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25 Years of sensory drive: the evidence and its watery bias

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Abstract

It has been 25 years since the formalization of the Sensory Drive hypothesis was published in the *American Naturalist* (1992). Since then, there has been an explosion of research identifying its utility in contributing to our understanding of inter- and intra-specific variation in sensory systems and signaling properties. The main tenet of Sensory Drive is that environmental characteristics will influence the evolutionary trajectory of both sensory (detecting capabilities) and signaling (detectable features and behaviors) traits in predictable directions. We review the accumulating evidence in 154 studies addressing these questions and categorized their approach in terms of testing for environmental influence on sensory tuning, signal characteristics, or both. For the subset of studies that examined sensory tuning, there was greater support for Sensory Drive processes shaping visual than auditory tuning, and it was more prevalent in aquatic than terrestrial habitats. Terrestrial habitats and visual traits were the prevalent habitat and sensory modality in the 104 studies showing support for environmental influence on signaling properties. An additional 19 studies that found no supporting evidence for environmental influence on signaling traits were all based in terrestrial ecosystems and almost exclusively involved auditory signals. Only 29 studies examined the complete coevolutionary process between sensory and signaling traits and were dominated by fish visual communication. We discuss biophysical factors that may contribute to the visual and aquatic bias for Sensory Drive evidence, as well as biotic factors that may contribute to the lack of Sensory Drive processes in terrestrial acoustic signaling systems.

Key words: animal communication, sensory drive, sensory ecology, sexual selection

The Origins of Sensory Drive

When reviewing the evidence or impact of a particular scientific hypothesis, it is useful to provide the historical context in which it originated. At the time of the late 1980s, there were three main models for the evolution of female mate choice and the traits that males evolve to secure matings; Fisher's runaway, Direct benefits, and Indirect benefits (good genes). For all three of these, the specific features of the male signal evolved to either genetically run away with female choice genes, indicate direct benefits to females, or indicate indirect benefits to offspring, and the direction of evolution was assumed to be arbitrary (Bradbury *et al.*, 1987). At the time, the purpose of all of these

models was to explain how male signaling traits could become common within a population. Meanwhile, there was little scientific discussion put forth for proposing models to predict which traits, or the specific features of male traits, that would be selected for under sexual selection, nor was there much interest in the effects of the signalling environment and sensory processes.

At the same time that sexual selection models in the 1980s were largely blind to sensory inputs, the field of sensory ecology was already well established and fully focused on how signaling traits and sensory systems are shaped by environments. Interest in the diversity of birdsong led researchers to test whether differential transmission

properties of species' habitats was at the source of this variation ("the environmental selection hypothesis" Morton 1975; Richards and Wiley 1980). Similarly, visual ecology pioneers such as John Lythgoe, William McFarland, and others were taking a highly quantitative approach to determine whether visual pigments covaried with different underwater optical environments (McFarland and Munz 1975; Lythgoe 1979). Given the highly predictive power of sensory ecology coupled with the absence of predictive sexual selection models at this time, it is perhaps not surprising that a number of "sensory-"based models for female mate choice/male signaling trait evolution emerged on the scene in the early 1990s. Endler presented Sensory Drive in a discussion during the Dahlem Conference on Sexual Selection in 1987 and a follow-up symposium (Endler 1992a) from which the first formal description of Sensory Drive emerged (Endler 1992b). The idea spread and features of this model were explored in more detail by several people. Among these were Sensory Exploitation (Ryan and Rand 1990); Pre-existing Bias (Basolo 1990, 1995) and Sensory Traps (Christy 1995). All of these "sensory" models can be placed in the Sensory Drive scheme (see Endler and Basolo 1998 for a comparative review of these models), but for the purposes of this review we will restrict our focus to describing and accumulating evidence for the overall Sensory Drive model (Figure 1). While all sensory or receiver bias models contend that male signal evolution is predicted by female sensory biases, only the Sensory Drive model (described in detail below) explicitly describes from where those sensory biases arise and include the effects of the environment on both the signaller and senses (Endler 1992b; Endler and Basolo 1998).

What is Sensory Drive?

The Sensory Drive model outlined by Endler (1992b, 1993) was a truly comprehensive and predictive model for the origins of communication traits. In this model, *both* signal receiver preference functions *and* signal transmitter traits are predictable characters based on features of a species' environment. The two main components of a communication dyad (receiver behavior and signaling traits) both co-evolve under the constraints of the abiotic (physical) and biotic (predatory and foraging) environment. While this model built upon previous sensory ecology insights into how the environment is likely to shape sensory systems and imposes constraints on signal transmission properties, it broadened the model to include how these environmental features influence key behaviors involved in the sexual selection process (mate choice and display behavior) and put it together in a larger evolutionary model. To quote directly from Endler (1992b), "These suites of traits should coevolve in predictable directions, determined by environmental biophysics, neurobiology and the genetics of the suites of traits- hence the term 'sensory drive'."

The critical feature that encapsulates the Sensory Drive hypothesis is the environment. As shown in Figure 1 (modified from Endler 1992b), the environmental conditions during communication events place selective pressures on the sensory systems to detect important features in its specific habitat (foraging items or other important traits under natural selection) and this influences receiver responses during mate choice encounters. Receivers with a sensory bias shaped by the biophysical properties of their habitat are likely to detect some stimuli better than others. This detection bias will result in receiver biases during mate choice and other choice encounters. For example, males that have communication features that match a female's detectability bias will enjoy a detectability advantage (seen, heard, smelled or felt first and/or with the greatest sensory
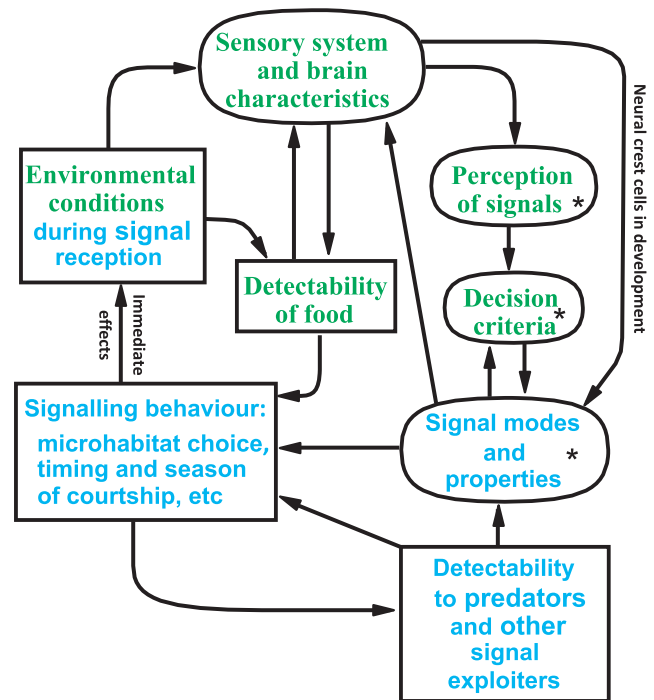
Figure 1. The Sensory Drive Model (modified from Endler 1992b). Steps coded in green represent the sensory component of the Sensory Drive model as the environment places selective forces on the evolution of sensory system properties for food detection but that also influences female mate choice criteria. Steps of the model that incorporate sensory exploitation are indicated by asteriesk. Steps colored in blue represent the signalling component of the Sensory Drive model describing the evolution of signaling characteristics (ornament features, behavioral displays, and choice of microhabitat for display) that are predictable products of environmental constraints and/or responses to environmentally shaped female response biases. Note that the environment is featured in both components (sensory and signal tuning), hence that box is bi-colored. Except for those arrows with text, the arrows indicate evolutionary relationships. The combined effects of microhabitat choice and behaviour have immediate effects on the signalling environment. Neural crest cells affect colour patterns directly but are developmentally related to other cells in the neural system. This is a new component of Sensory Drive.

stimulation); this portion of Sensory Drive is known as Sensory Exploitation (Endler 1992b; Endler and Basolo 1998).

Part of the difficulty in reviewing the presence or absence of support for Sensory Drive is clarifying which portion of the Sensory Drive model is under examination; and/or whether researchers are able to test Sensory Drive in its entirety. There are many interacting steps involved in Sensory Drive (Figure 1) and researchers have taken a number of different approaches or have emphasized different subsets of steps in the model. To organize our discussion we divide Sensory Drive into two components, sensory and signalling. The sensory component of the Sensory Drive model predicts a tight correlation between receiver sensory detection properties and features within a species' physical environment outside the realm of reproduction. The other major component of the Sensory Drive model, the signaling component, relates to the evolution of signaling traits in the communication dyad. It focuses on the strength of environmental constraints in shaping signal evolution to both match environmentally-induced sensory biases of the signal receiver and environmental transmission or other habitat features. Here, we present the evidence that has accumulated over 25 years in more detail, and examine some of the patterns that are emerging across habitats, modalities, and taxa.

Evidence for Sensory Drive

Since the early 1990s, much work has examined whether environmental variation can predict variation in the coevolution of sensory systems and signal design. Recent reviews of the model have found much empirical support for Sensory Drive processes (Cole 2013; Ryan and Cummings 2013; Price 2017), as well as some studies finding little evidence for its role in signal differentiation (Ey and Fischer 2009; Malone et al. 2014). In our review, we decided to examine the evidence for Sensory Drive in its most classic form — with an emphasis on environmental influence. Hence, we have limited our review to studies that examine whether environmental variation can predict variation in sensory tuning, signal characteristics or both. This means that several excellent studies that study Sensory Exploitation/Pre-existing Bias without an environmental component are not included in this current review (e.g., Basolo 1990; Ryan and Rand 1990; Rosenthal and Evans 1998; and others reviewed in Ryan and Cummings 2013). This exclusion is not meant to diminish the importance of Sensory Exploitation *sensu strictu* (the binding glue between sensory and signal coevolution) but rather focus our review around the feature that sets this coevolutionary process in motion (according to Sensory Drive) — the environment. It also allows us to ask questions about habitat bias in Sensory Drive studies, and whether some habitats show more support for Sensory Drive processes than others. We also ask whether certain components in the Sensory Drive model are better supported than others; and whether the support for Sensory Drive is biased for specific sensory modalities or taxonomic groups.

To examine the evidence for Sensory Drive and probe for habitat, modality, and taxonomic bias, we conducted a literature review of empirical studies in the field. For habitat classification, we categorized organisms communicating in either terrestrial or aquatic (both marine and freshwater) ecosystems. We searched for taxonomic bias by comparing the evidence for and against Sensory Drive between invertebrates and the major vertebrate classes; there were insufficient invertebrate studies to subdivide them by taxa. We restricted our analysis to the two most commonly investigated sensory modalities — vision and audition (with a modicum of vibration) due to the relative paucity of studies in other modes such as electroreception and chemoreception. While tests of Sensory Drive within chemoreception are beginning to accumulate (see references within Cole 2013), they are both few and relatively recent and we encourage future reviews to probe for habitat or taxonomic biases for chemosensory Sensory Drive processes.

Overall, we identified 154 studies that examined the evidence for some (or most) steps in the sensory drive model. Of these studies, 132 (86%) found evidence for Sensory Drive and 22 (14%) did not (Tables 1 and 2). While we should expect some portion of this lop-sided ledger to be driven by a reporting bias for positive results, our aim with this review is to identify any patterns that are emerging in terms of where, in what sensory modality, and with what organism do we see greater or lesser support for the sensory drive model. We examine the evidence for and against sensory drive in each of the main components of sensory drive (sensory and signaling) separately as well as the model as a whole. For each of these examinations, we then compare the evidence in terms of habitat, modality and taxonomic support.

Evidence for the environment influencing sensory components

We identified 56 empirical studies (Table 1) that directly tested the sensory component predictions of the sensory drive model (green steps in Figure 1). These studies found overwhelming support for the sensory component of the sensory drive model with 53 studies identifying support of sensory drive while 3 did not. Researchers interested in testing this component of the Sensory Drive hypothesis have often compared biophysical measurements from species-specific habitats with physiological measurements of sensory perception (e.g., Cummings and Partridge 2001; Cheroske et al. 2003; Fuller et al. 2003, 2004; Cummings 2004, 2007; Carleton et al. 2005; Seehausen et al. 2008; Fuller and Noa 2010; Veilleux et al. 2013; Veilleux and Cummings 2012; Bloch 2015; Bloch et al. 2015a; Sandkam et al. 2015; Tuset et al. 2016). Yet, in order to determine if this detectability bias has pleiotropic effects spilling into the sexual selection domain requires determining if these biases play a role in mate choice decisions. A few researchers have comprehensively tested this logistically complex question (e.g., Boughman 2001; Rodd et al. 2002; Garcia and Ramirez 2005; Maan et al. 2006; Seehausen et al. 2008; Arnqvist and Kolm 2010).

Of the studies that found evidence for sensory drive processes influencing sensory system tuning, 57% were in aquatic environments (Figure 2) and 83% involved vision (Figure 3). These studies were also dominated by teleost fish (45%) followed by invertebrates (19%), birds (15%), mammals (9%), and reptiles (8%, Figure 4). Using a Freeman–Halton exact test to compare the evidence for and against the sensory component of sensory drive, we found no significant differences in habitat, modality, or taxonomic group (Table 2). However, given so few studies in the "no evidence" column, a statistical approach to identify patterns is anemic from the beginning. Nonetheless, it is worth noting that the vast majority of these sensory studies fell in the domain of vision. Is this because human researchers are visually biased? Or is it because visual tuning is an easier modality to test in the lab and field? Or does vision respond more to the optical environment than the auditory senses to the auditory environment? Patterns could be entirely different in other sensory modes, for which there are still few data.

Environmental tuning mechanisms favor vision over other modalities?

Is there a mechanistic advantage of vision to respond to the environment more than the other sensory modalities? Vision scientists have been able to document how responsive the visual pathway is to environmental inputs in a number of taxa. Since the 1960s, it has been well documented that many teleosts employ a mixed chromophore strategy (different proportions of A1 and A2 prosthetic groups in photoreceptor outer segments) to tune their spectral sensitivity to ambient light conditions (Dartnall et al. 1961; Bridges 1965, 1972; Munz and Beatty 1965; Allen 1971; Loew and Dartnall 1976; Levine and MacNichol 1979; Muntz and Mouat 1984). More recent work has also shown how differential expression of multiple opsin proteins in photoreceptor outer segments is biased based on optical inputs during development (Carleton and Kocher 2001; Fuller et al. 2004; Shand et al. 2008; Hofmann et al. 2010) as well as dietary influences (Sandkam et al. 2016). And we have become even more aware that sensory tuning can shift across the course of a day (Johnson et al. 2013); or as a function of steroid hormonal exposure (e.g., Friesen et al. 2017).

Note that many of these visual "tuning" mechanisms are restricted to certain aquatic taxa. Some fish and amphibian species contain dual chromophores in their retina (A1 and A2). By changing the ratio of A1:A2 in each photoreceptor's outersegment, these aquatic and semi-aquatic species can tune the absorption maxima of the photoreceptor to match properties of their ambient light

Table 1. Characterization of 154 studies evaluating sensory drive processes by taxonomic grouping, sensory modality, habitat, and whether they demonstrated support for the sensory, signaling components of the sensory drive model.

Major taxonomic group	Species group	Sense	Habitat	Sensory support	Signal support	Citation
Invertebrates	Beetle	Vision	Terrestrial	Yes	Yes	Théry et al. (2008)
Invertebrates	Bladder grasshoppers	Auditory	Terrestrial		Yes	Couldridge and van Staaden (2004)
Invertebrates	Butterflies	Vision	Terrestrial		Yes	Rutkowski et al. (2007)
Invertebrates	Cicadas	Auditory	Terrestrial		No	Sueur and Aubin (2003)
Invertebrates	Crabs	Vision	Terrestrial		Yes	Christy (1988)
Invertebrates	Crabs	Vision	Terrestrial	Yes	Yes	Christy (1995)
Invertebrates	Crabs	Vision	Terrestrial		Yes	Christy et al. (2002)
Invertebrates	Crabs	Vision	Terrestrial	Yes	Yes	Christy et al. (2003)
Invertebrates	Crabs	Vision	Terrestrial			Kim et al. (2007)
Invertebrates	Crickets	Auditory	Terrestrial		No	Forrest (1991)
Invertebrates	Crickets	Auditory	Terrestrial		No	Jain and Balakrishnan (2012)
Invertebrates	Crickets	Auditory	Terrestrial		No	Mendelson and Shaw (2005)
Invertebrates	Green Lacewings	Auditory	Terrestrial		No	Noh and Henry (2010)
Invertebrates	Green Lacewings	Auditory	Terrestrial		No	Henry and Wells (2004)
Invertebrates	Moths	Auditory	Terrestrial	Yes		Conner (1987)
Invertebrates	Water Mites*	Vibratory*	Aquatic	Yes	Yes	Proctor (1991)
Invertebrates	Water Mites*	Vibratory*	Aquatic	Yes	Yes	Proctor (1992)
Invertebrates	Spiders	Vision	Terrestrial		Yes	Scheffer et al. (1996)
Invertebrates	Spiders	Vision	Terrestrial		Yes	Clark (2011)
Invertebrates	Spiders	Vision	Terrestrial		Yes	Wilgers and Hebets (2011)
Invertebrates	Spiders*	Vibratory*	Terrestrial		Yes	Elias et al. (2010)
Invertebrates	Stomatopods	Vision	Aquatic	Yes		Cronin et al. (2001)
Invertebrates	Stomatopods	Vision	Aquatic	Yes		Cronin and Caldwell (2002)
Invertebrates	Stomatopods	Vision	Aquatic	Yes		Cheroske et al. (2003)
Invertebrates	Stomatopods	Vision	Aquatic	Yes		Cheroske et al. (2006)
Invertebrates	Treehoppers*	Vibratory*	Terrestrial		Yes	Sullivan-Beckers and Cocroft (2010)
Invertebrates	Treehoppers*	Vibratory*	Terrestrial		Yes	McNett and Cocroft (2008)
Fish	Characins	Vision	Aquatic	Yes	Yes	Arnqvist and Kolm (2010)
Fish	Lake Malawi Cichlids	Vision	Aquatic	No		Smith et al. (2012)
Fish	Lake Victoria Cichlids	Vision	Aquatic		Yes	Seehausen et al. (1997)
Fish	Lake Victoria Cichlids	Vision	Aquatic	Yes	Yes	Maan et al. (2017)
Fish	Lake Victoria Cichlids	Vision	Aquatic	Yes		Carleton et al. (2005)
Fish	Lake Victoria Cichlids	Vision	Aquatic	Yes	Yes	Seehausen et al. (2008)
Fish	Lake Victoria Cichlids	Vision	Aquatic	Yes	Yes	Maan et al. (2006)
Fish	Goodeids	Vision	Aquatic	Yes	Yes	Garcia and Ramirez (2005)
Fish	Guppies	Vision	Aquatic		Yes	Endler (1980)
Fish	Guppies	Vision	Aquatic	Yes	Yes	Endler (1983)
Fish	Guppies	Vision	Aquatic		Yes	Endler (1987)
Fish	Guppies	Vision	Aquatic	Yes	Yes	Endler (1991)
Fish	Guppies	Vision	Aquatic	Yes	Yes	Endler (1995)
Fish	Guppies	Vision	Aquatic		Yes	Cole and Endler (2016)
Fish	Guppies	Vision	Aquatic		Yes	Long and Rosenqvist (1998)
Fish	Guppies	Vision	Aquatic		Yes	Chapman et al. (2009)
Fish	Guppies	Vision	Aquatic	Yes	Yes	Rodd et al. (2002)
Fish	Guppies	Vision	Aquatic	Yes	Yes	Gamble et al. (2003)
Fish	Guppies	Vision	Aquatic	Yes		Sandkam et al. (2015)
Fish	Killifish	Vision	Aquatic	Yes		Fuller et al. (2003)
Fish	Killifish	Vision	Aquatic	Yes		Fuller et al. (2005)
Fish	Killifish	Vision	Aquatic	Yes	Yes	Fuller and Noa (2010)
Fish	Killifish	Vision	Aquatic		Yes	Fuller (2002)
Fish	Killifish	Vision	Aquatic		Yes	Fuller and Travis (2004)
Fish	Ornate Rainbow Fish	Vision	Aquatic		Yes	Hancox et al. (2013)
Fish	Reef fish	Vision	Aquatic	Yes	Yes	Marshall (2000)
Fish	Rockfish	Auditory	Aquatic	Yes		Tuset et al. (2016)
Fish	Southern Pygmy perch	Vision	Aquatic		Yes	Morrongiello et al. (2010)
Fish	Sticklebacks	Vision	Aquatic		Yes	Reimchen (1989)
Fish	Sticklebacks	Vision	Aquatic	Yes	Yes	Boughman (2001)
Fish	Sticklebacks	Vision	Aquatic	Yes	Yes	Smith et al. (2004)
Fish	Sticklebacks	Vision	Aquatic	Yes		Veen et al. (2017)
Fish	Sticklebacks	Vision	Aquatic	Yes	Yes	Brock et al. (2017)

(continued)

Table 1. (continued)

Major taxonomic group	Species group	Sense	Habitat	Sensory support	Signal support	Citation
Fish	Suluwesi Fish	Vision	Aquatic		Yes	Gray et al. (2008)
Fish	Surfperch	Vision	Aquatic	Yes		Cummings and Partridge (2001)
Fish	Surfperch	Vision	Aquatic	Yes		Cummings (2004)
Fish	Surfperch	Vision	Aquatic	Yes	Yes	Cummings (2007)
Amphibians	Bolivian frogs	Auditory	Terrestrial		No	Bosch and Riva (2004)
Amphibians	Central Amazon frogs	Auditory	Terrestrial		No	Zimmerman (1983)
Amphibians	Central Amazon frogs	Auditory	Terrestrial		No	Kime et al. (2000)
Amphibians	Chorus frogs	Auditory	Terrestrial		No	Malone et al. (2014)
Amphibians	Concave-eared Torrent frog	Auditory	Terrestrial	Yes	Yes	Feng et al. (2006)
Amphibians	Cricket frogs	Auditory	Terrestrial		Yes	Ryan et al. (1990)
Amphibians	Cricket frogs	Auditory	Terrestrial		Yes	Gamble et al. (2008)
Amphibians	Cricket frogs	Auditory	Terrestrial	Yes		Witte et al. (2005)
Amphibians	Green toads	Auditory	Terrestrial		No	Castellano et al. (2003)
Amphibians	Poison Frogs	Vision	Terrestrial		Yes	Maan and Cummings (2012)
Amphibians	Poison Frogs	Vision	Terrestrial		Yes	Cummings and Crothers (2013)
Amphibians	Rock Frogs	Vision	Terrestrial		Yes	Grafe et al. (2012)
Amphibians	Rock skipper frog	Auditory	Terrestrial		Yes	Boeckle et al. (2009)
Amphibians	South American frogs	Auditory	Terrestrial		No	Penna and Solis (1998)
Amphibians	Streambank frogs	Auditory	Terrestrial		Yes	Odendaal et al. (1986)
Amphibians	Thailand frogs	Auditory	Terrestrial		Yes	Sun and Narins (2005)
Amphibians	Toads	Auditory	Terrestrial		Yes	Ryan and Sullivan (1989)
Amphibians	Treefrogs	Auditory	Terrestrial		Yes	Ziegler et al. (2011)
Amphibians	Tree-hole frogs	Auditory	Terrestrial		Yes	Lardner and Lakim (2002)
Reptiles	Anolis lizards	Vision	Terrestrial	Yes	Yes	Sigmund (1983)
Reptiles	Anolis lizards	Vision	Terrestrial	Yes	Yes	Leal and Fleishman (2002)
Reptiles	Anolis lizards	Vision	Terrestrial	No		Steinberg and Leal (2016)
Reptiles	Anolis lizards	Vision	Terrestrial	Yes	Yes	Fleishman (1992)
Reptiles	Anolis lizards	Vision	Terrestrial	Yes	Yes	Leal and Fleishman (2004)
Reptiles	Anolis lizards	Vision	Terrestrial		Yes	LeBas and Marshall (2000)
Reptiles	Anolis lizards	Vision	Terrestrial		Yes	Ord et al. (2007)
Reptiles	Anolis lizards	Vision	Terrestrial		Yes	Peters and Evans (2003)
Reptiles	Anolis lizards	Vision	Terrestrial		Yes	Peters et al. (2007)
Reptiles	Chameleons	Vision	Terrestrial		Yes	Stuart-Fox et al. (2007)
Reptiles	Chameleons	Vision	Terrestrial		Yes	Stuart-Fox and Moussalli (2008)
Birds	Amazonian birds	Auditory	Terrestrial		Yes	Tobias et al. (2010)
Birds	American redstarts	Auditory	Terrestrial		No	Date and Lemon (1993)
Birds	Antbirds	Auditory	Terrestrial		Yes	Nemeth et al. (2001)
Birds	Blue tits	Auditory	Terrestrial		No	Doutrelant and Lambrechts (2001)
Birds	Bowerbirds	Vision	Terrestrial	Yes	Yes	Madden and Tanner (2003)
Birds	Bowerbirds	Vision	Terrestrial	Yes	Yes	Endler and Day (2006)
Birds	Bowerbirds	Vision	Terrestrial		Yes	Doucet and Montgomerie (2003)
Birds	Bowerbirds	Vision	Terrestrial		Yes	Endler et al. (2010)
Birds	Bowerbirds	Vision	Terrestrial		Yes	Kelley and Endler (2012)
Birds	Bowerbirds	Vision	Terrestrial		No	Borgia and Keagy (2006)
Birds	Carolina Wren	Auditory	Terrestrial		Yes	Gish and Morton (1981)
Birds	Chickens	Vision	Terrestrial	Yes		Hart et al. (2006)
Birds	Finches	Auditory	Terrestrial		Yes	Snell-Rood and Badyaev (2008)
Birds	Finches	Auditory	Terrestrial		No	Podos (2010)
Birds	Flycatchers	Auditory	Terrestrial		Yes	Francis et al. (2011)
Birds	Forest Birds	Auditory	Terrestrial		Yes	Ryan and Brenowitz (1985)
Birds	Forest Birds	Vision	Terrestrial		Yes	Endler and Théry (1996)
Birds	Forest Birds	Vision	Terrestrial		Yes	Gomez and Théry (2004)
Birds	Forest Birds	Vision	Terrestrial		Yes	Gomez and Théry, 2007.
Birds	Forest Birds	Vision	Terrestrial		Yes	Uy and Stein (2007)
Birds	Great tits	Auditory	Terrestrial	Yes	Yes	Mockford and Marshall (2009)
Birds	Great tits	Auditory	Terrestrial		Yes	Slabbekoorn and Peet (2003)
Birds	Great tits	Auditory	Terrestrial		Yes	Slabbekoorn and der Boer-Vissor (2006)
Birds	Green hylia	Auditory	Terrestrial		Yes	Kirschel et al. (2009)
Birds	Grey breasted wood wren	Auditory	Terrestrial		Yes	Dingle et al. (2008)
Birds	House finches	Auditory	Terrestrial		Yes	Bermudez-Cuamatzin et al. (2011)
Birds	Juncos	Auditory	Terrestrial		Yes	Slabbekoorn et al. (2007)

Table 1. (continued)

Major taxonomic group	Species group	Sense	Habitat	Sensory support	Signal support	Citation
Birds	Mannakins	Vision	Terrestrial		Yes	Uy and Endler (2004)
Birds	Mannakins	Vision	Terrestrial		Yes	Heindl and Winkler (2003)
Birds	Nightingales	Auditory	Terrestrial		Yes	Brumm (2004)
Birds	Nightingales	Auditory	Terrestrial		Yes	Sorjonen (1986)
Birds	North American oscines	Auditory	Terrestrial		Yes	Wiley (1991)
Birds	Robins	Auditory	Terrestrial		Yes	Fuller et al. (2007)
Birds	Silvereyes	Auditory	Terrestrial		Yes	Potvin et al. (2011)
Birds	Song Sparrows	Auditory	Terrestrial		Yes	Shy and Morton (1986)
Birds	Song Sparrows	Auditory	Terrestrial		Yes	Patten et al. (2004)
Birds	South African birds	Auditory	Terrestrial		No	Saunders and Slotow (2004)
Birds	Warblers	Vision	Terrestrial		Yes	Marchetti (1993)
Birds	Warblers	Auditory	Terrestrial		No	Fotheringham et al. (1997)
Birds	Warblers	Vision	Terrestrial	Yes		Bloch (2015)
Birds	Warblers	Vision	Terrestrial	Yes		Bloch et al. (2015a)
Birds	Warblers	Vision	Terrestrial	Yes		Bloch et al. (2015b)
Birds	Warblers	Vision	Terrestrial	Yes		Price (2017)
Birds	White Crown Sparrows	Auditory	Terrestrial		Yes	Derryberry (2009)
Mammals	Baboons	Auditory	Terrestrial		Yes	Ey et al. (2009)
Mammals	Bats	Auditory	Terrestrial	Yes		Arlettaz et al. (2001)
Mammals	Bats	Auditory	Terrestrial	Yes		Jacobs et al. (2017)
Mammals	Bats	Auditory	Terrestrial	No		Puechmaille et al. (2011)
Mammals	Japanese macaques	Auditory	Terrestrial		Yes	Sugiura et al. (2006)
Mammals	Lemurs	Vision	Terrestrial	Yes		Veilleux et al. (2013)
Mammals	Marmots	Auditory	Terrestrial		Yes	de la Torre and Snowdon (2002)
Mammals	Marmots	Auditory	Terrestrial		Yes	Daniel and Blumstein (1998)
Mammals	New World Monkeys	Auditory	Terrestrial		Yes	Brumm et al. (2003)
Mammals	Nocturnal mammals	Vision	Terrestrial	Yes		Veilleux and Cummings (2012)
Mammals	Primates	Vision	Terrestrial	Yes		Fernandez and Morris (2007)
Mammals	Primates	Auditory	Terrestrial		Yes	Waser and Waser (1977)
Mammals	Primates	Auditory	Terrestrial		Yes	Mitani and Stuht (1998)
Mammals	Rain forest monkeys	Auditory	Terrestrial		Yes	Brown et al. (1995)
Mammals	Savannah monkeys	Auditory	Terrestrial		No	Brown et al. (1995)
Mammals	Whales	Auditory	Aquatic		Yes	Miller et al. (2000)

Asterisk refers to examples of sensory drive that involve the vibratory sensory system (included in this table, but not included for statistical analyses in table 2 owing to small numbers).

conditions. Evidence for chromophore mixing to match spectral properties of the underwater environment has been found in freshwater (Bridges 1972; Loew and Dartnall 1976), saltwater (Cummings and Partridge 2001) and anadromous fish (Munz and Beatty 1965; Muntz and Mouat 1984). Furthermore, teleosts have shown greater plasticity than any other taxon in spectral tuning via differential expression in opsin proteins within their photoreceptors (Fuller et al. 2004, 2010; Hofmann et al. 2009, 2010; Carleton 2009; Parry et al. 2005). Moreover, marine invertebrates, such as stomatopods, have multiple means to alter spectral sensitivity via modification to intrarhabdomal filters, allowing for extensive tunability (Cronin et al. 2001; Marshall et al. 2007).

While terrestrial vertebrates (amphibians, reptiles, birds, and mammals) do not possess as many tuning mechanisms as some of the marine organisms [e.g., only a single chromophore (A1)], they still exhibit tunable variation in visual sensitivities. Warblers exhibit differential opsin expression between species that vary in optical habitats (Bloch 2015), as well as genetic variation in opsin genes that is functionally linked to changes in habitat use (Bloch et al. 2015a). Birds, in general, exhibit tremendous genetic variation in UV-sensitive cone opsins (SWS1, Hart and Hunt 2007), and variation in the proportion of different photoreceptor cone types. This

variation has been attributed to variation in foraging ecology (Hart 2001). Furthermore, many birds and reptiles contain pigmented oil droplets in the inner segments of their photoreceptors that reduce the intensity and narrow the spectrum of light impinging upon the visual pigment in the outer segment (Liebman and Granda 1971; Bowmaker 1977; Loew et al. 2002); and the amount of this inner segment colored pigment appears to vary by ambient light intensity (Hart et al. 2006).

Interestingly, there is robust evidence of olfactory systems being tuned to their physical environment. Since early work in the 1970s (Scholz et al. 1976), we have seen that the fish olfactory epithelium responds to sensory input by a positive feedback process that allows salmon to tune their olfactory pathway to detect the olfactory signatures of their specific birth tributary (Harden et al. 2006). The olfactory system may well be set up to be primed by early developmental conditions to recognize certain odors for later olfactory discrimination (e.g., kin selection, Hinz et al. 2013). In fact, this phenomenon may occur in a variety of taxa, including insects at various developmental stages (Davis and Stamps 2004).

What is the evidence for sensory tuning to the acoustic environment? It is clear that the auditory systems from invertebrates (Schmidt et al. 2011) to vertebrates (Witte et al. 2005; Bar-Yosef

Table 2. Results of freeman-halton exact test results comparing differences in habitat, modality, and taxonomic group characteristics of supporting (yes) and non-supporting (no) studies testing the sensory (A), signaling (B), or both components (C) of the sensory drive model

A. Number studies testing the first component of Sensory Drive (Sensory systems tuned to environmental parameters)

Habitat	Yes	No	$P = 0.58$
Aquatic	30	1	
Terrestrial	23	2	
Order	Yes	No	$P = 0.31$
Invertebrates	10	0	
Fishes	24	1	
Amphibians	2	0	
Reptiles	4	1	
Birds	8	0	
Mammals	5	1	
Sense	Yes	No	$P = 0.33$
Vision	44	2	
Auditory	7	1	

B. Number of studies testing the second component of Sensory Drive (Signalling traits varying by environmental parameters)

Habitat	Yes	No	$P = 0.0036$
Aquatic	30	0	
Terrestrial	74	19	
Order	Yes	No	$P = 0.0055$
Invertebrates	14	6	
Fishes	27	0	
Amphibians	12	6	
Reptiles	10	0	
Birds	32	6	
Mammals	9	1	
Sense	Yes	No	$P < 0.0001$
Vision	59	1	
Auditory	40	18	

C. Number of studies testing both components of Sensory Drive (sensory and signaling coevolution)

Habitat	Yes	No	n.a.
Aquatic	18	0	
Terrestrial	11	0	
Order	Yes	No	n.a.
Invertebrates	5	0	
Fishes	16	0	
Amphibians	1	0	
Reptiles	4	0	
Birds	3	0	
Mammals	0	0	
Sense	Yes	No	n.a.
Vision	25	0	
Auditory	2	0	

Note vibratory studies listed in Table 1 are excluded for this analysis; and n.a. refers to inapplicability of the statistical test when only 1 column has numbers > 0.

and Nelken 2007; Mockford and Marshall 2009) are modified by background noise levels. Auditory systems can be selectively tuned to respond to conspecific signals (e.g., auditory imprinting, Batista et al. 2016), as well as be modified by steroid hormones (Coffin et al. 2012). And some of the best examples of sensory tuning to the environment include the evolution of selective ultrasonic hearing capabilities among several species preyed upon by echolocating bats (Conner 1987; Windmill et al. 2006).
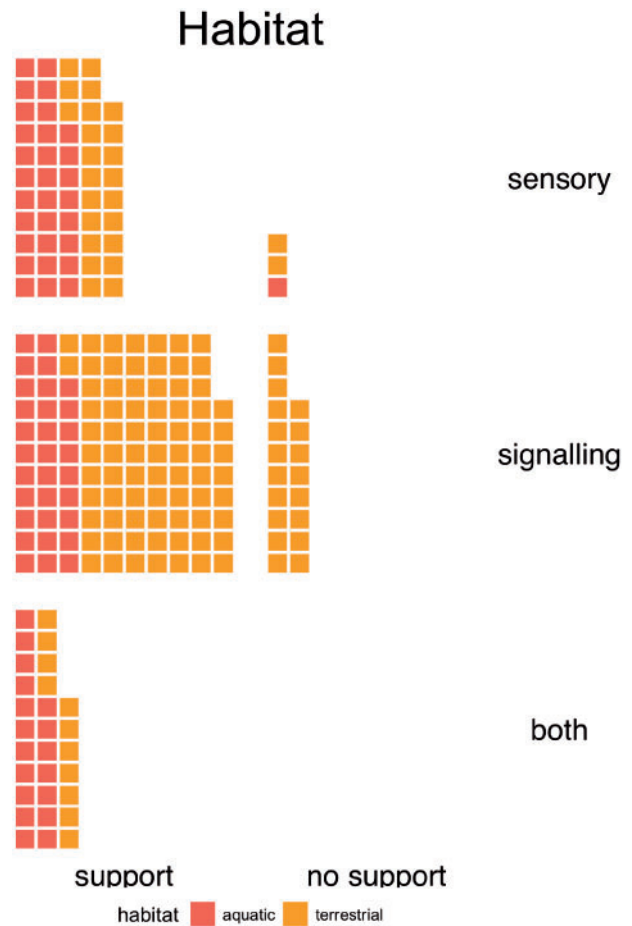
Figure 2. Frequency waffle plots of studies supporting and not supporting the sensory drive model by aquatic (red) or terrestrial (orange) habitats, including studies that evaluated the sensory component of the sensory drive model, studies that evaluated the signaling components of the sensory drive model, and studies that evaluate the complete model (both major components). Note for color blind readers (either deutanomaly or protanomaly) the aquatic blocks will appear a dark green and the terrestrial a dark yellow).

Evidence for the environment influencing signal components

Our literature search found more than twice the number of studies exploring the signal components of the sensory drive model than the sensory components (Table 1, Figures 2–4). We identified 126 empirical studies that directly tested the signal predictions of the sensory drive model (blue components in Figure 1). Of these studies, 107 found support for sensory drive while 19 did not. Many researchers have tested this part of sensory drive by examining correlational patterns between male signaling characteristics and environmental parameters (Table 1: Morton 1975; Gish and Morton 1981; Reimchen 1989; Wiley 1991; Fleishman 1992; Marchetti 1993; Seehausen et al. 1997; Slabberkoorn and Peet 2003; Fuller 2002; Leal and Fleishman 2004; Gomez and Théry 2004, 2007; Ord et al. 2007; Stuart-Fox et al. 2007; Gray et al. 2008; Derryberry 2009; Ey et al. 2009; Elias et al. 2010; Morrongiello et al. 2010; Tobias et al. 2010; Potvin et al. 2011; Hancox et al. 2013; Brock et al. 2017); or species-specific detection biases (Madden and Tanner 2003; Feng et al. 2006; Cummings 2007; Arnqvist and Kolm 2010), or female mate preference functions (Boughman 2001; Maan et al. 2006; Seehausen et al. 2008; Kelley and Endler 2012).
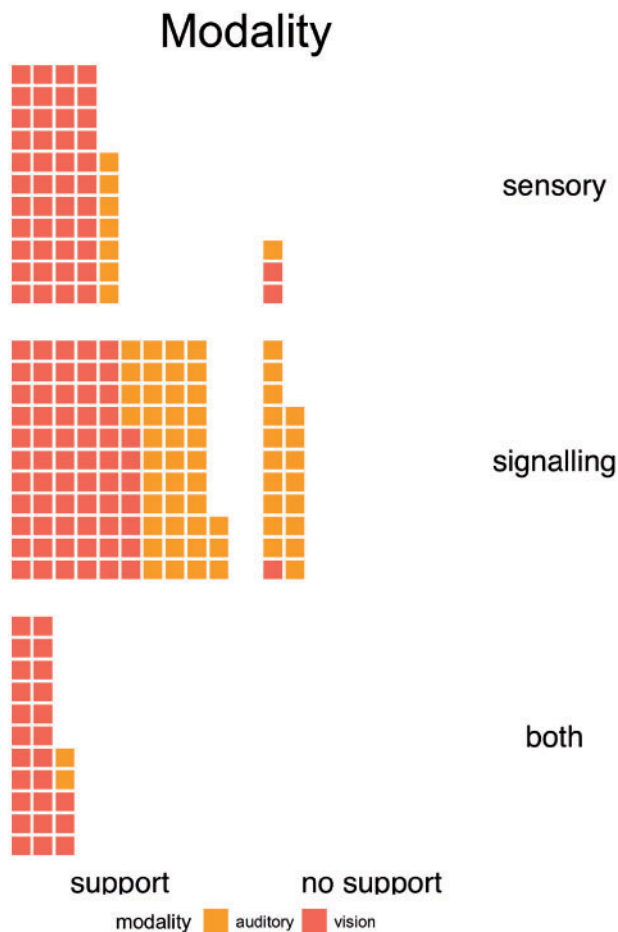
Modality

Figure 3. Frequency waffle plots of studies supporting and not supporting the sensory drive model by sensory modality [vision (red), auditory (orange)] including studies that evaluated the sensory component of the sensory drive model, studies that evaluated the signaling components of the sensory drive model, and studies that evaluate the complete model (both major components). Note for color blind readers (either deutanomaly or protanomaly) the vision blocks will appear a dark green and the auditory a dark yellow).

Still others have focused on the time and place of male signaling, to determine whether or not signaling behavior maximizes conspicuousness to females (Endler and Théry 1996; Long and Rosenqvist 1998; Doucet and Montgomerie 2003; Heindl and Winkler 2003; Lardner and Lakim 2002; Uy and Endler 2004; Sun and Narins 2005; Heinsohn et al. 2005; Ord et al. 2007; Peters et al. 2007; Rutkowski et al. 2007; Chapman et al. 2009; Cole and Endler 2016).

Of the supporting studies, 71% were in terrestrial systems (Figure 2), 57% involved visual signaling (Figure 3), and taxonomic representation was quite broad (31% birds, 26% fish, 13% invertebrates, 12% amphibians, 10% reptiles, and 9% mammals, Figure 4). All of the 19 studies finding no support for sensory drive were in terrestrial environments and 95% (18) involved auditory signals across three taxonomic groups (invertebrates, amphibians, and birds). Comparing the supporting and non-supporting studies (Table 2), we found significant non-independence of support by habitat ($P = 0.0036$), modality ($P < 0.0001$), and taxon ($P = 0.0055$).

The terrestrial environment dominated the studies finding support for the signal components of the sensory drive model

(Figure 2). This is a reverse pattern from the relative habitat representation observed for sensory component studies (Figure 2). Why the difference? The difference may be a matter of human accessibility between these two habitats. Or simply driven by the taxonomic foci of different researchers (e.g., birds, reptiles, amphibians, and several invertebrate orders are not found in the sea). In addition, acoustic signaling is far more common in the terrestrial environment than the aquatic environment, allowing signal researchers a broader range of signal forms to study. While recent research is beginning to discover the broad range of underwater sounds (Smith and van Staaden 2009; Danley et al. 2012), the field of underwater acoustics is still nascent relative to the long history of studying amphibian, bird, and insect calls in terrestrial habitats.

3.4 Auditory signals and the biotic versus abiotic design pressures

The terrestrial environment significantly dominated the category of non-supporting sensory drive studies concentrating on signal components ($P = 0.0036$, Table 2). The high concentration of these non-supporting studies involved auditory signals, a pattern that significantly deviated from random expectations ($P < 0.0001$; Table 2). Why do we find a disproportionate number of auditory studies (of which most are in terrestrial environments) representing this category of no support for sensory drive? One important feature to consider is how sensory modes differ; auditory signals frequently compete simultaneously with both biotic and abiotic noise. Unlike a visual signal, which is directional and whose detection is based on how it is perceived against highly localized abiotic backgrounds (the adjacent surrounding area), auditory signals are essentially omnidirectional so it is more difficult to disentangle them from background noise coming from all directions. It is the competition to stand out against the biotic din of competing signals that has been shown to be the dominant predictor of divergence in a number of different auditory signalling systems (e.g., insects: Greenfield 2015; frogs: Wollerman and Wiley 2002; Amézquita et al. 2011; Malone et al. 2014; birds: Luther 2009; Grant and Grant 2010). As a general rule, acoustic signal reception has to contend with significantly more biotic interactions than visual signals. Hence, signal design in ecosystems crowded with auditory communicators should be associated with the biotic environmental soundscape being the better predictor for signal differentiation than the abiotic factors. This has been born out in a number of different animal taxa (Amézquita et al. 2011; Wilkins et al. 2013). One of the most thorough examinations of this principle comes from a large-scale comparison of 82 species of tropical forest birds, wherein Luther (2009) found that bird song divergence at dawn chorus was predicted by the composition of competing songs at each given time interval, rather than physical location or phylogenetic relatedness. Hence, for auditory signaling, the communication environment is often dominated by biotic factors more than abiotic features, and it is the selective factor driving signal diversification in predictable directions. However, auditory evolution may be less predictable than visual signal evolution because the auditory biotic factors are often more variable in space, and in both short-term and evolutionary time, than the largely physical factors affecting vision.

Evidence for complete sensory drive model (co-evolution of sensory and signaling features)

Of the 154 studies examining sensory drive processes, 29 tested and found support for the complete sensory drive model (Table 1).
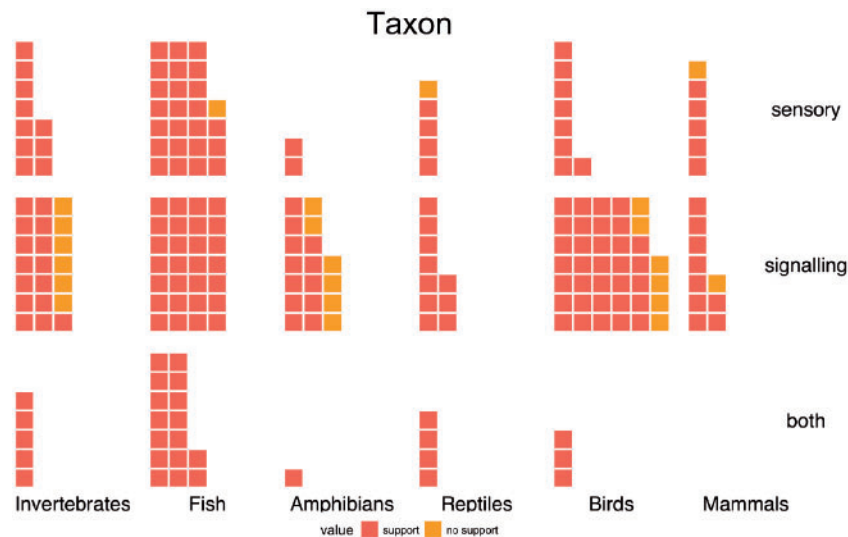
Figure 4. Frequency waffle plots of studies supporting and not supporting the sensory drive model by taxonomic group [supporting (red) and non-supporting (orange)] including studies that evaluated the sensory component of the sensory drive model, studies that evaluated the signalling components of the sensory drive model, and studies that evaluate the complete model (both major components). Note for color blind readers (either deuteranomaly or protanomaly) the supporting blocks will appear a dark green and the non-supporting a dark yellow).

Either tests not supporting the full model haven't yet been conducted or the authors could not publish their negative results. The supporting studies were overwhelmingly focused in visual traits (86%, Figure 3) with a bias for aquatic environments (62%, Figure 2) and a majority (55%, Figure 4) of fish representatives [followed by invertebrates (17%), reptiles (14%), birds (10%), and amphibians (3%)].

The close similarity between characteristics of studies finding support for sensory components and the complete sensory drive model is not surprising. After all, the sensory drive model starts with the environment placing a directional change on sensory systems in specific environmental conditions. To find evidence for the complete Sensory Drive model, one needs to first find a match between sensory system bias predicted by environmental constraints and then a match between signals and that environmentally induced sensory bias. To tackle both components is a daunting endeavor, so it should come as no surprise that the subset of studies that completed this challenge is not very large (about 1 per year since the inception of Sensory Drive).

It is also not surprising that the majority of these few "full support studies" are mostly in aquatic environments. Since the early days of sensory drive, it was noted that aquatic environments place a more constraining force on the sensory environment than terrestrial habitats, particularly in visual systems. The water medium, unlike air, differentially absorbs and scatters wavelengths of light as a function of depth as well as biotic and abiotic factors in the water medium itself, such as tannins. Phytoplankton and zooplankton blooms along with detritus and other inorganic materials can also stain the waters in particular ways, leaving a very limited optical spectrum for the visual senses to process. When spectra are restricted, then sensory systems have fewer options for tuning and the predicted direction of tuning and signals becomes predictable based on first principles. However, when the spectrum is broad, the system is permissive and multiple solutions are equally plausible (Endler 1993a,1993b).

A comparison across the different types of cichlid fish and the optical environments they inhabit demonstrate this principle quite well. The Lake Victorian cichlids differ in optical environment due to a predictable (and unidirectional) change in ambient spectra with depth. As species-specific depth ranges increase, ambient spectral bandwidth becomes narrower and redder. In this system, visual pigments follow this depth gradient shift as well as predictable shifts in male color reflectance to contrast against the shift in background spectra (Seehausen et al. 2008) that is also reflected in female choice for these signals (Maan et al. 2006). Meanwhile, in the Lake Malawi cichlids that inhabit clearer waters with a broader spectrum of ambient light, the optical environment is less constrained, and the multiple (6 main opsins) show no correlated pattern with expression and optical environment (Smith et al. 2012). This point was brought up by Endler in the early stages of Sensory Drive (Endler 1993a, 1993b), that environments that are optically constrained to narrow irradiance spectra favor a very specific color component for signal evolution, whereas environments containing broad spectra are very permissive, favouring diversity and making predictions more difficult. This same principle explains why there is strong support for sensory drive in the surfperch fishes optically extreme environment of an underwater kelp forest (Cummings 2007), yet more muted support in birds dwelling in tropical terrestrial forests (Gomez and Théry 2004; Maia et al. 2016).

Conclusions and Future Directions

There is broad support for the process of sensory drive in a variety of taxa and environments but the distribution among taxa and environments is uneven. The unevenness results from variation among habitats as well as in sensory capacities and sensory biophysics. Some combinations restrict what form sensory drive can take, making it predictable, but other combinations are very permissive, making predictions difficult or impossible. There may even be a tradeoff between environmental constraints and diversity. This predicts more diversity of senses and signals, and more diversity of species, in permissive habitats and species with multiple sensory modes than those with fewer modes or which live in more restrictive

habitats. These ideas need testing in as many taxa and habitats as possible. We also note that there is comparatively little work on sensory drive in chemoreception, vibration reception, and electroreception, and little work on the evolution of microhabitat and habitat choice relative to sensory drive. There is clearly a lot more to be done in exploring the directions and rates of sensory drive.

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