

## Article

# Evolutionary ecology of chemosensation and its role in sensory drive

Laurel R. YOHE<sup>a,b,\*</sup> and Philipp BRAND<sup>c,\*</sup>

<sup>a</sup>Department of Ecology and Evolution, Stony Brook University, Stony Brook, NY 11790, USA, <sup>b</sup>Department of Geology & Geophysics, Yale University, New Haven, CT 06511, USA and <sup>c</sup>Department of Evolution and Ecology, Center for Population Biology, University of California, Davis, CA 95616, USA

Address correspondence to Laurel R. Yohe. E-mail: laurel.yohe@stonybrook.edu; laurel.yohe@yale.edu

\*Both the authors equally contributed to this article.

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## Abstract

All behaviors of an organism are rooted in sensory processing of signals from its environment, and natural selection shapes sensory adaptations to ensure successful detection of cues that maximize fitness. Sensory drive, or divergent selection for efficient signal transmission among heterogeneous environments, has been a useful hypothesis for describing sensory adaptations, but its current scope has primarily focused on visual and acoustic sensory modalities. Chemosensation, the most widespread sensory modality in animals that includes the senses of smell and taste, is characterized by rapid evolution and has been linked to sensory adaptations to new environments in numerous lineages. Yet, olfaction and gustation have been largely underappreciated in light of the sensory drive hypothesis. Here, we examine why chemosensory systems have been overlooked and discuss the potential of chemosensation to shed new insight on the sensory drive hypothesis and vice versa. We provide suggestions for developing a framework to better incorporate studies of chemosensory adaptation that have the potential to shape a more complete, coherent, and holistic interpretation of the sensory drive.

**Key words:** chemical signaling, chemoreceptor, chemosensation, sensory drive, olfaction

## Introduction

All animals must find food and reproduce while avoiding predators and pathogens that threaten their survival. Sensing, perceiving, and processing environmental cues are critical to these fitness-related behaviors (Dangles et al. 2009). However, environmental stimuli must be filtered in cluttered environments in which relevant cues may be drowned out by many extraneous signals (Endler 1992). Fine-tuned sensory systems are required to filter and maximize the detection of cues and signals that are important for survival and reproduction. In a heterogeneous world, signal and noise can be highly habitat-specific. Sensory systems can play a critical role in controlling the functional ecology of an organism as a response to new or changing environments, leading to local adaptation, sexual

selection, and eventually speciation (Endler 1992; Endler and Basolo 1998; Boughman 2002).

The sensory drive hypothesis, first presented by Endler (1992), provides a framework to articulate how evolution influences signal production and signal detection in a dynamic world and predicts that selection favors mechanisms that facilitate communication depending on the environmental background. The coadaptation of highly specific signals and sensory systems with respect to background “noise” may even establish barriers to gene flow between populations in different environments and eventually lead to speciation (Boughman 2002; Fuller et al. 2005). Although there are numerous examples of visual and acoustic sensory systems that evolved via sensory drive (Kingston et al. 2001; Scott 2001; Fuller et al. 2005; Seehausen et al. 2008; Tobias et al. 2010; Wilkins et al. 2013; Price 2017), the effects

of sensory drive on the evolution of other sensory modalities have been largely neglected in this context (Dangles et al. 2009; Cummings and Endler 2018). Chemosensation, although arguably the most commonly used sensory modality in animals (Hildebrand and Shepherd 1997; Yarmolinsky et al. 2009), has received little attention in the sensory drive literature, and we argue that this is largely due to a combination of methodological difficulties in assessing environmental chemical diversity and the complexity of chemical signals and perception mechanisms relative to acoustic and visual systems.

Chemosensation involves the transduction of a chemical stimulus from the environment into a neurological signal interpreted by the organism. Chemosensory systems directly interact with environmental chemical cues and regulate behaviors essential for survival and reproduction, such as finding food, avoiding predators, identifying conspecifics, caring for offspring, and attracting mates (Hart and Chao 2010; Hansson and Stensmyr 2011; Li and Liberles 2015; Meister 2015). Chemosensation is ubiquitous across the Tree of Life, from a unicellular budding yeast that initiates mating with a chemical signal (Bardwell 2004), to male orchid bees collecting environmental scents to produce their own “perfume” (Vogel 1965; Eltz et al. 1999; Roubik and Hanson 2004); from a female garter snake that chemically signals reproductive viability (Parker and Mason 2014), to felines rubbing facial pheromones to mark territory (Soini et al. 2012). This great diversity highlights the important role of chemosensation in fitness-related behaviors (Figure 1), and it is highly likely that the sensory drive hypothesis influences the evolution of the senses of smell and taste and chemical signaling in animals. Rapid rates of molecular evolution and exceptional gene turnover through duplication and loss of chemical-detecting receptor genes lay the groundwork for rapid local adaptation that may even influence sexual selection and facilitate reproductive isolation. Yet, how environmental conditions and the chemical background interfere with or facilitate signal transmission and detection are relatively unexplored. Here, we highlight the underestimated, yet pervasive role of chemosensation in sensory adaptation and how it can be tested in light of the sensory drive hypothesis.

## Challenges in Bringing Chemosensation to Sensory Drive

Variation in signal production, signal transmission, and signal detection is shaped by natural selection in heterogeneous environments. The sensory drive hypothesis predicts that the local adaptation of signals and signal detection can evolve within populations of the same species in differing environments due to environmentally mediated divergent selection on signaling specialization. There are three predictions of the sensory drive hypothesis:

1. habitat-induced background “noise” influences efficient signal transmission and signal detection;
2. divergent selection on sensory perception in response to heterogeneous sensory environments leads to local adaptation of sensory systems; and
3. altered perception abilities and specializations select for signals that match changes in perception, which in turn may eventually lead to reproductive isolation between lineages.

The past and current focus on visual and acoustic systems has revealed convincing evidence for sensory drive as a mechanism in sensory-mediated local adaptation and also reproductive isolation (Boughman 2002; Dangles et al. 2009). Yet, chemosensory evolution has been virtually untested under the sensory drive hypothesis,

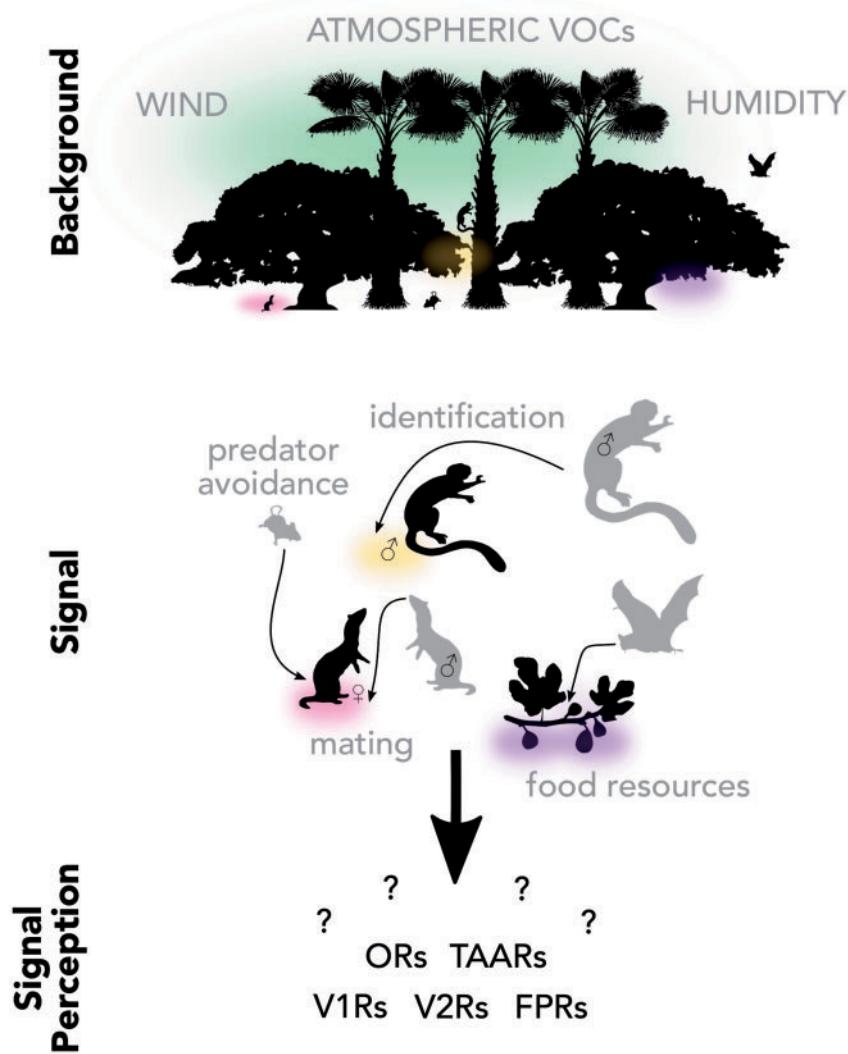
despite its relevance in the functional ecology across animals. We argue that there are two main reasons for this: 1) chemical background, chemical signals, and chemosensory gene function and evolution are highly complex in comparison to vision and hearing, which makes the connection between environmental changes and sensory evolution more convoluted and 2) sophisticated methods to reliably determine chemical background, signals, and gene function are only recently emerging. We argue that with the development of methods to analyze and integrate environmental chemicals and chemical signals with the molecular evolution and function of chemosensory genes, we are at an exciting point in time where it is becoming increasingly feasible to test the extent of sensory drive in chemosensory evolution and thus better understand the role of sensory drive in sensory evolution in general.

### Challenge #1: the complexity of the chemical background

A key component of sensory drive is the influence of the environment on the evolution of signals and signal detection. Chemical signals and cues must stand out against the chemical background, and the recipient must detect the cue in time before the signal is diffused (Figure 1). The chemical environment is a dynamic and complex system influenced by various abiotic and biotic factors. Besides spatial variation of the abundance and composition of biotic chemicals between (micro-) habitats (Guenther 1997; Kesselmeier and Staudt 1999), the chemical environment varies across time (Proffit et al. 2008; Riffell et al. 2008), and is significantly influenced by rapidly changing and highly interconnected abiotic conditions including temperature, humidity, and wind (Cetin et al. 2003). Diurnal convection dynamics of the atmosphere influence how chemicals move through the air, such that the movement of chemicals at sunrise will not be the same as at sunset (Riffell et al. 2008). Similarly, water turbulence has a critical impact on chemical concentrations in aquatic systems (Weissburg and Zimmer-Faust 1993; Zimmer-Faust et al. 1995). Furthermore, while influencing atmospheric movements and air pressure, temperature alters the chemical background on the basis of volatility (the tendency of a chemical to evaporate), which varies with molecular weight and functional groups.

In addition to the chemical background, abiotic factors also affect animal physiology and perception abilities. Humidity has been shown to be critical to olfaction in hermit crabs leading to low electrophysiological responses of the antenna when humidity is low (Krång et al. 2012). Although this might present a special case due to a recent shift from a marine to terrestrial lifestyle, it demonstrates how the chemical environment not only changes but also is perceived differently with respect to changes in physical abiotic factors.

This complexity renders the characterization and quantification of the chemical background and the transmission efficiency of chemical signals through the background of a nontrivial task (Riffel et al. 2008). The demonstration of empirical evidence of sensory drive and the effects of the chemical background on signal transmission will require the determination of multiple complex environmental factors that are highly specific to the organism, locality, and time. Although the qualification and quantification of light and sound are highly standardized through measurements of well-known physical properties (i.e., waves, wavelengths, and amplitudes), there is presently no unbiased way of capturing the entire breadth of chemicals from the environment, presenting a significant challenge for testing the effects of sensory drive on chemosensory evolution. The detection of chemicals with current scent-trapping methods is highly dependent on the type of trap, adsorbent, and solvent used, not only complicating



**Figure 1.** The three components of sensory drive through the perspective of olfaction and how they may relate to one another in a mammalian community. Chemical signals must be transmitted through a complex chemical background composed of a general background of volatile organic compounds (VOCs) and intra- and interspecific chemical signals, all interacting with abiotic conditions such as wind and humidity. The perceiver expresses hundreds of different genes in a number of different chemosensory receptor gene families under selection to maximize individual fitness. Sensory drive research in chemosensory systems is required to understand how changing environments influence the evolution of chemical communication. Abbreviations of mammalian chemosensory receptors: ORs: olfactory receptors; TAARs: Trace amine-associated receptors; V1Rs: vomeronasal type-1 receptors; V2Rs: vomeronasal type-2 receptors; FPRs: formyl peptide receptors.

replication, but also biasing the outcome of the analysis (Agelopoulos and Pickett 1998). Nevertheless, these methods have been successfully implemented to study chemical ecology in a plethora of organisms (Raguso et al. 2015), and recently they have been modified for the determination of the chemical environment. Methods to capture the breadth of the volatile and nonvolatile chemical environment are emerging and becoming slowly available and applicable to macrohabitats (Barreira et al. 2017; Hellén et al. 2017). It is now possible to study the temporal changes in atmospheric volatile organic compounds across large spatial scales of the rainforest (Jokinen et al. 2015; Yáñez-Serrano et al. 2015; Alves et al. 2016) or to characterize the “volatilome” of an animal (Amann et al. 2014; Angle et al. 2016), paving the way for sensory drive research.

The relevance of the sensory drive hypothesis has become increasingly important as discoveries show that chemical cues can indeed be drowned out by environmental changes and hinder the detection of relevant odorants (Atema 1995; Riffell et al. 2008,

2014). For example, the male tobacco budworm *Heliothis virescens* must identify females located on host plants from long distances, but some host plant volatiles interfere with the efficient detection of pheromones emitted by females (Pregitzer et al. 2012). Conversely, the silkworm *Bombyx mori* demonstrates a synergistic response with host plant cues, in which pheromone detection is enhanced by the presence of specific plant volatiles (Namiki et al. 2008). Human-produced pollutants can mask floral scents, drastically reducing signal transmission and impacting navigation in foraging moths (Riffell et al. 2014). It is becoming more obvious that the chemical background has a strong effect on signal transmission, and this is not only restricted to terrestrial habitats. In marine systems, pesticide-derived chemical pollutants disrupt olfactory signals used in navigation by salmon *Oncorhynchus mykiss* in British Columbia depending on concentration and pollutant mixtures (Tierney et al. 2008). Lobsters *Homarus americanus* generate their own currents of urine signal delivery for precise dispersal of chemical cues, creating

odorant “patches” that can be more readily sampled by conspecifics in a turbid marine environment (Atema 1995).

Identification and quantification of environmental chemicals and their dynamics with respect to atmospheric and aquatic conditions over different temporal and spatial scales are essential to test the role of sensory drive in chemosensory evolution. Although quantification of the chemical background is nontrivial, substantial technological advances have been made to facilitate our understanding of chemical signaling in nature.

### Challenge #2: the complexity of chemical signals

Visual and acoustic sensory systems process signals that can be readily quantified through well-understood inherent physical properties (e.g., electromagnetic waves and air pressure), and it is often straightforward to predict and test how these signals change in time and space. Chemosensory systems, in contrast, process signals composed of chemical molecules from a multidimensional chemical space that is virtually infinitive. Chemosensory signals can range from a single compound to complex mixtures of different compounds with diverse functional groups and varying concentrations. Pheromones, chemical signals emitted by many animal species to mediate intraspecific behaviors (Karlson and Lüscher 1959; Liberles 2014; Stowers and Kuo 2015), are often composed of dozens of compounds that may vary between individuals (Wyatt 2003). Determining which compounds are relevant with respect to sexual communication versus territoriality versus parental care versus metabolic byproduct (i.e., noise) is not trivial and often impossible. The isolation of behaviorally active compounds or compound mixtures in signals can be a tedious endeavor, due to often-unknown chemical structures of naturally occurring chemicals new to science. Although the manipulation of complex signals in visual and acoustic communication systems is relatively straightforward, the manipulation of chemical blends depends on the ability to produce or isolate the involved single compounds, which is often impossible and thus may be unfeasible. However, manipulations of signal mixtures are necessary to disentangle signal function in behavioral experiments, which may take considerable effort to conduct. For example, the functional characterization of the behavioral agents of the queen pheromone bouquet in honey bees *Apis mellifera* required decades of focused investigation, highlighting the difficulty in identifying the function of single components of signal mixtures. Early chemical analysis of the mandibular pheromone excreted by the queen revealed 9-oxo-(*E*)-2-decanoic acid as the dominant compound (Butler and Fairey 1963; Slessor et al. 2005). However, 9-oxo-(*E*)-2-decanoic acid alone is neither attractive to drones (male honey bees) nor does it lead to a response from worker bees. Behavioral experiments showed that for a response in workers to occur, four additional compounds are required (Slessor et al. 1988). However, it became evident that these results were not applicable to all honey bees. Although the five-ingredient mixture elicits behavioral responses in some subspecies, multiple additional subspecies-specific compounds were required to consistently elicit attraction in workers of other subspecies (Keeling et al. 2003; Slessor et al. 2005). This example further highlights how signal mixtures may vary between populations of the same species, which might be a result of local adaptation due to sensory drive. Although rarely studied, it is becoming more apparent that signals used in the same behavioral context can vary geographically within species (Ramírez et al. 2010; Pokorný et al. 2013; Duménil et al. 2014; Groot et al. 2014). In order to disentangle the evolutionary mechanisms driving this interpopulation

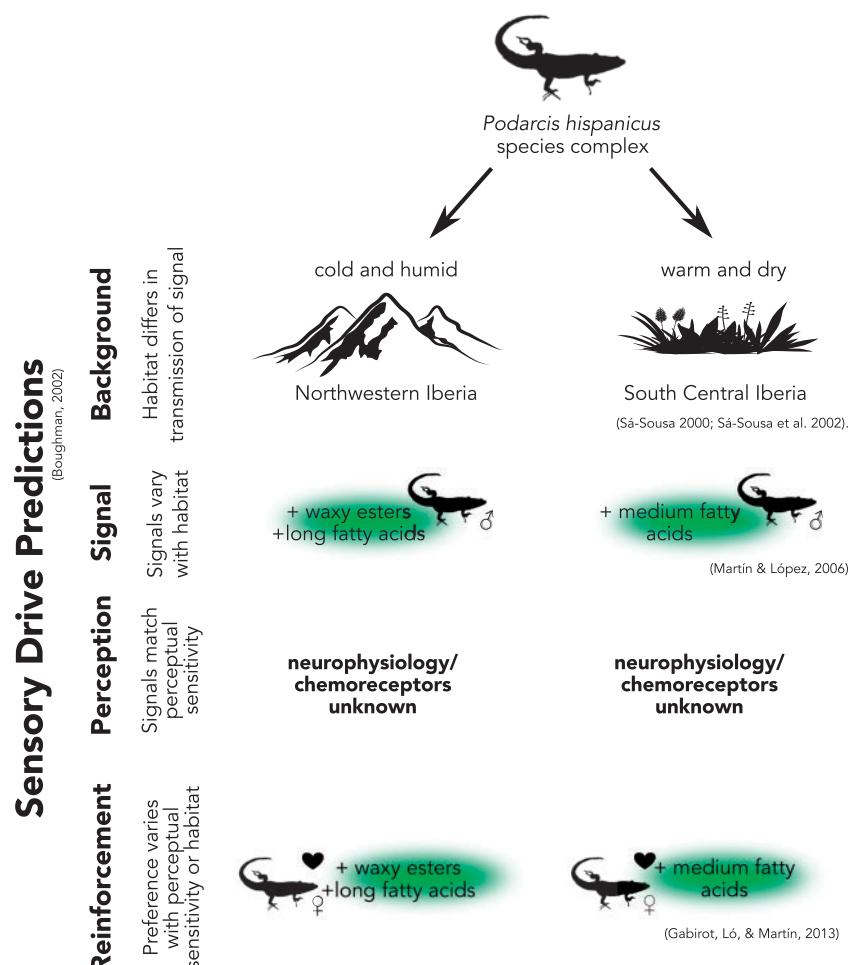
variation in chemical signaling, future investigations must explicitly test how the environment contributes to the evolution of variation in signaling and signal perception.

### Challenge #3: the complexity of the genetic basis of chemosensation

Once the chemical cue is emitted and transmitted through time and space, it must be detected and processed by the perceiver. In vertebrates and invertebrates alike, the detection of volatile and nonvolatile chemicals is based on the interaction of chemicals with proteins encoded by genes of large multi-copy chemosensory gene families expressed in sensory neurons and supporting cells of the olfactory and gustatory systems (see Kaupp 2010 for review). Although the number of genes underlying vision and acoustics is comparatively small and stable among lineages (Parker et al. 2013; Ramirez et al. 2016), the number of genetic loci involved in chemoreception can vary by orders of magnitude (Niimura 2012). Throughout animal evolution, the number of opsin paralog copies, for example, is highly conserved and rarely exceeds 10 per gene family (Ramirez et al. 2016). In contrast, tens to thousands of chemosensory genes of several fast evolving multigene families are involved in chemosensation (Nei et al. 2008; de Bruyne et al. 2010; Ota et al. 2012; Brykczynska et al. 2013; Niimura et al. 2014; Yoder et al. 2014; Derby et al. 2016). The origin of gene families involved in chemical detection occurred at different points in phylogenetic history independently in vertebrates and invertebrates (Eisthen 1992; Strausfeld and Hildebrand 1999; Grus and Zhang 2006, 2009; Sánchez-Gracia et al. 2009; Eyun et al. 2017; Brand et al. 2018). This includes several mostly G-protein-coupled receptor gene families in vertebrates (Grus and Zhang 2006; Niimura 2009, 2012) and non-G-protein-coupled receptor gene families in invertebrates (Sato et al. 2008; Cummins and Degnan 2010; Derby et al. 2016). New chemoreceptor gene families are still being discovered (Benton et al. 2009; Greer et al. 2016), emphasizing how much more there is still to learn about the molecular basis of chemosensation.

The widespread chemosensory receptor diversity is a result of rapid evolutionary rates through high gene turnover and rapid sequence diversification of homologous genes (Nei et al. 2008; Sánchez-Gracia et al. 2009; Bear et al. 2016; Brand and Ramírez 2017). The convergently evolved odorant receptor gene families in vertebrates and insects (Sato et al. 2008; Dehara et al. 2012; Niimura et al. 2014), for example, demonstrate some of the most extraordinary patterns of gene duplication and pseudogenization (i.e., gene turnover) in animals, constantly expanding and contracting over time (Nei et al. 2008). This birth-death evolution and the subsequent diversification are responsible for odorant receptors accounting for the largest gene families in animals encoding for up to 5% of the protein-coding genome in mammals, for example (Hayden et al. 2010; Niimura 2012; Niimura et al. 2014).

Although the evolutionary dynamics of chemosensory gene families in animals are well described based on an ever-increasing amount of genomic data for a diverse array of taxa (Guo and Kim 2007; Young et al. 2010; Brykczynska et al. 2013; Niimura et al. 2014, 2018; Picone et al. 2014; Yoder et al. 2014; Brand et al. 2015; Derby et al. 2016; Brand and Ramírez, 2017; Yohe et al. 2018), linking molecular patterns of sequence evolution to gene function is still a nontrivial task. One contributing factor is that the identification of ligands which individual chemosensory receptors respond to was initially limited to model organisms and experiments focused mainly on the mechanistic understanding of chemosensation (Dobritsa et al. 2003; Hallem and Carlson 2006; Touhara 2007;



**Figure 2.** The Iberian wall lizard *Podarcis hispanicus* illustrates a strong candidate for sensory drive promoting chemosensory divergence and local adaptation. Compounds of the male femoral gland excretions differ based on the environment, in which northern populations have waxier and bulkier compounds that are less volatile and enable more viable signals in the given habitat. Receptors of the perceivers are unknown, but behavioral evidence has demonstrated female preference and male–male recognition of signals based on their own environments. Silhouettes are from vecteezy and all-free-download.com.

Wang et al. 2010; Launay et al. 2012; de Fouchier et al. 2017; Pask et al. 2017; Slone et al. 2017; Fleischer et al. 2018). Early experiments functionally characterizing the entire chemosensory receptor repertoires in mice and vinegar flies revealed that the encoding of the senses of smell and taste is more complex than the number of genes initially indicated (Malnic et al. 1999; Dobritsa et al. 2003; Hallem and Carlson 2006). The detection of a single chemical can either be dependent on a single highly specialized receptor or multiple receptors acting in a combinatorial fashion (Malnic et al. 1999; Hallem and Carlson 2006; Malnic 2007; Ullah et al. 2015). Thus, the number of compounds detected by an animal is likely vastly exceeding the number of receptor genes in the genome (Malnic et al. 1999; Hallem and Carlson 2006; Nara et al. 2011; Magklara and Lomvardas 2013; Rodriguez 2013; McClintock et al. 2014; Bushdid et al. 2016; Haverkamp et al. 2018), and the loss or gain of receptor genes might have severe effects on the sensory ecology of an organism. Indeed, the high gene turnover of chemosensory gene families among animal lineages has been linked to changes in sensory abilities including the adaptation of novel food resources (McBride 2007; McBride and Arguello 2007; Hayden et al. 2014; Goldman-Huertas et al. 2015) or specializations in the pheromone communication system (Gould et al. 2010; Ferrero et al. 2011).

With neurophysiological methods being constantly refined and adapted for use in nonmodel species (de Fouchier et al. 2017; Pask et al. 2017; Slone et al. 2017), the field is moving toward a better understanding of how selection influences chemosensory evolution on a functional level. For example, it has become evident that even single mutations in olfactory receptors can lead to adaptive shifts in olfactory tuning (Pellegrino et al. 2011; Leary et al. 2012; McBride et al. 2014). Furthermore, chemosensory genes can be highly diverse within populations of the same species, leading to variable sensitivity to chemical stimuli (Rollmann et al. 2010; Logan 2014; Mainland et al. 2014), and thus representing variation for natural selection to act on when environments and/or signals change. With an increasing understanding of the molecular dynamics and a methodological toolkit becoming available for broad application, it will be possible to understand how chemosensation is evolving with response to local environments.

## Future Opportunities in Bringing Chemosensation to Sensory Drive

Through a combination of genomic, biochemical, and neurophysiological advances, the integrated study of chemosensory evolution is

now becoming tractable, and testing the role of sensory drive in chemosensory system evolution represents a new frontier in evolutionary biology. We are only beginning to understand the extent of variability in the chemical environment, chemical signals, and chemosensory genes and how their interplay is shaping the evolution of chemical communication. Although challenging, we believe that studying the role of sensory drive in chemosensory systems is possible with the careful choice of study systems in combination with well-designed experiments.

As we outlined above, there is an increasing number of examples of chemosensory-based local adaptation, chemical signal divergence, and molecular signatures of selection on chemosensory receptors. However, the majority of these studies focus on host-shift adaptation or the evolution of pheromone communication and its role in speciation, including analyses of intraspecific signaling variation among geographically (and environmentally) distinct populations (see Smadja and Butlin 2009 for summary). Although most systems partially align with the predictions of sensory drive, it is usually not explicitly tested for in the system. One such example is the Iberian wall lizard *Podarcis hispanicus*, a species complex that includes two populations that inhabit neighboring but differing environments (Figure 2), in which one population inhabits cold and humid environments of the highlands in northern Iberia and the other population inhabits a warmer and dryer Mediterranean climate of central and southern Iberia (Sá-Sousa 2000; Sá-Sousa et al. 2002). These divergent environmental conditions have led to differences in the chemical composition of femoral gland excretions of male lizards used for marking territory, conspecific identification, and female choice (Martín and López 2006). Males in colder, wetter climates have less volatile femoral gland excretions compared with those in drier climates, likely an environmentally driven adaptation for efficient signal deposition and signal stability (Martín and López 2006; Martín et al. 2015). Males of each respective population elicit a more aggressive response toward signals from conspecific in their own habitat (Martín and López 2006; Gabirot et al. 2012), and similarly females show preferences for signals specific to their habitat type (Gabirot et al. 2013; Martín et al. 2015). These preferences reinforce the boundaries likely initially established by more efficient signaling based on their habitat type, leading to reproductive isolation among the populations and potential cryptic speciation (Gabirot et al. 2012; Martín and López 2015; Martín et al. 2015). Accordingly, this system corroborates many of the criteria outlined by Boughman (2002) for speciation via sensory drive (Figure 2), and we encourage follow-up studies on neurophysiology and chemoreceptor evolution to test for selection driving divergent chemical perception mechanisms between habitats and to exclude genetic drift.

Similar to the Iberian wall lizard, many known cases of intraspecific pheromone evolution show patterns that meet the predictions of the sensory drive theory, emphasizing the disparity between the study of chemosensory adaptations and sensory drive literature. Environmental changes are likely often a part of interpopulation divergence in chemosensory systems from latitudinal gradients (Lavagno et al. 2008) to sympatric host shifts (Olsson et al. 2006; Tait et al. 2016) and thus have the potential to be affected by sensory drive.

## Concluding Remarks

Over the past 25 years, a focus on visual and acoustic systems has generated convincing evidence for the role of sensory drive as a mechanism in sensory-mediated local adaptation and potential reproductive isolation. However, the importance of sensory drive as a

hypothesis that explains sensory adaptations based on environmental differences, in general, remains uncertain until the hypothesis is rigorously tested in all sensory modalities, including chemosensation. The traditional lack of studies on sensory drive in chemosensory evolution likely results from the complexity of chemosensory signals and their detection alongside the only recently emerging technology needed for the combined analysis of both phenotypic and molecular evolution of chemosensory communication. We find that precisely these technological advances have led to a deeper understanding of chemosensation and the underlying molecular basis in the recent past, paving the way for future research on chemosensory evolution with respect to the variability of natural habitats. Ultimately, we will need to link chemosensory evolution of signaling and perception to the complex chemical background of the environment to truly demonstrate how sensory drive is a critical mechanism of chemosensory evolution.

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