2011), classifying the role of different sensory modes based on whether they convey the same (redundant signalling) or complementary (nonredundant signalling) information about the sender (Møller & Pomiankowski 1993; Partan & Marler 1999, 2005).

This content-based approach, however, does not consider how multimodal signals are processed by different individuals or how they may be adaptive in different environments. While recent work considers multimodal processing across different ecological contexts (Munoz & Blumstein 2012) or different receivers (Hebets & Papaj 2005; Miller & Bee 2012), the impact of individual variation in sensory processing on multimodal signal evolution is relatively less studied (Dangles et al. 2009). By overlooking individual variation in multimodal processing, we have implicitly assumed that variation in signal perception has no effect on signal evolution (Bateson & Healy 2005). Unfortunately, this assumption is unlikely to hold in many circumstances, and thus our understanding of mate choice may need to be reevaluated.

True communication involves a sender and receiver (Bradbury & Vehrencamp 2011). Therefore, understanding receiver signal processing is vital to evaluating courtship interactions (Akre et al. 2011; Miller & Bee 2012). Nevertheless, many past communication models assume receiver signal detection is accurate and equivalent across individuals (Johnstone 1994). However, the complexity of sensory physiology and environmental variability may cause significant individual differences in central and peripheral signal processing (Phillmore et al. 2003; Dangles et al. 2009; Toomey & McGraw 2009; Henry & Lucas 2010; Perrachione et al. 2011). Moreover, as information encoded in different sensory modalities can interact (e.g. one modality is dominant or the modalities combine to produce a new, emergent response; Partan & Marler 2005), changes in aspects of the signal encoded in one modality cannot only influence the sensory processing in that modality but also in the interpretation of the combined signal. For instance, the McGurk effect demonstrates that altering the visual component of a phoneme processed using both acoustic and visual cues can generate the perception of a phoneme encoded by neither the visual nor the acoustic part of the signal (McGurk & MacDonald 1976). This review will show that differences in a receiver's ability to process multimodal signals (Guilford & Dawkins 1991; Rowe

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1999; Widemo & Sæther 1999) may influence receiver and sender fitness if these differences lead to variation in mate selection. Individual variation and plasticity in mate choice could alter the rate and direction of signal evolution (Wagner 1998; Bateson & Healy 2005).

We demonstrate a critical link between individual variation in sensory physiology and individual variation in mate choice. Our goals are to (1) discuss recent research on individual variation in mate choice and highlight the lack of sensory-based hypotheses explaining this variation, (2) review the sensory biology literature to establish a link between individual variation in sensory processing and variation in development and current condition, (3) propose novel predictions as to how variability in the sensory system would affect preference functions and choosiness in a multimodal signalling context and (4) discuss the theoretical implications of individual variation in the sensory system on inter- and intrasexual selection, particularly considering sensory bias, honest signalling and assortative mating. To accomplish these goals, we focused on multimodal signal use where males are signallers and females are receivers, although we acknowledge there are exceptions to this pattern. Moreover, while our focus is mainly on auditory and visual processing, we believe our discussion is applicable to all sensory modalities.

INDIVIDUAL VARIATION IN MATE CHOICE

Many scientists are beginning to recognize the relevant role of individual variation (Dangles et al. 2009; Biro & Stamps 2010; Violle et al. 2012), including those studying mate choice. Indeed, the number of Web of Science articles containing ‘individual variation’ and ‘mate choice’ in their titles, abstracts or keywords nearly tripled over the last decade, from 25 in 2001 to 74 in 2011.

Female mate choice can be affected by external factors such as the physical and social signalling environment (Herb et al. 2003; Matos et al. 2003; Gordon & Uetz 2011; Clark et al. 2012) and previous experience (Tudor & Morris 2009; Rutledge et al. 2010; Bailey 2011; Wong et al. 2011). Female mate choice can also be affected by internal factors such as genetics (Tregenza & Wedell 2000; Chenoweth & Blows 2006; Horth 2007) and female condition (Cotton et al. 2006a). Additionally, mate choice can be further complicated if these internal and external factors interact with one another (Moskalik & Uetz 2011; Wilgers & Hebets 2012b) or if females are plastic in their decisions. Regardless, we still know relatively little about the physiological mechanisms behind these sources of variation.

Individual variation studies typically evaluate two parameters that influence mate choice: (1) preference functions and (2) choosiness (Jennions & Petrie 1997). A preference function is a ranked order of prospective mates with respect to traits relevant to the mate choice decision (Wagner 1998). For example, a female’s preference function can be generated by plotting a measure of female preference (e.g. number of female copulatory solicitation displays) in relation to the males evaluated (Fig. 1). Preference functions are often described in terms of preference strength: the slope of the preference function (Robinson et al. 2011). Females that choose mates randomly have low preference strength; females that consistently rank males have high preference strengths. Choosiness is the effort an individual invests in mate assessment in terms of the number of mates sampled and time spent per mate (Jennions & Petrie 1997; Castellano & Cermelli 2011). Choosiness is influenced by the assessment cost (Fawcett & Johnstone 2003; Härdling & Kokko 2005) and the receiver’s motivation (Dukas 2004). Choosiness can be represented by plotting a measure of female choosiness (e.g. time spent per male) in relation to the males evaluated (Fig. 1).

Preference functions and choosiness may be associated in different ways. They may be positively related when females with greater preference strength also spend more time evaluating mates. Preference functions and choosiness may be negatively related when females spend less time with each male because they evaluate males quickly. This could occur if the female has high resolution in a sensory modality that allows her to assess males quickly. However, mate choice studies typically do not link variation in the relationship between preference functions and choosiness to individual variation in perception. Nevertheless, as evidence continues to show that individuals vary in sensory processing, there will be a need for studies to show how this variation can contribute to mate choice variation (Archer et al. 1987; McNamara & Houston 2009).

Sensory physiology variation could result in receivers differing in their capacity to process and integrate multimodal signals. The perceptual variability hypothesis (Hebets & Papaj 2005) proposes that multimodal signals may have evolved to target receivers that differ in their sensory processing (i.e. signallers should be selected for their ability to reach multiple receivers). The only study to test this hypothesis found that female sagebrush lizards, *Sceloporus graciosus*, are more attentive to male motion-based displays than males are (Martins et al. 2005) because females are faster than males at visually detecting motion (Nava et al. 2009). Thus, differential signal detection may be driven by sexual variability in the capacity to detect different display properties (Nava et al. 2009). Multiple studies now illustrate sex differences in sensory processing (Doty & Cameron 2009; Gall & Lucas 2010; Muchlinski et al. 2011); thus, variation between sexes may be common. Variation within sexes has also been documented. Henry et al. (2011) showed that within-sex variation in frequency specificity is correlated with variation in temporal resolution of auditory signals.

An individual’s sensory processing and eventual mate choice could be related to its developmental history or current condition. For example, developmental stress could lead to long-term differences in visual or acoustic perception, consequently altering that individual’s lifetime preference functions and choosiness. In contrast, current condition (e.g. differences in nutritional availability, hormone profiles and age) is likely to affect sensory processing and mating decisions on a scale finer than variation in developmental factors (Lailvaux & Kasumovic 2011).

INDIVIDUAL SENSORY VARIATION DUE TO ONTOGENY

Selective pressures on sensory systems are likely to be greatest during early life history (Dangles et al. 2009). For instance, resource availability can constrain the developing sensory system, providing a mechanism by which individual variation in sensory processing can arise. Several studies demonstrate that manipulation of the developmental environment and stress can affect later sensory capabilities (Nowicki et al. 2002; Holveck & Riebel 2010). However, no studies link variation in multimodal sensory capabilities due to development and differences in mate choice (but see Grant & Grant 1997; see below for discussion on unimodal sensory capabilities). Nevertheless, stress can alter the amount or timing of sensory stimulation in one modality, which could have significant consequences for other modalities (Verzijden & Rosenthal 2011).

Animals can compensate for deficits in certain modalities by redirecting energy to alternative sensory modes (compensatory plasticity hypotheses) (Rauschecker & Kniepert 1995; Lessard et al. 1998). For example, females with auditory deficits could compensate by investing more in visual system development. Thus, individuals engaged in mate choice decisions may emphasize the signal modalities that developed more fully in their ontogeny. Here we discuss how differences in the development of sensory processing may lead to differences in mate choice.

Ontogeny of Acoustic Signals and Perception

Two approaches have been used to study the link between development and auditory function in mate choice. The first approach involves manipulating available acoustic information during ontogeny and then measuring adult sensory functioning. Studies using this approach show that sensory stimulation provided by kin can influence the perceptual functioning and hemispheric processing of acoustic information during prenatal and postnatal periods (Lickliter 2005; Phan & Vicario 2010; Harshaw & Lickliter 2011). For example, black-capped chickadees, *Poecile atricapillus*, reared in isolation could not perceive relative pitch of song (Njegovan & Weisman 1997). Similarly, female zebra finches, *Taeniopygia guttata* (Sturdy et al. 2001) and field crickets, *Teleogryllus oceanicus* (Bailey & Zuk 2008) reared apart from adult males failed to discriminate between male songs.

The second approach links developmental stress to variation in female preference functions and choosiness for auditory signals. Stress in ontogeny (e.g. deficit in nutrition) can constrain developing sensory systems, resulting in a malfunctioning of sensory learning (developmental stress hypothesis; Nowicki et al. 2002; Buchanan et al. 2003). For example, female black field crickets, *Teleogryllus commodus*, reared on a high-protein diet had stronger preferences for male call rate than did females reared on a low-protein diet (Hunt et al. 2005).

Developmental stress can also be altered by manipulating brood size, as large brood size is correlated with reductions in mass and immune response (Riebel 2009). Riebel (2009) showed that zebra finches from small broods had stronger preferences for song than did those from larger broods.

Manipulation of stress during development can also change the direction of female mate preferences. Holveck & Riebel (2010) found that zebra finches reared in small and large broods preferred the songs of males reared in small and large broods, respectively, despite all females showing similar choosiness. Interestingly a follow-up study showed rearing background did not affect male zebra finch preferences. This suggests that the sexes differ in their susceptibility to rearing conditions and subsequently display different preference functions (Holveck et al. 2011). Additionally, stressed females can also express less choosiness than nonstressed females. Zebra finch females reared under nutritional stress made fewer sampling visits to stimulus males (Woodgate et al. 2010), but no differences in preferences were found between the treatment and control group (also see Woodgate et al. 2011).

While these studies demonstrate that stress during development can cause differences in female mate choice, they make conclusions on the role of auditory processing without explicitly

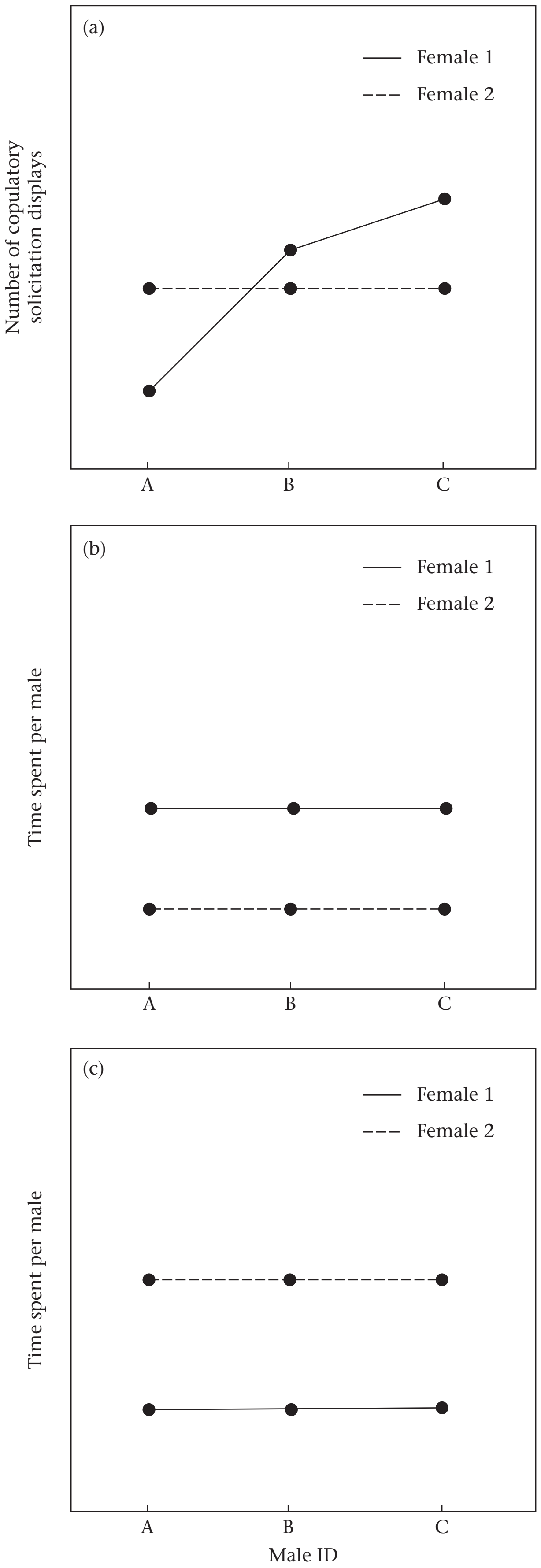

Figure 1. Individual variation in female preference functions and choosiness. (a) Preference functions (as measured by the number of copulatory solicitation displays) of two hypothetical females for three males, A, B and C. Preference functions are often described in terms of preference strength, which is the slope of the preference function. Female 1 prefers male C over male B, and male B over male A, and thus the slope of her preference function is much steeper than the preference function of female 2, who ranks all three males the same. (b) Female choosiness (measured as time spent per male) and preference strength can be positively related, so that as preference strength increases, the time a female spends with potential males increases (e.g. female 1 shows greater choosiness than female 2). (c) Female choosiness and preference strength can also be negatively related, so that as preference strength increases, a female spends less time with each male, potentially because the female has high resolution in a sensory modality that allows her to evaluate males quickly (e.g. female 2 shows greater choosiness than female 1).

testing the receiver's sensory functioning. We need explicit experimental evaluations of the connection between development, sensory functioning and mate choice. Assessing female sensory capabilities is a prerequisite for advancing our understanding of mate choice (Jennions & Petrie 1997).

Ontogeny of Visual Signals and Perception

Just as acoustic stimuli during ontogeny can shape auditory functioning, visual stimuli are important for the development of functional visual systems. Individuals can experience different developmental lighting conditions, and such differences could lead to variation in visual processing and subsequent variation in mate choice. Fuller & Noa (2010) found that preference strength in the bluefin killifish, *Lucania goodei*, is an interaction between an individual's genetics and the lighting conditions it experiences during development and during mate choice. Moreover, exposure to visual stimuli (i.e. novel male phenotypes) during development influenced adult female mating preferences in the wolf spider *Schizocosa rovneri* (Rutledge et al. 2010). Hart et al. (2006) found that lighting conditions during development can explain variation in carotenoid concentration in the cone oil droplets of domestic chickens, *Gallus gallus domesticus*. In general, carotenoid pigments filter incoming light before it reaches the visual pigment (Goldsmith 1984), effectively enhancing colour discrimination and colour constancy in variable lighting environments (Vorobyev et al. 1998). As each oil droplet type is associated with a specific photoreceptor type, the combination of oil droplets and visual pigments play a unique role in the perception of colour (Goldsmith & Butler 2005).

Recent evidence suggests that there could be substantial individual differences in colour perception resulting from individual differences in the sensitivity of the oil droplets of these organisms (Hart et al. 2006; Knott et al. 2012). Visual chromatic contrast models have been used to predict how changes in the sensitivity of the visual system (i.e. peak sensitivity of visual pigments, absorbance of oil droplets, relative densities of photoreceptors) can affect colour perception (Vorobyev & Osorio 1998; Endler & Mielke 2005), typically at the species level (Lind & Kelber 2009). In general, chromatic contrast is a measure of an animal's ability to perceive an object against a visual background under particular ambient light conditions (Endler 1990). Higher chromatic contrast values indicate that the signal is more visually salient for the visual system of the receiver.

We determined whether the degree of individual variation in the visual system could lead to individual variation in the perception of chromatic signals using chromatic contrast models and published information on the sensitivity of the domestic chicken's visual system (see details in Supplementary Material). Specifically, we modelled (following Vorobyev & Osorio 1998) how changes in the absorbance properties of oil droplets and in the retinal density of cone photoreceptors can lead to individual differences in the perception of chromatic signals in relation to the visual background (Fig. 2). The percentage variation in colour perception from changes in visual physiology varied from 1.3% for a signal peaking at 550 nm to 29.3% for a signal peaking at 700 nm. Such individual differences are predicted to have a profound effect on colour discrimination.

We found a greater level of variation in the processing of longer wavelength signals (500–650 nm). Many organisms have visual signals in this wavelength range (Griffith et al. 2006), thus individual variation in the perception of these wavelengths may provide a mechanism for variation in receiver behaviour. These modelling results show that between-individual variation in wavelength sensitivity and photoreceptor density in the retina can result in differences in colour perception, which may in turn influence female mate choice.

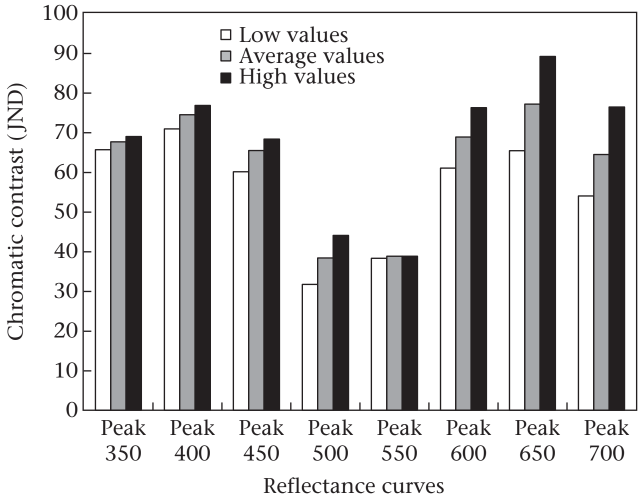

Figure 2. Individual variation in chromatic contrast. Chromatic contrast for artificial objects having reflectance peaks at 350, 400, 450, 500, 550, 600, 650 and 700 nm. Values correspond to parameters showing the lowest, average and highest values in the range of between-individual variability in λ_o and relative photoreceptor density. All other factors (i.e. peak absorbance of visual pigments, λ_{max}, the reflectance of the visual background and the spectral properties of ambient light) were held constant in our calculations. See Supplementary Material for a description of the model.

INDIVIDUAL SENSORY VARIATION DUE TO CONDITIONAL DIFFERENCES

Recent studies have started to address how changes in condition affect mature, rather than developing, sensory systems (e.g. Lynch & Wilczynski 2008; Knott et al. 2010; Yoder & Vicario 2012). Changes in sensory processing could generate condition-dependent receiver preferences (Bro-Jørgensen 2009). For example, female Ipswich sparrows, *Passerculus sandwichensis princeps* (Reid & Weatherhead 1990) and lark buntings, *Calamospiza melanocorys* (Chaine & Lyon 2008) show yearly variation in the signals they use to distinguish among males. Reid & Weatherhead (1990) found that females choose mates based on the trait showing the greatest variability between males in a given year. One possibility is that the trait females assess as the most variable could be dependent on their sensory system. For instance, a female with low visual resolution may discriminate between males using auditory signals. This prediction provides a mechanism by which different females could use different modalities to choose a mate. A validation of this prediction would support the perceptual variability hypothesis.

Variation among females can in part derive from short-term changes in condition. A number of factors can directly or indirectly alter a receiver's condition, but many past studies have neglected to demonstrate how these factors may combine or interact to affect overall fitness (Wilson & Nussey 2010), or how they are influenced by different environments or selective contexts (Lailvaux & Kasumovic 2011). Nevertheless, understanding how single variables such as resource availability, hormone profile or age alters a receiver's condition and influences variation in sensory capability will provide the basis for more complex studies where multiple variables over a particular context are examined.

Resource Availability and Sensory Variation

The availability of high-quality food sources can have a profound effect on a female's current body condition and mate choice (Lerch et al. 2011; Pruitt et al. 2011) perhaps by precipitating disparities in sensory processing. For example, dietary carotenoid levels can alter oil droplet pigmentation (Bowmaker et al. 1993; Knott et al. 2010) as animals cannot inherently synthesize carotenoids (Goodwin 1984). Carotenoid supplementation in two bird species increased the carotenoid concentration of the P-type oil droplet (Knott et al. 2010), which is thought to be associated with motion detection (Campenhausen & Kirschfield 1998; Vorobyev et al. 1998). Additionally, house finches, *Carpodacus mexicanus*, given a low carotenoid diet had lower retinal carotenoid levels (Toomey & McGraw 2010) and showed decreased choosiness during mate choice (Toomey & McGraw 2012).

Mate choice differences resulting from individual variation in other visual properties have also been described. For instance, individual preference strength in the stalk-eyed fly, *Diasemopsis meigenii*, is positively correlated with female eyespan, a trait dependent on diet quality that is linked to higher visual acuity (Cotton et al. 2006b). Large-eyespan females rejected only small-eyespan males whereas small-eyespan females rejected males randomly. Cotton et al. (2006b) reasoned that the number of ommatidia increases with female eyespan; thus, large-eyespan females may have higher visual resolution that allows for greater discrimination between males.

Quality matching in mating pairs is an example of assortative mating. Female midwife toads, *Alytes mulentensis* (Lea et al. 2000), cricket frogs, *Acris crepitans* (Ryan et al. 1992) and African painted reed frogs, *Hyperolius marmoratus* (Jennions et al. 1995) have size-dependent preferences that result in larger, more fecund females preferring larger, more fecund males. In anurans, body size is negatively correlated with the dominant frequency of a frog's advertisement call and the best excitatory frequency of the basilar papilla (Ryan 1980). Thus, large females may prefer large males that produce the lower-frequency songs that stimulate their basilar papilla the most.

These studies provide a fundamental link between diet and condition, condition and sensory system variability, and, in some cases, individual variability in sensory processing and mate preferences. This evidence suggests that high-quality females often show the strongest mate preference (Hedrick & Kortet 2012). We suggest that this is partly due to their enhanced ability to discriminate between males.

Hormones and Sensory Variation

Fluctuations in hormone levels play a large role in reproductive behaviour and may mediate mate choice by increasing sexual responsiveness as oviposition/ovulation approaches (Trivers 1972). Some of these changes result from hormones modifying how females process signals (Lynch & Wilczynski 2008; Yoder & Vicario 2012).

Hormones regulate auditory processing in a variety of taxa including fish (Sisneros 2009; Ramsey et al. 2011; Rohmann & Bass 2011; Maruska et al. 2012), birds (Vyas et al. 2009; Caras et al. 2010; Donna & Raphael 2011) and mammals (Miranda & Liu 2009; Al-Mana et al. 2010). Steroid receptors in these organisms' inner ears provide a direct pathway for these hormones to act on the auditory system (Maruska & Fernald 2010). Research in anurans demonstrates a specific link between preferences for auditory signals and hormone changes (i.e. Lynch & Wilczynski 2008; Arch & Peter 2009; Chakraborty & Burmeister 2009). Female túngara frogs, *Engystomops pustulosus*, with higher oestrogen levels showed less choosiness and increased the range of mate calls they were willing to accept; moreover, increased choosiness was not due to decreased discrimination of male calls (Lynch et al. 2006). Likewise, recently mated green tree frogs, *Hyla cinerea*, show reduced behavioural responsiveness to male calls; this may be because these females show reduced neural responses in the auditory midbrain compared to gravid females (Miranda & Wilczynski 2009).

In comparison to the auditory-based research, the role of hormone-mediated changes in the visual system has been less studied. Experiments using the optimotor response in female sticklebacks (Rick et al. 2011) and túngara frogs (Cummings et al. 2008) show that reproductive females have increased behavioural sensitivity to male visual displays. Interestingly, steroid receptors are present in fish and other vertebrate eyes (Wickham et al. 2000), thus fluctuations in hormone levels may mediate fluctuations in visual processing.

Variation in sensory biology mediated by changes in hormones may exacerbate or moderate decision making. For example, androgens often influence aggressive behaviour (Wingfield et al. 1990) and can also influence sensory perception (Hultcrantz et al. 2006), thereby affecting signal processing during an aggressive bout. Given that many aspects of condition affect mate choice and sensory biology, there is great potential for condition-mediated sensory changes to interact with condition-mediated behavioural decisions.

Age and Sensory Variation

Several studies show that sensory perception is influenced by age. In fish (Pankhurst & Eagar 1996), cephalopods (Groeger et al. 2005), birds (Brittan-Powell & Dooling 2004) and mammals (Hall 2007), optimal auditory and visual sensory functioning improves after early development. In comparison, sensory functioning typically declines after the peak reproductive age (Fitzgerald 2001). Old age is linked to visual decline and loss of photoreceptors in quail (Lee et al. 1997), pigeons (Porciatti et al. 1991) and humans (Panda-Jonas et al. 1995), among other species (Zhang et al. 2008). Additionally, decreased neuronal responsiveness to auditory stimuli has been noted in model species such as chickens (Smittkamp & Durham 2004) and gerbils (Boettcher et al. 1993). The ability of rats to process auditory amplitude modulation also decays with age (Parthasarathy & Bartlett 2011).

The sensory-related decline in advanced age may lead a female to rearrange her preference functions or have decreased choosiness (Kodric-Brown & Nicoletto 2001). This prediction is supported by life-history models showing that a decrease in choosiness can mirror the decline in reproductive value with age (Stearns 1992). As predicted, studies of the cockroach *Nauphoeta cinerea* (Moore & Moore 2001) and the house cricket *Acheta domestica* (Gray 1999) found reduced choosiness with reduced fertility. Female guppies, *Poecilia reticulata*, become less selective with age; this could result from decreased choosiness or a decreased ability to discriminate between males (Kodric-Brown & Nicoletto 2001). Studying the sensory functioning of these fish would help us to understand which of the two alternatives is correct.

Kodric-Brown & Nicoletto (2001) hypothesized that if older females are less responsive to male morphological traits, then males may engage in more vigorous displays to attract older females. Interestingly, male guppies increase their courtship displays towards older (Houde 1997), and perhaps more fecund, females (Hendry et al. 2001). This finding corroborates a study of satin bowerbirds, *Ptilonorhynchus violaceus*, which showed that males perform more intense behavioural displays towards older females (Patricelli 2002). Although these two signals are visually based, the fact that males switch to a signal most relevant for a given individual suggests there may be individual differences in sensory processing.

INDIVIDUAL VARIATION IN ADDITIONAL SENSORY PROCESSING MODALITIES

There is an emerging appreciation for the use of a broad range of sensory modalities involved in processing mating signals, including mechanoreception (Kekäläinen et al. 2011; Gleason et al. 2012), electroreception (Moller 2002; Wong & Hopkins 2007), vibration reception (Wilgers & Hebets 2012a) and chemoreception (Johansson & Jones 2007). However, while there is much evidence of sender-dependent signalling in these modalities (i.e. Johansson & Jones 2007; Allee et al. 2009; Schlupp et al. 2010; Kekäläinen et al. 2011; Gallant et al. 2011; Gibson & Uetz 2012), relatively few data exist addressing individual variation in receiver-dependent reception. One exception is individual variation in chemical reception in model organisms (i.e. humans and mice) (Dematte et al. 2011; Lundström et al. 2012). Chemical perception is altered by developmental (Bigiani et al. 2002; Bertin et al. 2012) and conditional factors such as age (Doty et al. 1984; Murphy et al. 2002) and hormone profile (De Groof et al. 2010; Maruska & Fernald 2010; Kasurak et al. 2012). Additionally, female hunger state has also been shown to influence receptivity to chemical signals of well-fed males in female rock lizards, *Iberolacerta cyreni* (Mártin & López 2008) and swordtail fishes, *Xiphorus birchmanni* (Fisher & Rosenthal 2006). Given the importance of olfactory signals in multimodal signalling during mate choice across taxa (Brennan & Kendrick 2006; Whittaker et al. 2010; Chouinard 2012), individual variation in chemical reception may affect female mate choice in ways similar to acoustic and visual processing. Moreover, we expect the same to be true for other modalities as further research illustrates the developmental and conditional dependence of processing in these sensory modes.

IMPLICATIONS FOR SEXUAL SELECTION

Developmental and conditional factors have the potential to alter sensory system processing drastically, possibly impacting the preference functions and choosiness of an individual. Individual variation in mate choice is common (Jennions & Petrie 1997); however, we have yet to determine the role of variation in multimodal sensory processing on subsequent mate choice. Several techniques, such as neural networks theory, provide a tractable way to simulate the evolution of sensory systems (Phelps 2007; Gurney 2010), but empirical data are necessary to draw definite connections between individual variation in development/condition, variation in multimodal sensory system functioning and subsequent variation in mate choice. Identifying hypotheses that can link individual variation in sensory processing and mate choice can enhance our understanding of preference functions, choosiness and several sexual selection hypotheses.

Preference Functions and Choosiness

Although the idea that individual sensory variation can lead to differences in mate choice has been proposed (Widemo & Sæther 1999; Dangles et al. 2009), hypotheses have typically been framed at the population level and have not included individual variation in multiple sensory modalities. Here we propose novel predictions from existing hypotheses about the effects of individual variation in the sensory system on preference functions and choosiness in a multimodal context. We take into consideration (1) the degree of signal variation, (2) the degree of sensory variation in each of the receiver's processing modalities, (3) whether variation in processing is caused by development or condition and (4) how these components combine to affect the preference functions and choosiness of an individual (Table 1).

Following the working definition of condition by Wilson & Nussey (2010), we consider females to be in 'good condition' or 'high quality' when a multiple regression analysis of conditional traits creates an axis of variation among individuals that is positively related to overall fitness. We also expect female condition to be correlated with female sensory processing; for instance, females in good condition may have a greater ability to resolve different signals (i.e. visual or auditory resolution), which could affect the amount of time they assess mates as well as their ability to tell different signals apart. Finally, we are making our predictions in a sexual selection context and thus our definition of 'good condition' may not extend to scenarios outside of mate choice (e.g. survivorship) (Lailvaux & Kasumovic 2011). This broad definition of quality will allow our preference functions and choosiness predictions to have wider applicability to researchers who can determine the most appropriate conditional traits to measure for their particular system.

Additionally, although there are important examples of nonredundant multimodal signal use in mate choice (e.g. Rowe 1999; Hebets & Papaj 2005), our predictions are based on the assumption that the combination of two equal and redundant sensory components (A and B) leads to an enhanced behavioural response (e.g. 'enhancement'; Partan & Marler 2005). Redundant signals may serve as 'backup' to one another in situations where there is a sender deficiency in encoding information, environmental variability or receiver assessment errors (Hebets & Papaj 2005). Following this assumption allows us to predict how development and condition may affect one or both sensory modalities without making further, unsupported assumptions as to whether developmental or conditional factors play a larger role in determining sensory processing or whether the composite signal illustrates dominance, independence, emergence or modulation of the multimodal components (Partan & Marler 2005). Moreover, the literature suggests redundant multimodal signals may be more common than nonredundant multimodal signals (Partan & Marler 2005; MacDougall-Shackleton et al. 2009; Alonso et al. 2010; Elias et al. 2010; Wilgers & Hebets 2011); therefore, our predictions should be applicable across many multimodal mate choice contexts. Our framework rests on the idea that selection should favour sensory receptors that maximize the received signal relative to the background noise and minimize signal degradation (Endler 1992a). Thus, we assume that high sensory resolution (the ability to resolve two signals in a particular modality) will increase the quality of information the receiver gets, which will ultimately affect preference functions and choosiness (Castellano et al. 2012). Generally, we consider females with greater sensory resolution to be able to resolve fine differences between males and thus have steeper preference functions. Additionally, we also expect females with high sensory resolution to show greater choosiness because they are selected to maximize their chances of mating with a high-quality male and may therefore sample a greater number of males before making a final mate choice decision.

First, we consider the 'standard' assumption (Johnstone 1994) to be that females do not vary in their sensory processing and all have an average ability to resolve male signals. Under these conditions, we predict that directional selection will lead all females to have equal preference function slopes and to prefer the highest-quality male (Table 1). Therefore, any variation in mate choice should result from differences in female choosiness. For example, females in poor condition may not be able to expend as much effort in mating as females in good condition.

However, when we consider the scenario where females vary in a single sensory processing mode (e.g. high variability in A, average variability in B), we could have several outcomes depending on the cause of the variation and the information females have about potential mates. First, following the redundant signalling hypothesis, if females are in good condition and developmental factors cause variation in sensory processing, females with poor resolution in modality A should resolve differences between males using modality B and thus should have preference function slopes less

Table 1
Effects of variation in sensory processing on mate choice via changes in preference functions and choosiness

Individual female variation in sensory processing		Cause of variation	Sensory resolution	Female condition	Mate choice pattern	Preference function	Choosiness
Modality A	Modality B						
No variation	No variation	N/A	Average resolution in A and B	Variable between females	Directional selection[*] for multimodal signal	All females have equal preference functions and prefer the highest-quality male; this function has a steep slope, which we consider the standard	Females in better condition have greater choosiness
Higher than average	Average	Development	Poor resolution in A; average resolution in B	Good	Directional selection[*] on signal B	Preference function slopes are less than the standard	Choosiness decreased: less information available about males
			High resolution in A; average resolution in B	Good	Directional selection[*] on signal A	Preference function slopes are steeper than the standard	Choosiness increased: more information available about males
Higher than average	Average	Condition	Poor resolution in A; average resolution in B	Poor	Directional selection[*] on signal B	Preference function slopes are less than the standard	Choosiness greatly decreased: compromised female condition and less information available about males
					Assortative mating[†] based on signal B	Females prefer condition-matched males; preference function slopes are less than and the opposite to the standard	
			High resolution in A; average resolution in B	Good	Directional selection[*] on signal A	Preference function slopes are steeper than the standard	Choosiness greatly increased: females in good condition and more information available about males
Higher than average	Higher than average	Development	Poor resolution in A or B; greater resolution in A or B (compensatory plasticity hypothesis[‡])	Poor	Directional selection[*] on modality with highest resolution	Preference function slope less than the standard	Choosiness greatly decreased: compromised female condition and less information available about males
					Assortative mating[†] based on modality with highest resolution	Females prefer condition-matched males; preference function slopes are less than and opposite to the standard slope	
				Good	Directional selection[*] on signal with highest resolution	Preference function slopes are the same or slightly less than the standard	Choosiness the same or slightly less than the standard: less information available about males
			Poor resolution in A and B	Good	Random mating[§]	Preference function slopes close to 0	Choosiness decreased: no benefit to being choosy
			High resolution in A and B	Good	Directional selection[*] for multimodal signal	Preference function slopes greater than the standard	Choosiness increased: more information available about males
Higher than average	Higher than average	Condition	Poor resolution in A or B	Poor	Directional selection[*] on modality with highest resolution	Preference function slopes are less than the standard	Choosiness greatly decreased: compromised female condition and less information available about males
					Assortative mating[†] based on modality with highest resolution[‡]	Females prefer condition-matched males. Preference function slopes are less than and opposite of the standard	
			Poor resolution in A and B	Poor	Random mating[§]	Preference function slopes close to 0	Choosiness greatly decreased: compromised female condition and no benefit to being choosy
			High resolution in A and B	Good	Directional selection[*] on multimodal signal	Preference function slopes greater than the standard	Choosiness increased: more information available about males

We assume that multimodal signals to females vary between males and that multimodal displays are additive (e.g. a multimodal display is more potent than a display consisting of a single modality). We define ‘choosiness’ as the amount of time females could spend sampling different males, and we assume that the number of males available for mating does not differ across situations. Females with ‘average’ variation in a given sensory-processing mode (A or B) distinguish between males at a rate that does not differ substantially from that of other females in a population. Females with ‘higher-than-average’ variation in a sensory-processing mode could differ from the average female and either be less capable of resolving differences between male signals in that modality, or be more capable of resolving differences between males.

[*] Andersson (1994).

[†] Burley (1983).

[‡] Rauschecker & Kniepert (1995).

[§] Bennett (1954).

than the ‘standard’ female and should show decreased choosiness because they have less information available to them about the potential mates (Table 1). In contrast, females with high resolution in modality A should place more emphasis on this modality during mate choice and subsequently express increased preference function slopes and increased choosiness because they can resolve fine differences between males and benefit from choosing the highest-quality male (Table 1). Second, according to the redundant signalling hypothesis, if a conditional factor leads to variation in sensory processing, we would expect poor-condition females to be have low sensory resolution to distinguish males based on A, hence choosing mates based on B. Preference function slopes for these females would be less than the ‘standard’ female and their choosiness would be further decreased because of the combination of the females’ poor condition and loss of information from one sensory modality (Table 1). However, if females follow an assortative mating strategy, males may still be chosen based on modality B but prefer quality-matched males. In this case, we would still expect to see preference function slopes less than the standard female and greatly decreased choosiness (Table 1), but females will rank males differently from a low-quality female that still prefers high-quality males. Lastly, high-quality females with a higher resolution in modality A may put more emphasis on modality A in mate choice as this modality provides the female with the most information about potential mates. For these females, preference function slopes would become steeper than the standard and choosiness should increase because of the combination of the female’s good condition and information from multiple sensory modalities (Table 1).

These predictions become more complex when we consider how individual females may vary in both sensory processing modalities due to developmental or conditional factors, which may interact to produce alternative predictions of preference functions and choosiness. For instance, if we assume that a developmental factor causes sensory-processing variation in modalities A and B, we predict that a female with poor resolution in A or B may have greater resolution in the alternative modality (following the compensatory plasticity hypothesis). This greater sensory resolution in modality A or B may compensate for the decreased resolution caused by the development factor, and subsequently lead to her having the same or slightly lower preference function slopes. Moreover, she could have the same or slightly decreased choosiness relative to the standard because the amount of information in one sensory modality may allow her to discriminate finely between males or she may still need the information that would have been provided by the second modality to make fine discriminations between potential mates (Table 1).

However, if females that undergo compensatory plasticity in one sensory mode experience a conditional situation that decreases their resolution in the alternative modality, then their preference functions will decrease relative to the standard if their mate choice follows a directional selection pattern, or they may be in the opposite direction of the standard if their mate choice follows an assortative mating pattern (Table 1). In both of these scenarios, female choosiness should be greatly reduced because of the combined loss of information about the available males and the reduction in the females’ condition.

We predict that females that have poor resolution in both modalities due to a developmental factor but are in good condition will choose mates randomly and have preference function slopes nearing zero and decreased choosiness (i.e. random mating strategy; Table 1). In comparison, females in good condition with high resolution in both modalities due to a developmental factor should have increased preference function slopes and increased choosiness (Table 1) because these females are able to discriminate accurately between males and can hence devote more time to mate choice.

Instead of developmental factors affecting variation in sensory processing, a conditional factor may increase sensory processing variation in both modalities. Given the short timescale of the influence of conditional factors on sensory capabilities, there will be little opportunity for compensatory allocation of resources that enhances unaffected sensory modalities. This lack of compensatory allocation could in turn alter expected outcomes for preference functions and choosiness. In general, females in poor condition that are unable to resolve one modality may (1) choose males based on the modality that provides the most information or (2) choose quality-matched mates (i.e. assortative mating). In either case, preference function slopes will be less than the standard (although females choosing mates assortatively may have the opposite-sign preference function) and choosiness will be greatly reduced because of the combined effects of poor condition and less information available about males (Table 1). In comparison, (3) females with poor resolution in both modalities could choose mates randomly and have preference function slopes nearing zero and greatly reduced choosiness because these females gain no benefit from time sampling males that they cannot resolve differences between, or (4) females with high resolution in both modalities have increased preference function slopes and increased choosiness because they have more information with which to evaluate males quickly and accurately, as predicted by the redundant signalling hypothesis (Table 1).

Table 1 demonstrates that when we consider individual variation in multimodal sensory processing, the predictions on mate choice vary substantially from situations in which we assume that there is no individual variation or population-level variation in the sensory system of females (Endler 1992a; Stuart-Fox et al. 2007). Ultimately, individual differences in sensory processing influences how we interpret results of mate choice studies and could alter hypotheses underlying sexual selection. We will now consider important hypotheses that illustrate the potential relevance of sensory physiology on mate choice patterns.

Sensory Drive Hypothesis

The sensory drive hypothesis proposes that male courtship signals may have evolved to exploit preexisting female sensory biases that increase the probability that a female will choose a particular male as a mate (Endler 1992b). As such, the sensory drive hypothesis is often invoked to explain population-level female preferences for a male trait (Egger et al. 2011; MacLaren et al. 2011).

Such studies often make two critical assumptions when discussing sensory drive. The first is that greater sensory stimulation results in preferences for mates with the stimulating trait (Endler & Basolo 1998). Exaggerated displays are expected to have greater signal value and generate more matings because they elicit a stronger response from the female’s sensory system (Ryan & Keddy-Hector 1992). The second assumption is that biases arising from sensory-processing mechanisms are relatively fixed (Sherman & Wolfenbarger 1995) and therefore show limited developmental plasticity (ten Cate & Rowe 2007). However, neither of these assumptions is likely to hold in all circumstances.

First, while sensory drive theory suggests that all females will prefer intense displays, the specific components of multidimensional signals preferred by females may change over time. For example, mate choice in satin bowerbirds is age dependent: young females place an emphasis on decorations around the male’s bower, whereas older females evaluate a male’s exaggerated behavioural display (Coleman et al. 2004). Second, with respect to the assumption about fixed processing mechanisms, recent evidence suggests that individual variation in sensory processing could be common (reviewed above) and could result in individual differences in preference functions due to receiver differences in signal processing (Widemo & Sæther 1999).

Endler (1995) originally suggested that the sensory drive hypothesis does not assume that sensory biases are fixed. Nevertheless, most empirical studies only evaluate its predictions at the population level (Egger et al. 2011; MacLaren et al. 2011). We suggest that the degree to which a sensory bias can act as a selective mechanism in female choice could be diminished when the salient components of a sensory trait are condition dependent. Thus, when individual variation in sensory processing is large, the strength of a population-level bias will be weaker and less likely to result in directional selection.

Honest Signalling Hypothesis

The honest signalling hypothesis predicts that only high-quality males should produce expensive signals as they are too costly for low-quality males (Searcy & Nowicki 2005). For example, in birds, testosterone regulates song and plumage, but signal production is costly as testosterone is immunosuppressive (Folstad & Karter 1992). Therefore, only high-quality males can incur the cost of testosterone and still produce high-quality sexual signals.

While the honest signalling hypothesis provides a mechanism for male signal variability, it overlooks how these signals are perceived by different receivers. Indeed, females varying in quality may process signals differently depending on the cost of processing (Phelps 2007). For example, carotenoids contribute to immune system functioning in addition to playing a role in avian vision. Evidence suggests that only high-quality individuals can allocate carotenoid use for vision rather than for immunoprotection (Toomey et al. 2010). Such sensory variation among females imposes variation in males' signal design, because males display to females that are not homogeneous in their perception of the signal. Thus, honest signalling is complicated by the fact that information derived from the signal can be modified by variation in female sensory capabilities. Ideally, the honest signalling hypothesis should be expanded to include a mechanism that relates female condition, her sensory processing and her variable responses to the study of male signals. If enhanced perception of male traits leads high-quality females to choose high-quality males, this mechanism could lead to assortative mating patterns.

Assortative Mating

Variation in development or condition often results in high-quality females pairing with high-quality males, a pattern called positive assortative mating (Burley 1983). Individual differences in sensory discrimination and its link to quality provides a unique mechanism for understanding these patterns. For example, northern cardinals, *Cardinalis cardinalis*, mate assortatively by plumage colour (Jawor et al. 2003). One explanation is that pairing is based on the active choice for a mate that matches the perception of one's rank. However, this assortative pattern could also be maintained by a physiological mechanism where all females prefer high-quality males but are variable in their ability to distinguish between them.

Cardinal plumage brightness is maintained by a high-quality diet that includes carotenoids (Jawor et al. 2003). As discussed, there is a positive relationship between plumage redness and retinal carotenoid concentration, suggesting a common biochemical basis of colour vision and plumage coloration (Toomey & McGraw 2009). Thus, high-quality females will be better at distinguishing between males and subsequently, more likely to mate with higher-quality males.

This sensory mechanism is a potentially new approach to the basis of assortative mating. It differs from classical models because it assumes directional selection on mate choice, but also posits that the strength of selection varies with the distribution of sensory capabilities in the female population. In contrast, classical assortative mating assumes frequency-dependent stabilizing selection. The evolutionary consequences of these two mechanisms could be different as the sensory mechanism allows for variation but proposes that there is an optimal mate choice that confers the highest fitness. In assortative mating, however, stabilizing selection predicts phenotype matching by organisms with a diversity of preference functions. Studies that evaluate the quality of the mating pair at the level of the sensory system and the eventual fitness benefits could distinguish between these two mechanisms and make an interesting case for which is most prevalent in a given population.

Intrasexual Selection

Sexual selection theory is framed to demonstrate how secondary sexual characteristics can evolve through both intersexual mate choice and intrasexual competition. While the currencies we use in this review (i.e. preference functions and choosiness) are fundamentally linked to mate choice, variation in multimodal signalling and reception in an intrasexual context can also be considered. In fact, there is an emerging literature base for female intrasexual competition outside the typical examples of sex-role reversal. This literature highlights the importance of considering individual variation in sexual selection (Edward & Chapman 2011; Rosvall 2011; Myhre et al. 2012). Indeed, competition between females for high-quality males that provide direct and indirect benefits may be more prevalent than previously thought (Rosvall 2011; Cain & Ketterson 2012). Such competition could lead to individual variation in female sensory processing. This was the case in a population of pollen katydids, *Kawanaphila nartee*, where sexual selection resulted in differences in the size of the females' thoracic spiracles, the main input into their auditory system, as well as in the females' ability to locate males (Gwynne & Bailey 1999). Greater degrees of individual variation in female sensory systems should be expected in populations where there is intense selection for the ability to locate a mate, perhaps because only some females are able to expend the resources necessary to locate mates. Females may even adopt an additional sensory modality to locate males in these situations; this has been proposed for females in the well-studied population of field crickets, in which males have nearly lost their ability to call because of intense selection against singing males by a parasitic wasp (Zuk et al. 2006). Investigating the role of intrasexual selection in shaping females' multimodal sensory biology may be a fruitful avenue for future research.

CONCLUSIONS

Overall, there is a general dearth of research linking mate choice variation to multimodal sensory processing variation. To better understand the direction and rate of sexual selection, estimates of sensory function need to be related to individual differences in mate selection (Dangles et al. 2009). Such studies would highlight the factors influencing variation in female preferences and how this variation impacts the evolution of male multimodal ornaments. Indeed, knowledge about receiver sensory functioning may require a reexamination of the basis of multimodal signalling, sensory drive, honest signalling, assortative mating and intrasexual selection. Research linking the heritability of sensory variation and mate choice would strengthen our understanding of how individual differences in sensory functioning can affect sexual selection.

Unfortunately, relatively few studies have determined the heritability of female mating preferences (Jennions et al. 1995). Ultimately, variation in sensory physiology may influence the fitness of the sender and receiver, thereby altering the rate and direction of signal evolution (McNamara & Houston 2009).

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Supplementary Material

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