Editorial

A perspective on sensory drive

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Introduction

In 1992, *The American Naturalist* published a special supplement entitled: "Sensory Drive. Does Sensory Drive Biology Bias or Constrain the Direction of Evolution?" organized by John Endler. The supplement contained a seminal paper on "sensory drive" by Endler (1992a) as well as several other well-cited papers on sensory exploitation (Ryan and Keddy-Hector 1992), background matching with respect to motion (Fleishman 1992), chemical cues in mammals and amphibians (Alberts 1992; Roth et al. 1992), and the relationship between auditory processing and call properties in frogs (Narins 1992). The paper by Endler was especially important; it has been cited over 1,200 times and has inspired research at many levels of ecology and evolution across diverse taxa and sensory modalities. In this paper and associated ones, Endler laid out the primary components that influence the evolution of signaling systems, placing a large emphasis on the environmental conditions under which signaling occurs (Endler 1992a, 1992b, 1993). Twenty-five years later, the American Society of Naturalists held a symposium on "25 Years of Sensory Drive" at the 2017 Evolution meetings in Portland, Oregon, organized by Becky Fuller. This special column in *Current Zoology* summarizes the work presented there as well as other contributions made for the column. In this editorial, we first review sensory drive and the state of the field when it emerged. We then summarize the work in this special column and suggest fruitful ways forward.

Figure 1 shows the sensory drive framework. In order for signaling to occur between a signaler and a receiver the following must happen: The signaler gives off signal(s) using one or more signal modalities, and those signals have particular properties (e.g., reflectance, pitch, degree of polarization, chemical structure, etc.). The signals are given off in particular times and places. In order for the signal to be successful, the signal must travel through the environmental conditions under which signaling takes place and be detected by the receiver against a background of other potential stimuli. The signal is then detected (or not) by the sensory system of the receiver and processed by the brain, which influences the perception of the signals and the resulting behavior (i.e., decision criteria). Of course, there are other things can influence the evolution of the signaler and the receiver, which are indicated in Figure 1. The receiver must do many things with its sensory systems other than merely detect signals used in communication. It must also find food, avoid predators, and find proper habitat, all of which can exert natural selection on sensory system properties. In Figure 1, this is exemplified by "Detectability of food" and foraging success (fs). In addition, the act of signaling may make signalers more conspicuous to predators and other actors that would exploit signals. The environmental conditions under which signaling takes place can affect the roles of predators and eavesdroppers just as it can with signalers and intended receivers.

At the time of its publication, there was a debate among biologists as to why females evolved mating preferences for males with costly secondary traits. Both Cummings and Endler (this column) and Rosenthal (this column) discuss the state of the field at the time of publication. On one side of the debate were folks modelling and testing the Fisher–Lande–Kirkpatrick, Good Genes-Handicap, and direct benefits models, which emphasized the costs and benefits of female mate choice and male traits, the levels of genetic variation in preferences and traits, and the extent to which there were genetic correlations/gametic disequilibria between the alleles for traits and the alleles for preferences (Lande 1981; Kirkpatrick 1982, 1985; Pomiankowski 1987a, 1987b; Kirkpatrick et al. 1990; Pomiankowski et al. 1991). On the other side of the debate were the sensory exploitation (West-Eberhard 1984; Ryan 1990), sensory trap (Christy 1988; Christy 1995), and pre-existing bias (Basolo 1990a, 1990b) models that emphasized the manner in which male traits stimulated sensory systems and induced female mating. Sensory drive was published in the middle of this debate and had the ultimate effect of bringing the two sides together. By presenting a more complete view of signaling dynamics, it incorporated the sensory exploitation, sensory trap, and sensory bias hypotheses as a subset of possible phenomena. It also allowed for feedbacks between the evolution of signals and receiver properties, thus accommodating evolutionary genetic models. In retrospect, the debate was perhaps a bit misplaced due to the fact that the different sides were understanding the same phenomena at different levels of biological
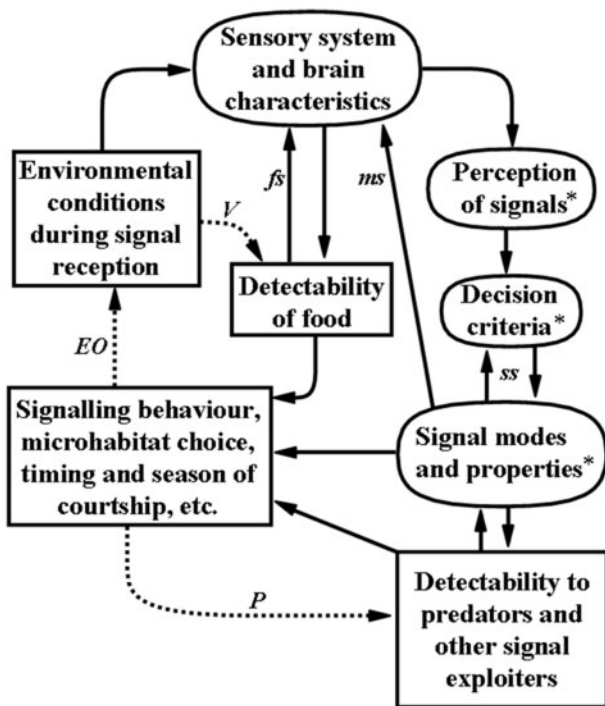
Figure 1 Diagram of the main processes in sensory drive, modified and revised from Endler (1992). Solid arrows indicate evolutionary processes. Dashed arrows with upper case symbols indicate immediate or functional effects: *Eo*: immediate effects of ecological and optical conditions on signalling conditions. *V*: immediate effect of microenvironment on the visibility of prey. *P*: immediate effect of microenvironment on visibility to predators, and also natural selection caused by microenvironmental conditions acting on predator senses and behaviour. Lower Case Symbols: *Fs*: feeding success that directly affects the evolution of the senses. *Ms*: mating success that affects sensory evolution directly. *Ss*: sexual selection (Good Genes, Fisher Process, etc.) That influences mate-choice criteria evolution directly. The asterisks identify the three components of sensory exploitation, a well-studied subset of sensory drive.

organization, similar to the debates between Lorenz, Tinbergen, and the American behaviorists (Tinbergen 1963).

Today, regardless of whether one is modelling the evolution of female mating preferences for costly male traits, mapping preferences, traits and signaling environments onto a phylogeny, or dissecting the neurological pathways underlying female mating preferences, there is widespread agreement on the following: 1) Natural and sexual selection readily occur in populations provided that there is genetic variation in traits (i.e., signals, receiver systems, preferences) that is associated with fitness; 2) The levels of genetic variation and the genetic architecture of traits, preferences, and their underlying component parts can have large influences on the subsequent evolutionary dynamics of preferences and traits; 3) Traits that originally evolved for one purpose may be co-opted for other purposes; 4) Female mating preferences (and male–male competition rules) rely on the detection of signals at the peripheral sensory system, their processing and interpretation in the brain, and the resulting motor output; these neural mechanisms are often complex; 5) The sensory system of the receiver determines which signals can be detected; 6) In the majority of cases, sensory systems serve multiple purposes and must be capable of detecting many types of different stimuli (i.e., mates, food, habitat, etc.); 7) The environment under which signaling takes place may have large influences on

determining which signals can be readily transmitted and detected over background noise; these effects may alter the costs and benefits of preferences and traits across populations; 8) Understanding the sensory experiences and signal interpretation of other animals (i.e., non-humans) is difficult, and this is particularly so for sensory modalities where humans lack sensitivity (e.g., polarized vision, lateral line, chemosensation, electroreception). Evolutionary theory, neurobiology, and sensory ecology co-exist in many labs studying sensory drive, and this is reflected in the articles in this special column. Three main themes emerge in this column: the effects of signaling environments on signals and receiving systems (Cummings and Endler 2018; Gunderson et al. 2018; Mitchem et al. 2018), the potential for sensory drive in sensory modalities other than vision and acoustics (Cronin 2018; Yohe and Brand 2018), and the inferences concerning sensory drive that can be drawn by understanding the neurobiology underlying signal reception, perception, and discrimination (Gunderson et al. 2018; Rosenthal 2018; Sandkam et al. 2018).

The importance of sensory environments

Cummings and Endler (2018) lead off the special column with a review of the evidence for sensory drive across study systems and ask whether there are particular taxa or environments where sensory drive is particularly prevalent. Cummings and Endler (2018) ask two simple questions. The first is whether elements of the sensory system vary between different environmental conditions—either among populations within species or among closely related species. The overwhelming answer is yes. In 53 of 56 tested study systems, there was evidence for variation in sensory system properties. The vast majority of these studies focused on visual signals and the most abundant taxonomic group was fishes. The second question was whether properties of signals differed with environmental conditions, including temporal variation. Again, the vast majority of tested study systems (107 of 126) found good evidence for sensory drive. Both terrestrial and aquatic systems were well represented as were various taxa. However, the most telling fact was that the systems lacking support for sensory drive (i.e., differences in signal between environments) were all terrestrial, 95% involved acoustics, and fish were not among the taxa represented by these studies. Finally, only 29 study systems found "complete" evidence for sensory drive (i.e., both the sensory system and the signal varied between environments). These studies were primarily on vision in aquatic environments with fish being the dominant taxon supporting sensory drive.

Why should sensory drive be so well-supported in vision in aquatic habitats? One possibility is that the result reflects the fact that humans are visually oriented and can more readily detect patterns in coloration than they can in other sensory modalities (see Cronin 2018; Yohe and Brand 2018). However, Cummings and Endler (2018) had good sample sizes in acoustics as well as in terrestrial studies in vision. Hence, the abundance of studies supporting sensory drive in vision in aquatic systems must have a real biological basis—at least in comparison to acoustics and terrestrial studies of vision. Another explanation is that there is greater among population variation in aquatic lighting environments than there is in terrestrial lighting environments or in acoustic environments. Aquatic lighting environments experience similar sources of variation as do terrestrial environments (i.e., time of day, tree cover, differences in background coloration), but they also experience variation due to depth and to the inherent optical properties (i.e., algae, cDOM,

sediments) that restrict the wavelengths of light available for vision and visual signaling. The strong support for sensory drive in aquatic systems is in keeping with the fact that the pioneering work in visual ecology had a clear influence on the development of sensory drive.

For Cummings and Endler (2018), the defining attribute of sensory drive is that signals and receiver systems co-vary with sensory environments in a putatively adaptive manner. Such patterns can be generated by local adaptation, adaptive phenotypic plasticity, or a combination of the two. Echoing the approach of Cummings and Endler (2018) is the contribution from Mitchem et al. (2018) summarizing a body of work on bluefin killifish and presenting three new studies on components of sensory drive. Bluefin killifish are relevant to sensory drive because populations occur in both spring and swamp habitats that differ dramatically in lighting environment. Spring habitats are crystal clear with high levels of UV and blue light present in the water column, whereas swamp habitats are tannin-stained with the UV and blue wavelengths filtered by dissolved organic materials. Previous work in bluefin killifish had found that male coloration, foraging preferences, and elements of the visual system differed among populations. There was also some evidence that female mating preferences differed among populations as well. Mitchem et al. (2018) presented three new studies showing that 1) predation risk of different colour morphs likely varies due to lighting environment, 2) the outcome of male/male competition varies due to lighting environment, but 3) unlike previous studies, female mate choice did not vary due to lighting environments. Hence, in the bluefin killifish system, there is good support for most of the components of the sensory drive framework. The other compelling aspect of this system is that genetics, phenotypic plasticity, and an interaction between the two contribute to many of these traits in a manner that suggests adaptive plasticity as a function of the lighting environment.

Finally, Gunderson et al. (2018) present the most experimental study in the column that focuses on dewlap coloration in the Caribbean anole, *Anolis cristatellus*. This species has populations in both open xeric and shaded mesic forests that differ in dewlap coloration. Gunderson et al. created fake dewlaps that mimicked the spectral properties of dewlaps found in xeric and mesic habitats and then presented these back to live animals in the field. Mesic fake dewlaps were detected more often by anoles in mesic habitats and the same trend occurred in xeric habitats. This study shows the feasibility of experimentally evaluating the predictions of the sensory drive under natural conditions, including the validation of perceptual distance models which have been used widely to evaluate the conspicuousness of visual signals.

Other sensory modalities

The two manuscripts from Cronin (2018) and Yohe and Brand (2018) remind those of us working on visual signaling not to be too smug. While studies of colour pattern and colour vision are quite satisfying to us as visually oriented humans, we are likely missing vast amounts of patterns in signals and receiving systems that are present in other modalities to which humans are insensitive. Cronin (2018) discusses the nature of polarized light and the evidence indicating a possible role for sensory drive and sensory bias in polarized cues. Polarization refers to the orientation of photons as they travel through space. While humans can obviously tell which direction light is coming from (i.e., we can see shadows), we cannot determine the extent to which the photons are traveling in a similar orientation. Light can be polarized linearly (think of photons traveling

forward and vibrating in a single orientation as they pass through a slit in a filter) or circularly (think of photons traveling through a long helical stair case). Many invertebrates and a few vertebrates can use polarized light as a source of information and some employ polarized light in colour patterns that may act as signals. Our two favourite examples were those of nymphalid butterflies and stomatopods. In the case of nymphalid butterflies, there are compelling lines of evidence to suggest that polarized signals and polarized preferences have co-evolved and that differences in habitat (dim versus bright light) might play in role in determining when polarized cues are used. In stomatopods, Cronin and colleagues have shown that animals create circularly polarized light that conspecifics can detect. In some species, disrupting the structures with a hot pin (which does not hurt the appendage itself) results in males having to display for longer periods of time to females with shorter mating durations. There are all sorts of interesting patterns here—including the observation that the ability to detect circularly polarized light may be an artifact of the organization of the photoreceptor cells in the midband of the compound eye of stomatopods. The underwater world is naturally devoid of circularly polarized light, with the exception of that created by the mantis shrimp, which suggests that the initial biases in this system did not evolve due to natural selection to detect such cues in nature. In short, there are undoubtedly many fascinating patterns around us with respect to polarized signals, to which we are blind. The good news is that new methodologies are being developed to allow scientists insight into the polarized world (Brady et al. 2015; Daly et al. 2016; Ahmed et al. 2017).

While the challenges posed by polarized light are daunting, a good argument can be made as to why those posed by chemoreception are even greater. The term "chemoreception" refers to the sensory reception of chemical cues, but it disguises the fact that there are likely hundreds if not thousands of different signals that animals can detect with thousands of different chemoreceptors. Moreover, conditions and sensory biases may be very different for smell (media transport to the sensors) or taste (direct contact between the chemical and the sensors). Whereas color vision, polarized light vision, vibrational cues, and acoustics, rely on the comparisons of different spectra (i.e., waves, amplitudes, etc.), chemoreception relies on the differential binding between receptors and chemicals for thousands of different chemicals (Yohe and Brand 2018). For each chemoreceptor, one needs to know which chemicals bind to it and with what affinities. Are there other chemicals that can also bind to a given receptor, i.e., what are the levels of cross talk among receptors? A given "signal" might consist of a complex blend of a hundred compounds that must be received and distinguished from a background also containing hundreds of compounds. Within these blends, identifying the salient compounds and whether different compounds act as agonists is challenging. Moreover, different mixtures of the same compounds may transmit very different signals and mixture differences are often enough for species isolation (Lofstedt 1993). On the receiver side, most organisms possess hundreds to thousands of different chemoreceptors. Trying to describe the basic binding properties of these is obviously challenging. Genomics approaches have been adopted for categorizing major classes of chemoreceptors and inferring function, but this is not easy because these chemoreceptors evolve rapidly due to gene duplication. In the ideal world, one would know the concentrations and ratios for many chemicals in the environment (both from the signal and the background), the binding properties for thousands of chemoreceptors, and the manner in which the neurological signal from

the receptors are compared by upstream processing. The complexity of chemoreception is staggering. It is, therefore, all the more impressive that good progress has been made in this area of sensory biology (Yohe and Brand 2018).

There are good reasons to suspect that sensory drive is important to chemoreception. Yohe and Brand (2018) review a number of intriguing studies that suggest complex interactions between compounds released by plants and the insects that either pollinate them, mate on them, or eat them. In these situations, the background (i.e., the plant) often releases compounds that alter the perception of the pheromones released by conspecifics. Similarly, pollutants released by humans can mask floral scents altering plant-pollinator systems in terrestrial systems. Yohe and Brand (2018) review systems where pheromones are involved in reproductive isolation between two close relatives where differences in abiotic environment that might play a role in signal evolution. As with polarized vision, there is undoubtedly a wealth of fascinating biological patterns to be unraveled. We suspect that sensory drive will be a helpful framework for these endeavors.

The mechanisms of signal reception, processing, and preference

Two contributions focused on the physiological/neurological basis of sensory reception, perception, and discrimination as they related to mating preferences. The two papers take very different views, particularly with respect to the importance of the peripheral sensory system on mate choice. (Rosenthal 2018; Sandkam et al. 2018). Sandkam et al. (2018) review the large body of work on guppy colour vision. This is particularly appropriate for this column as Endler's original paper on sensory drive had a large subsection devoted to the topic of color patterns, colour vision, and sensory ecology in guppies. Sandkam et al. (2018) review the manner in which light passes through the eye and is absorbed (or not) by photoreceptors. In doing so, they point out the steps via which variation in sensory reception can occur. For some of these elements, there is good evidence for either variation among populations or phenotypic plasticity as a function of light, diet, and/or age. Most notable are patterns seen in densities of ellipsosomes (which filter light prior to absorption by the photoreceptors), allelic variation at the LWS-1 locus, and variation in opsin expression. The take home message is that there are many ways that the visual system can vary among populations and individuals. There is very good evidence for phenotypic plasticity in visual system properties, but there is also evidence for genetic variation. The implication is that variation among populations in visual system properties might account for variation among populations in female mating preferences.

Rosenthal (2018) takes a different view on this topic. While there is often variation among populations and species in sensory system properties, Rosenthal argues that there is little direct evidence that the causative variation in mating preferences lies at the peripheral sensory system (see also Rosenthal 2016). Rather, Rosenthal (2018) presents a very compelling review indicating that the evaluative mechanisms of mate choice that assign positive and negative values to a given stimulus lie in the brain. On the surface, the articles by Sandkam et al. (2018) and Rosenthal (2018) would seem to contradict one another. However, we argue that these two vantage points raise compelling questions for sensory drive, and just reflect different levels of organisation in sensory-cognitive processes.

This column and other reviews clearly indicate that there are measurable levels of variation in sensory system properties that are often associated with environmental conditions and with different aspects of male signals in many taxa (Ryan and Cummings 2013). In fact, over the past 25 years, our collective endeavours indicate that—despite their complexity—sensory systems are often variable across populations and species. What can we infer from this variation? The temptation has been to assume that these differences result in differences in mating preferences. Population/species differences in sensory system properties that are correlated with environmental conditions, male traits, and preferences provide compelling candidates for the mechanisms of preference (e.g., Lofstedt 1993; Seehausen et al. 2008). However, an alternative explanation is that these differences simply represent adaptations in the sensory system to different environmental conditions. In other words, there is selection on sensory systems to efficiently capture relevant stimuli in the environment, whether it be related to mates, food, predators, or habitat. The sensory system captures information from the environment, which is then processed by downstream neurological processes. Applied to guppies, one could hypothesize that, while there are important elements of the retina that vary between high and low predation streams and different lighting/food environments, preference for orange males over drab males occurs in the brain and not in the retina. Population differences in orange preference may therefore involve changes in the evaluations made in the brain and not in the retina. This is made more complex by the different light environments and other physical differences between high and low predation locations, which may favour sensory divergence, affecting the perceived appearance of alternative mates, which may favour divergence in the choice mechanisms in the brain. This is a testable hypothesis.

Would such a scenario undercut sensory drive? Not necessarily. Sensory drive predicts local adaptation (or adaptive phenotypic plasticity) as a function of variation in sensory environments. The fact that the causative mechanisms of mate choice lie in the brain is not necessarily a death knell for sensory drive. Rather, it forces us to ask how such differences in evaluative mechanisms evolve and whether we can detect the signature of local adaptation as a function of sensory environments. This is a challenging task, but one that is worth pursuing. Population differences in mating preferences—and their underlying neural/physiological mechanisms—can evolve for many reasons, including reinforcement, differential sexual selection independent of the sensory environment, local adaptation to different sensory environments, and correlated effects due to selection in other contexts. Determining the relative importance of these processes would be very interesting.

Going forward—the next 25 years

In many ways, sensory drive represented the merger of sensory ecology and ecological/evolutionary genetics. We argue that this merger has been tremendously successful and has led to a wealth of integrated approaches to understanding animal behaviour, sexual selection, and the functioning of sensory systems in nature. There are clear challenges that lay ahead. We still have a rudimentary understanding of many senses for many organisms. This special column focused on two: the detection of polarized light (Cronin 2018) and chemoreception (Yohe and Brand 2018). Others sensory modalities would benefit from increased attention including the sense of vibration, water movement, and magnetic reception. Even with well-studied sensory systems such as vision, many of our models that allow us to infer the experiences of other animals (Vorobyev and Osorio 1998; Maia et al. 2013) rely on parameters that have been

estimated in only a handful of organisms (Land and Nilsson 2012; Cronin et al. 2014). Given that variation in sensory system properties is common, further studies into the basic biology of sensory systems are warranted.

Yet, even without knowing the precise details of the sensory biology of every organism, we can still make predictions with regards to sensory drive. The basic premise of sensory drive is that variation in the environmental conditions under which signaling takes place can have profound effects on the evolution of signals, receiver systems, and behavior as well as costs due to predators and other eavesdroppers. Below, we provide a series of predictions concerning sensory drive. Some of these were made when the original paper was published, and we have updated these with our current understanding.

1. There should be correlations between the sensory system+-brain, signal perception, decision criteria, signal properties, microhabitat choice, and foraging detection methods. These correlations might be present at multiple levels: among closely related species, among populations, among individuals. However, different levels may or may not diverge, depending upon evolutionary history and genetic variation. While there is good evidence for compelling patterns among populations and closely related species, there is less evidence for these correlations at the within-population among-individual level. This raises the question of whether multiple traits evolve as a function of local adaptation or whether there are strong pleiotropic relationships among traits (Fuller and Noa 2010). The resolution to this question is important to understanding the extent to which trade-offs between different functions act as constraints (Fuller et al. 2005). The answer to this question is also central to the issue raised by Sandkam et al. (2018) and Rosenthal (2018) above, and is an inherent part of the sensory drive diagram where perception and decision-making are treated as separate processes (Figure 1). Again, not all components of the sensory drive process will necessarily evolve; just those components which make the system work should evolve.

2. Testing sensory drive on a phylogeny is informative as it provides compelling patterns of repeated evolution of traits. In general, there ought to be a repeated sequence of character state transitions starting from any point on the diagram (Figure 1) and running through the main cycle and network in the same direction as the arrows in the figure. The precise patterns that emerge will depend on the levels of genetic variation and strength of selection on traits as well as on the branching rates that capture transitions in trait values.

3. Sensory drive could be divided roughly into two component groups: 1) based upon receiving and processing signals (sensory system and brain, signal perception, decision criteria, food detection) and 2) based upon making and transmitting signals (signal modes and properties, predator detectability, microhabitat choice and use, and environmental conditions during signal reception). Evolutionary relationships within each of these two groups of processes may evolve faster and more in concert than processes running between them. Consequently, character change sequences on a phylogeny might be more orderly between the two groups than within them.

4. Phenotypic plasticity as a function of the sensory environment may be common, particularly for organisms that have a high probability of experiencing multiple environmental conditions (Mitchem et al. 2018). Sensory modalities that experience high levels of diurnal, seasonal, or spatial variation in environmental conditions (i.e., vision, chemoreception) may be particularly likely to be plastic. Theoretical treatments are needed to determine the implications of plasticity versus genetic effects in different elements of the sensory drive process.

5. Local adaptation should evolve among most of the components; divergent environments should lead to divergent suites of traits involved in sensory drive (Endler 1992a; Maan et al. 2006; Maan et al. 2017; Cummings and Endler 2018; Gunderson et al. 2018; Mitchem et al. 2018; Yohe and Brand 2018). But which components diverge will be a function of evolutionary history and genetics so higher taxa may diverge in very different ways, in addition to using different sensory modes. In addition, the local community may alter the sensory drive process in unanticipated ways.

6. Background noise will influence the direction of sensory drive when there are wavelength bands which have relatively less noise and can be used for signalling. For chemoreception very rare chemicals or chemical mixtures rare in the background would be favored for signalling. In addition, sensory drive will proceed most rapidly in the sensory modes which work best in the presence of the background noise (Yohe and Brand 2018). For example, in a habitat with a lot of noise in sound and vibration modes, visual and chemical mode sensory drive may proceed more rapidly and yield more divergence. Physical properties of the environment and how sensory processing works will affect the efficacy of signal emission, transmission, and reception (Endler 1992a, 1993, 2000; Cronin 2018; Gunderson et al. 2018).

7. The mutually reinforcing joint evolution of all the suites in sensory drive could lead to speciation if choosing the best mate incidentally results in one set of populations no longer interbreeding with another set of populations, or if divergent changes in genes affecting any of the components of sensory drive diverge sufficiently for genetic incompatibility in "hybrids" (Endler 1992a; Boughman 2001; Boughman 2002; Servedio and Boughman 2017; Yohe and Brand 2018).

8. "Restrictive" sensory environments allow for predictions concerning signals and sensory receptors, where as "permissive" environments preclude good predictions because sensory drive can evolve in many different directions. For example, with respect to vision, some environments, especially aquatic and sub-canopy terrestrial (and kelp forests), have restrictive visual environments (with a narrow range of wavelengths), while others, such as open areas and shallow pelagic marine, have permissive visual environments (with the full solar spectrum). The same principle applies to other sensory modes. However, there is not a simple link to diversity and speciation. Restrictive environments allow predictions about the direction of sensory drive hence the properties of species evolved in those conditions. However, this predicts relatively low diversity under those conditions because multiple lineages will experience similar sensory drive (with the same sensory modes). On the other hand, in permissive environments, sensory drive can run in many different directions, aided by the Fisher–Lande–Kirkpatrick Process, so the details of species in permissive environments are not particularly predictable, but diversity is favored. In summary, restrictive environments allow predictability in details but prevent diversity, unless habitats are diverse, whereas permissive environments allow diversity but prevent predictability.

9. Much of the work surrounding sensory drive has involved the documentation of pattern. Gunderson et al. (2018) refer to this as the "correlational" approach. Of course, good science involves the combination of pattern, experimentation, and theory. Theoretical treatments of sensory drive that are motivated by natural patterns and tested with rigorous experimental approaches are the benchmark to which we should all strive.

Clearly, more work is needed on a variety of taxa, sensory systems, and environments to fully understand sensory drive, and eventually use it to predict the direction of evolution and rates of

speciation. Still, we are heartened by the progress made, the integration of sensory ecology and evolutionary genetics, the creative application of mathematical and genomic tools to questions in this field, and the collaborative nature of these endeavours. We are excited to see what the next 25 years brings.

Acknowledgments

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