

Chemical communication and its role in sexual selection across Animalia

Tyler J. Buchinger ^{1,2}✉ & Weiming Li ¹

Sexual selection has been studied as a major evolutionary driver of animal diversity for roughly 50 years. Much evidence indicates that competition for mates favors elaborate signaling traits. However, this evidence comes primarily from a few taxa, leaving sexual selection as a salient evolutionary force across Animalia largely untested. Here, we reviewed the evidence for sexual selection on communication across all animal phyla, classes, and orders with emphasis on chemoreception, the only sense shared across lifeforms. An exhaustive literature review documented evidence for sexual selection on chemosensory traits in 10 of 34 animal phyla and indications of sexual selection on chemosensory traits in an additional 13 phyla. Potential targets of sexual selection include structures and processes involved in production, delivery, and detection of chemical signals. Our review suggests sexual selection plays a widespread role in the evolution of communication and highlights the need for research that better reflects animal diversity.

Animals interact with mates and sexual rivals using diverse and often elaborate traits¹. These traits are among the most striking displays of animal biodiversity (e.g., courtship dance of peacock spider²) and inspired Darwin's theory that sexual selection arising from variation in access to mates (or gametes)³ (Box 1) acts alongside selection for survival and fecundity⁴. The last few decades have brought an outpouring of research on the evolution of sexual ornaments, displays, and calls^{5,6} and, as Darwin suggested, overwhelming evidence indicates such traits often evolve under sexual selection. Having garnered empirical support as a salient evolutionary force underlying signaling traits¹, sexual selection continues to hold the keen focus of evolutionary biologists due, in part, to the hypothesis that its effects on sexual signals and preferences drive reproductive isolation and ultimately speciation^{7,8}. As important products of sexual selection and substrates for sexual selection to drive speciation, signaling traits are often at the center of discussions on the evolution of animal biodiversity^{9–11}.

Despite its broad scope, theory around animal signals and sexual selection has advanced largely through the intensive study of relatively few taxa. Animals such as frogs, fish, and arthropods have proven particularly useful for developing and testing models of sexual selection^{12,13}. For example, studies on túngara frogs¹⁴, Trinidadian guppies¹⁵, and fiddler crabs¹⁶ revealed that sexual signals can evolve to exploit receivers' sensory ecology rather than providing information about the signaler's quality as a mate¹⁷ (e.g., male guppies have orange spots that mimic fruit¹⁸). Largely lost amongst the mechanistic details of sexual selection, however, is the fundamental question of whether sexual selection acts as an important evolutionary force across all of Animalia. Importantly, all but one (Micrognathozoa) animal phyla include species that are known to reproduce sexually and therefore could be shaped by sexual selection¹⁹. The conspicuous signaling traits that originally captured Darwin's attention clearly illustrate a major role of sexual selection in some chordate and arthropod classes²⁰ but whether this role is common across the animal kingdom remains largely unexplored.

¹Department of Fisheries and Wildlife, Michigan State University, East Lansing, MI, USA. ²Biology Department, Albion College, Albion, MI, USA. ✉email: buching6@msu.edu

Box 1 | Glossary

Sexual selection: Selection that arises from fitness differences associated with nonrandom success in the competition for access to gametes for fertilization³.

Signal: A trait of one individual (sender) that evolved to influence the physiology or behavior of another individual (receiver) after being sensed by the receiver¹⁸¹.

Cue: A sensory stimulus (biotic or abiotic) that triggers a response in an animal but did not evolve for communication¹⁸¹.

Pheromone: A molecule that evolved for signaling to conspecifics and elicit a specific reaction when detected²⁴.

Allomorphone: Molecules from one individual that are transferred directly into a conspecific and that elicit a physiological or behavioral response without being detected by external senses^{134,182}.

Table 1 Mechanisms of sexual selection on chemosensory traits (modified from refs. 1,3).

Mechanism	Example	Species
Scramble competition	Males with more sensilla on antennae locate females quicker ⁸⁶	Mantid (<i>Pseudomantis albofimbriata</i>)
Contest competition	Eventual winning males jet urine at opponents during fights to induce defensive behaviors ¹⁶⁵	Crayfish (<i>Astacus leptodactylus</i>)
Gamete competition	Love dart injects mucous into mates to delay remating ¹⁶⁶	Snail (<i>Euhadra quaesita</i>)
Mate choice	Males prefer pheromones of virgin over mated females ¹⁶⁷	Nematodes (<i>Caenorhabditis</i> sp.)
Cryptic mate choice	Females differ in the production of sperm chemoattractant and males differ in sperm chemotactic ability ^{168,169}	Urchin (<i>Lytechinus pictus</i>)

In this Perspective, we review the evidence for sexual selection on traits involved in chemical communication across the animal Tree of Life. As we outline below, chemical communication is uniquely poised to be a possible target of sexual selection across all animals and therefore particularly important for evaluating the potential for sexual selection on communication at a macroevolutionary scale. Our primary objective is to review the evidence for sexual selection on signaling traits across Animalia. By focusing on chemical communication, our approach explicitly acknowledges differences in animals' sensory biology. After establishing chemosensation as the only possible target of sexual selection on communication that is common across all of Animalia, we review (1) the evidence for sexual selection on chemosensory traits in species from all phyla, classes, and orders of animals and (2) the mechanisms (e.g., mate choice; Table 1) and targets (e.g., scent glands; Table 2) of sexual selection on chemical communication. Our goal is to encourage the field of sexual selection to have a broader scope that spans Earth's diverse forms of animal life, and advocate that chemical communication be a key focus of the discussion.

Chemosensory traits as potentially universal targets of sexual selection. Despite much interest in visual and auditory signals, most animals cannot see or hear. High-resolution, image-forming eyes are present only in arthropods, chordates, and cephalopod mollusks²¹, and only vertebrates and some arthropods possess ears or analogs of ears²². Although some animals that lack eyes or ears can detect light and sounds^{21,23}, the sensitivity and specificity of these channels is unlikely sufficient for communication. For example, photoreception in most animal phyla can mediate internal physiological control (e.g., circadian rhythms), directional phototaxis, and habitat orientation but not interactions with specific objects or individuals (e.g., mates)²¹. In contrast, all single- and multicellular organisms have chemoreceptors that allow acute sensitivity to specific chemicals²⁴.

The capacity to sense specific molecules is a fundamental feature of life on Earth^{25,26}. Unicellular bacteria²⁷, archaea²⁸, protists²⁹, and fungi³⁰ express membrane-bound receptors that bind specific molecules, such as those related to social conditions (e.g., quorum-sensing pheromones)³¹. As first suggested by JBS

Haldane, the external chemoreceptors of unicellular organisms may be precursors to internal receptors that allow intercellular communication in multicellular organisms²⁵. This basic ability to detect chemicals in the milieu surrounding cells, whether internally or externally, has given rise to specialized chemosensory cells and organs in seemingly all animals, from the nerveless poriferans and placozoans to ctenophores and cnidarians, which have nerve nets, and the bilaterians with their centralized nervous systems^{32,33}. The mechanisms of chemoreception differ within and among taxa, and include solitary chemosensory cells, olfaction, gustation, and the vomeronasal system. However, these classifications are largely based on terrestrial vertebrates and insects and may not hold in other taxa³⁴, especially the many groups for which our understanding of chemoreception systems is limited (e.g., ctenophores)³⁵. Regardless, the ubiquity of chemoreception as a specific sensory channel makes it especially useful for studying the potential role of sexual selection across diverse animals.

How and where animals live further implicates chemosensory traits as common potential targets of sexual selection across higher taxonomic levels. Sexual signals evolve under selection related to animals' ecology—specifically how individuals interact with potential mates and the environment^{15,36}. In several phyla, individuals that already lack vision and hearing also have limited ability to interact with mates via touch as they are sessile as adults³⁷ (with some exceptions, such as sessile barnacles with extendable penises³⁸). Perhaps more surprising to visually oriented humans is evidence that the dominant sensory environment of animals favors communication via chemoreception³⁹; most invertebrates⁴⁰ and mammals⁴¹ are nocturnal and a large proportion of Earth's animal diversity is found in the perennial dark of the deep sea⁴² and underground⁴³. Although many animals have adaptations that allow vision in dim light⁴⁴, life in the dark is often associated with a predominant role of chemoreception^{45–47}. Numerous and interacting ecological conditions shape the evolution of signaling systems and visual, auditory, electrical, and tactile communication clearly play dominant roles in many taxa⁴⁸. However, the basic sensory capabilities and ecology of many animals suggest chemoreception is the only common channel

Table 2 Example targets of potential sexual selection on chemical communication.

Level	Trait type	Example	Species
Production	Enzyme	Female-specific expression of fatty acid elongase underlies sex pheromone production ¹¹⁰	Cockroach (<i>Blattella germanica</i>)
	Cell	Male-specific gill cells release sex pheromone ⁸¹	Lamprey (<i>Petromyzon marinus</i>)
	Gland	Male-specific leg glands secrete sex pheromone ¹¹⁶	Velvet worm (<i>Cephalofovea tomahmontis</i>)
Delivery	Organ	Large kidneys and hypertrophic urinary bladders mediate pheromone signaling by dominant males ¹²⁰	Tilapia (<i>Oreochromis mossambicus</i>)
	Apparatus	Calcareous dart injects allohormone that biases paternity ¹⁷⁰	Snail (<i>Helix aspersa</i>)
Transmission	Signaling behavior	Dominant males kick feces to increase active space of odor ^{127,128}	Rhino (<i>Ceratotherium simum</i>)
	Accessory molecule	Proteins delay scent evaporation and extend signal duration ¹³²	Mouse (<i>Mus domesticus</i>)
Detection	Sampling behavior	Eventual losers of fights flick sensory antennules more often to assess urine signal of competitor ¹⁷¹	Lobster (<i>Nephrops norvegicus</i>)
	Sensory structure	Long antennae improve male mate search ¹⁷²	Isopod (<i>Asellus aquaticus</i>)
	Accessory molecule	Male-specific binding proteins increases sensitivity to female pheromones ¹⁷³	Moth (<i>Chilo suppressalis</i>)
	Receptor	Female-specific expression of putative pheromone receptors on sensory tentacles ¹⁷⁴	Starfish (<i>Acanthaster planci</i>)
	Neural circuit	Sexually dimorphic neural circuit mediates sex-specific responses to a pheromone ¹⁷⁵	Fruit fly (<i>Drosophila melanogaster</i>)

for sexual communication across higher taxonomic levels of the animal Tree of Life.

Taxonomic distribution of chemosensory traits potentially under sexual selection

Literature review. We searched for studies indicating that chemosensory traits guide sexual interactions between competitors or mates. Our primary objective was to document evidence for sexual chemosensory traits across higher taxonomic groups of Animalia (phyla $n = 34$, classes $n = \sim 100$, orders $n = \sim 600$). As the animal kingdom includes immensely diverse life-forms and studies on these life-forms often use different terminology, achieving our goal required a flexible and exhaustive search rather than a structured review with restricted search terms and filtering steps. We followed the taxonomy of Ruggiero et al.⁴⁹ because it provided a unified classification down to the level of order and therefore allowed a taxonomically systematic search (Supplementary Data 1). To begin, we searched Google Scholar using both scientific and common names (when available), and keywords such as (but not limited to) “pheromone”, “chemical cue”, “chemosensory”, “olfactory”, and “scent”. At a minimum, we searched at the level of phyla and order. Searches for which the above keywords yielded few (or no) results were then repeated using more general keywords such as “reproductive behavior”, “mating”, and “spawning”. Often, these general searches yielded papers that were only tangentially relevant but either cited or were cited by studies that were directly relevant to our search. When available, we leveraged review papers^{50–54} and online resources (e.g., www.pherobase.com) that guided us to potentially relevant studies. In especially obscure taxa (e.g., Placozoans), we used Google Scholar or Google Search and no search terms other than their name to find if anything is known about how they reproduce and if chemosensory traits might be involved. Using these approaches, we searched exhaustively for the most direct evidence (see below for categories of evidence) of sexual selection on a chemosensory trait available for each order of animal. Importantly, our search was exhaustive in that we attempted to document, at a minimum, one example of a sexual chemosensory trait for each order but not exhaustive in compiling the available evidence within orders.

We included studies that fit into three categories according to the evidence they provided for sexual selection on a

chemosensory trait. The first category met the criteria for sexual selection set by Andersson¹: (i) evidence of a significant relationship between a trait and mating success and (ii) an identified mechanism of sexual selection, such as mate choice (Table 1). Consistent with Andersson¹ and more recent literature⁵⁵, this category included studies that used a proxy of mate choice (e.g., time near stimulus from a potential mate) but did not measure actual mating outcomes. To acknowledge known research biases towards certain taxa^{12,13,56}, we also included studies in two additional categories if they indicated potential for sexual selection on a chemosensory trait but did not provide direct empirical support per the established criteria¹. Specifically, studies considered to report potential for sexual selection on chemosensory traits included (i) documented behavioral or physiological responses to chemical traits of mates or competitors in a reproductive context (e.g., behavioral attraction of mature male *Nautilus* to female rectal extract⁵⁷) or (ii) suggestions of sexual chemosensory interactions based upon indirect evidence (e.g., sexually dimorphic leg glands in centipedes⁵⁸). We prioritized studies that fit in the first category, and sequentially included studies in the second and then third categories only if we were unable to find studies that met the criteria of the first category. Importantly, studies in the latter two categories do not provide direct evidence of sexual selection on chemosensory traits. Nevertheless, we included them to illustrate the state of the field across taxa and guide future work. Indeed, these relaxed criteria could produce an overestimate of the distribution of sexually selected chemosensory traits. For example, chemicals only documented to elicit responses in the opposite sex might turn out to guide sex or species recognition but not be shaped by sexual selection²⁰ (but see ref. ⁵⁹ regarding possible issues with the distinction between species recognition and mate choice).

Our review took a broad view of the chemosensory traits that guide sexual interactions. Although our primary focus was on signaling traits, we also included some chemosensory stimuli that may not fit classic definitions of signals (Box 1). In many cases, additional research is needed to determine whether a chemosensory stimulus is a signal that evolved for communication or a cue that elicits a response in receivers but did not evolve for that purpose. Indeed, traits detected by all sensory systems are often difficult to discretely categorize as cues versus signals⁴⁸. For example, female goldfish (*Carassius auratus*) excrete hormonal

metabolites via urine that attract males⁶⁰; these molecules were initially considered cues that males spied on⁶¹, but subsequent research revealed females control their release of urine to facilitate communication⁶². In other cases, sexual chemosensory traits strain the classic definition of signals. For example, male salamanders (*Plethodon shermani*) release pheromone proteins that increase courtship receptivity after being smelled by females⁶³; male frogs (*Rana temporaria*) produce closely related proteins suspected to also increase female receptivity but deliver them directly into females via spiny nuptial pads rather than releasing them into the environment⁶⁴. Although the proteins transferred into female frogs may not fit classic definitions of a signal as they are not sensed as an external stimulus, they conceivably evolved via similar selective mechanisms and, in our opinion, are relevant to our review. We also noted studies on chemosensory traits that guide interactions between gametes (e.g., sperm chemotaxis) as they are similar targets of sexual selection in diverse animals⁶⁵, though we only note these in our literature review if we were unable to find examples of chemosensory traits that guide interactions between individuals. Lastly, we did not distinguish between the various mechanisms involved in the detection of chemical traits (e.g., olfaction versus taste)²⁴. As discussed above, a flexible and inclusive approach was necessary to support a discussion on sexual selection across the diversity of Animalia.

Potential for sexual selection on chemosensory traits across Animalia. Potential for sexual selection on chemosensory traits spans across the Tree of Life (Figs. 1 and 2 and Supplementary Data 1 and 2). Altogether, our literature review included $n = 319$ studies on the potential for sexual selection on chemosensory traits. Studies on animals from 10 of 34 phyla provide evidence of sexual selection on chemosensory traits that meets the criteria set by Andersson¹. Among these phyla, 9 include animals with traits involved in communication (e.g.,

chemosensory-based mate preferences) and 1 (Echinodermata) includes animals with traits that guide gamete interactions (cryptic mate choice). An additional 6 phyla possess chemosensory traits that were found to guide interactions between mates or competitors (5 at the individual level, 1 at the gamete level), and therefore may be under sexual selection. However, a direct link between variation in these traits and mating success has yet to be established. Finally, sexual chemosensory traits have been suggested for 7 more phyla, though direct evidence for sexual communication remains lacking. Although our review focused on the animal kingdom, fungi⁶⁶, bacteria⁶⁷, protists⁶⁸, and plants⁶⁹ also have reproductive chemosensory traits that may be shaped by sexual selection. Importantly, our failure to find evidence for sexual selection on chemosensory traits in many taxa should not be interpreted as evidence against sexual selection in those taxa. Indeed, the literature shows evidence (Category 1) or potential indications (Category 2 or 3) of sexual selection on chemosensory traits across the Tree of Life and in most animal phyla (23 of 34).

Albeit relatively broad, the taxonomic distribution of evidence for sexual selection on chemosensory traits remains shallow, with most phyla represented by relatively few classes or orders (Fig. 3 and Supplementary Data 1). In phyla with chemosensory traits that meet the criteria for sexual selection (Category 1), only Annelida, Bryozoa, Nematomorpha, and Platyhelminthes had evidence from more than half of classes, and these four phyla each have <3 recognized classes. However, most classes ($\geq 50\%$) in phyla Cnidaria, Ctenophora, Porifera, Arthropoda, Nematoda, Tardigrada, Annelida, Bryozoa, Mollusca, Nemertea, Platyhelminthes, Rotifera, Chordata, Echinodermata, and Hemichordata have at least some potential indications (Category 2 or 3) of sexual selection on chemosensory traits, even if the indications are only suggestions based on indirect evidence. Phyla Placozoa, Chaetognatha, Nematomorpha, Onychophora, Cyclophora, and Gastrotricha showed potential indications of sexually selected

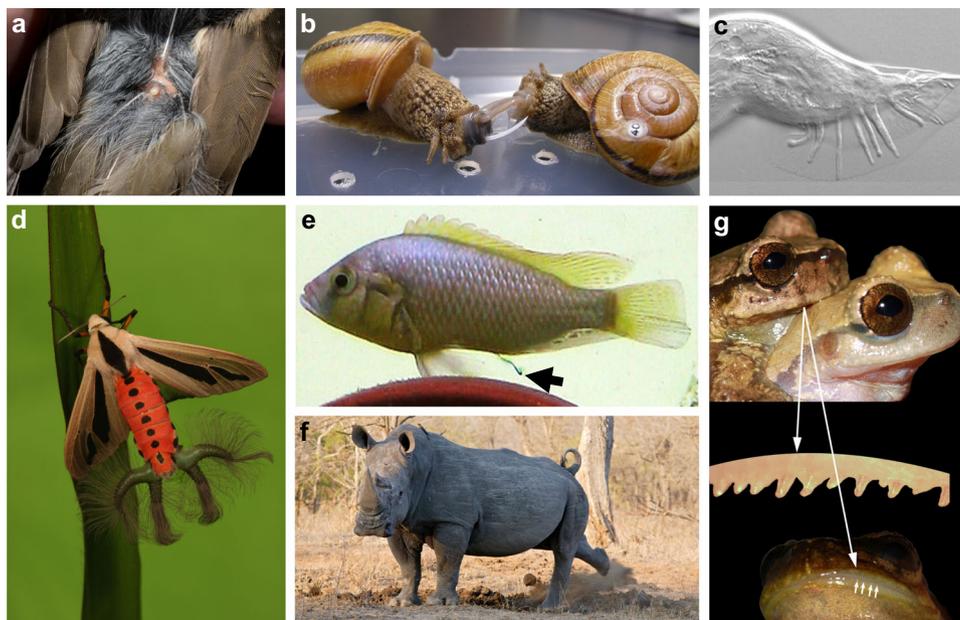


Fig. 1 Examples of chemosensory traits potentially under sexual selection in animals. **a** Preen gland involved in olfactory signaling in birds (Swainson's thrush, *Catharus ustulatus*; photo credit: Brock and Sherri Fenton). **b** love dart of land snail (*Bradybaena pellucida*) that injects allohormone into mate to increase paternity (photo credit: Kazuki Kimura). **c** sensory rays of male nematode (*Caenorhabditis elegans*) used in chemosensation of mates (image adapted with permission from ref. 176). **d** inflatable scent gland of male tiger moths (*Cretonotus gangis*; photo credit: Darren5907/Alamy). **e** pulse of urine released by dominant male cichlids (*Astatotilapia burtoni*; image adapted with permission from ref. 177). **f** Male white rhino (*Ceratotherium simum*) kicking dung to spread chemical signal (AfriPics.com/Alamy). **g** Protruding teeth and swollen lips in frogs (*Plectrohyla sagorum*) that males use to scratch females and deliver putative pheromones (reproduced from ref. 137, BMC).

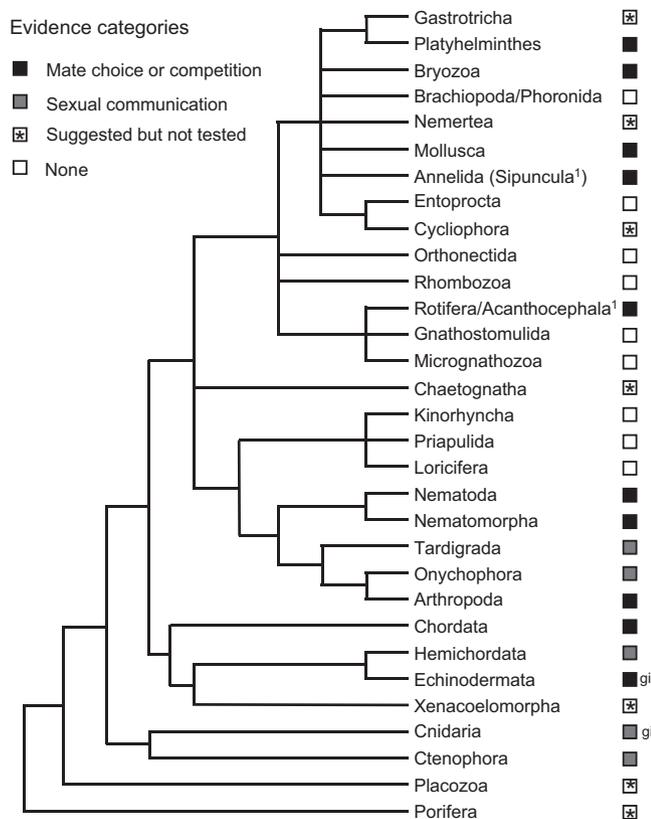


Fig. 2 Evidence and potential for sexual selection on chemosensory traits across animal phyla. Black-filled boxes indicate phyla for which evidence suggests chemosensory traits guide mate choice or competition. Gray-filled boxes indicate phyla for which chemosensory interactions between mates or sexual rivals have been documented. Asterisks indicate phyla for which chemosensory interactions between mates or sexual rivals have been suggested but remain without direct empirical support. *gi* indicates the trait with the strongest support in a phylum was involved in gamete interactions. Phylogeny based on ref. 178. ¹Sipuncula and Acanthocephala were considered distinct phyla in the taxonomy followed for our literature review⁴⁹ but are recognized in ref. 178 as part of Annelida and Rotifera. Sexual chemical communication has been documented in Acanthocephala but remains untested in Sipuncula.

chemosensory traits but have ≤ 1 recognized classes (see ref. 49; Supplementary Data 1), making the percentage of represented classes impossible or of little use to calculate. Finally, Acanthocephala and Xenacoelomorpha had indications of sexually selected chemosensory traits in $<50\%$ of classes.

In many taxa, the lack of evidence for sexual selection on chemosensory traits likely represents a lack of data rather than true absence. Indeed, the animal kingdom is rife with poorly understood life-forms. Phyla Loricifera, Cycliophora, and Micrognathozoa were only discovered in the last several decades^{70–72}. Furthermore, sexual reproduction has not yet been confirmed in Micrognathozoa⁷³ and was only recently documented in Placozoa⁷⁴. The monotypic cnidarian *Polypodium hydriforme*, a parasite found only in eggs of a small order of fishes (Acipenseriformes), may be exclusively parthenogenetic⁷⁵ and therefore not subject to sexual selection¹⁹. Coelacanth, one of only five classes of chordates for which indications of sexual selection on chemosensory traits are lacking, were thought long extinct before their rediscovery in 1938⁷⁶; today, basic questions about their reproductive behavior, such as how they interact with

mates, remain unanswered⁷⁷. Improving our basic understanding of some clades will almost certainly unveil more evidence of sexual selection on chemosensory traits.

Potential targets of sexual selection on chemosensory traits across Animalia. Sexual selection acts upon a diverse collection of chemosensory traits spanning molecules to behaviors (Table 2). Examining the specific targets of sexual selection is helpful for two primary reasons:

First, it shows where signatures of sexual selection might occur. By definition, sexually selected chemosensory traits influence individuals' success at accessing mates or gametes³. This influence on mating success arises from various traits at all levels of biological organization (e.g., from cells to behaviors), not just the signal or sensory structure directly involved in sexual interactions⁷⁸. For example, female preference for higher pheromone concentrations favors higher signaling rates in sea lamprey (*Petromyzon marinus*), but various physiological^{79–81} and behavioral traits^{82,83} that mediate pheromone production and release are likely the specific targets of sexual selection (Fig. 4). In lampreys, the traits underlying pheromone signaling show possible signatures of sexual selection, such as sexual dimorphism⁸¹ and relatively high inter-specific diversity⁸⁴. Studying the various traits underlying chemical communication can be especially useful for testing potential sexual selection when the specific identity of the signal is unknown.

Second, examining the targets of sexual selection can reveal the various mechanisms by which sexual selection can act upon communication across diverse taxa. Theory suggests that sexual selection acts on communication traits via several mechanisms of mate choice and competition^{3,6} (Table 1). Much evidence supports this theory, but the data come from relatively few animal groups¹. For chemical communication, mate choice using signals that provide or indicate benefits to the choosing sex has been of particular interest⁸⁵; however, other mechanisms (Table 1) of sexual selection are also important and may be more relevant for some animal groups. For example, large and elaborate sensory structures in male insects indicate a possible role of sexual selection via scramble competition (discussed below⁸⁶). Indeed, most studies focus on signals that attract mates or repel competitors²⁰ but such functions do not fully capture the diversity of sexual chemosensory traits. Below, we review the potential targets of sexual selection on chemical communication and the mechanisms by which sexual selection can act on each.

Molecular constituents. Animals use a diverse selection of molecules to interact with mates and sexual rivals²⁴. Chemical diversity in these traits arises from differences in attributes of individual compounds, such as their class (e.g., protein vs. steroid vs. ketone)^{87–89}, functional group⁹⁰, or stereochemistry⁹¹, as well as differences in mixture constituents or proportions⁹². Even different concentrations of a single compound can be perceived as distinct stimuli⁹³. High species specificity of many sexual chemical signals indicates they often diversify rapidly⁹⁴. This diversity has made chemical signals an especially useful model of studying the evolution of communication⁹⁴. However, the classical view on how chemical signals evolve emphasized species recognition⁹⁵ and only more recently has the scope broadened to include sexual selection^{85,96}. Nevertheless, a substantial body of evidence, largely but not exclusively from studies on insects⁹⁷, shows that sexual selection can influence the molecular identity of chemical signals.

Sexual selection can act through several mechanisms to influence the identity of chemical signals. In some cases, the molecular constituents of chemical signals are closely linked to

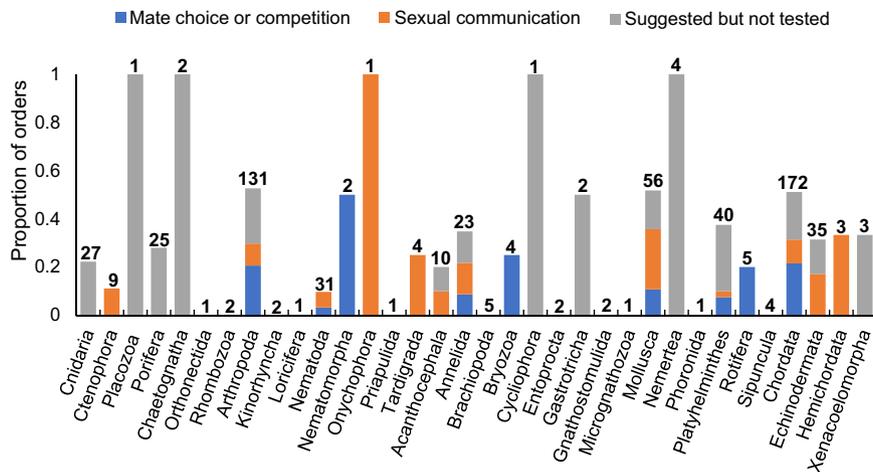


Fig. 3 Proportion of orders with evidence or potential for sexual selection on chemosensory traits across phyla. Studies are categorized according to whether they (1) report evidence that chemosensory traits guide mate choice or competition, (2) report evidence for sexual chemical communication, or (3) suggest sexual chemical communication without direct evidence. Numbers above bars indicate the number of orders within each phyla, based upon ref. 49. For clarity, only traits that mediate interactions between mates or competitors (not gametes) are included, though cryptic mate choice via gamete chemosensation has been shown or suggested in many orders of Echinodermata and Cnidaria (Supplementary Data 1).

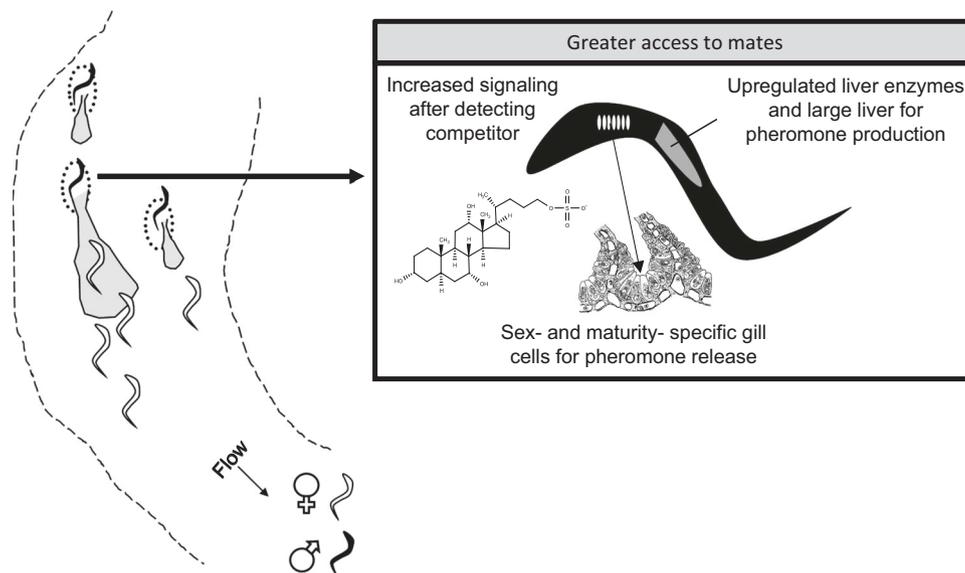


Fig. 4 Illustration of how sexual selection can act on various traits underlying sexual chemosensory interactions. During spawning, female sea lamprey (*Petromyzon marinus*) orient towards the bile acid 3-keto petromyzon sulfate (3kPZS). The lek-like mating system of lamprey and female preference for the more concentrated of adjacent 3kPZS plumes¹⁷⁹ appears to generate sexual selection for upregulation of bile acid synthetic enzymes^{79,84}, large livers (where bile acids are biosynthesized)⁸⁰, and sexually dimorphic gill cells involved in 3kPZS release⁸¹. Furthermore, males increase the attractiveness of their pheromone signal by releasing more 3kPZS after exposure to a competitor⁸³. Gill cell image adapted with permission from ref. 180.

the benefits the signal provides or indicates to receivers. Insect pheromones are often molecules sequestered from needed resources⁸⁵, such as the plant-derived alkaloids that deter predators and act as male sex pheromones in the moth *Utetheisa ornatrix*^{98,99}. In fish, hormonal metabolites directly indicate the reproductive status of the signaler⁶⁰ and peptides associated with major histocompatibility complex (MHC) molecules reflect genetic quality¹⁰⁰. Signals can also evolve to exploit pre-existing aspects of receivers' sensory biology without necessarily providing any benefit¹⁸, though evidence for this evolutionary mechanism of mate choice is not well-documented for chemical communication¹⁰¹. A few examples include prey molecules released by male beewolves (*Philanthus triangulum*) and rock lizards (*Iberolacerta cyreni*) to attract conspecific females

searching for food^{102,103} and a bile acid released by male sea lamprey to mimic a larval cue used to navigate to preferred habitats¹⁰⁴. Though the above studies focus on interactions between mates, similar mechanisms act upon chemical signaling between rivals; male goldfish (*Carassius auratus*) mediate aggressive interactions using reproductive hormones that are likely related to their reproductive status^{105,106} and male *Drosophila* manipulate competitors using an anti-aphrodisiac pheromone that exploits a pre-existing sensory bias¹⁰⁷. Finally, sexual selection might also drive elaboration of chemical signals if adding components increases signal information content or efficiency^{92,94,97}, though evidence that this occurs also remains limited¹⁰⁸. Unfortunately, a poor understanding of the specific chemical structures of chemical signals in most animals limits

broad inferences about the link between their molecular composition and the mechanisms of sexual selection that act upon them⁹⁴.

Traits related to the production of chemical signals. Chemical signals manifest through an assortment of molecular and physiological processes, cells, and organs that are shaped by sexual selection¹⁰⁹. Often, sexual chemical signals are produced via sex- and stage-specific upregulation of biosynthetic enzymes or transporters^{79,110}. These molecular processes can occur in cells with other functions or in sexually dimorphic cells that likely evolved to support chemosensory interactions between mates or sexual rivals^{81,111}. Similarly, cells involved in chemical signaling can be dispersed throughout the body, localized to common organs, or organized into specialized glandular tissues¹⁰⁹. Pheromone and scent glands likely shaped by sexual selection are often noted in insects and mammals²⁴ but also occur in fish¹¹², birds¹¹³, anurans¹¹⁴, reptiles¹¹⁵, non-insect arthropods (centipedes)⁵⁸, onychophorans¹¹⁶, nemerteans¹¹⁷, gastrotrichs¹¹⁸, and platyhelminths¹¹⁹. Common organs can also have adaptations for producing or emitting sexual chemical signals (e.g., large livers⁸⁰, hypertrophic urinary bladders¹²⁰). Adaptations for sexual signaling in common organs, albeit more cryptic than those associated with specialized glands, may be especially widespread given many chemical signals are released via routes linked to common physiological processes (e.g., feces, urine)²⁴.

Traits related to the delivery of chemical signals. Sexual selection can act upon physiological and behavioral traits that mediate delivery of chemical signals. Many chemical signals consist of molecules that also have non-communicative functions⁹² and leak out via sexual materials¹²¹, tears¹²², mucous¹²³, feces¹²⁴, urine¹²⁵, and respiratory waste¹²⁶. Release via seemingly unspecialized routes again points to selection for signals with direct links to the physiological status of signalers. As discussed above, chemicals that leak out may act as cues that receivers evolved to detect but not signals that involve any adaptations in releasers (Box 1). However, even unspecialized routes of release often involve finesse that evolved for communication; for example, dominant male white rhinos (*Ceratotherium simum*) defecate more often than females or nonterritorial males and kick their dung to increase the signal's active space^{127,128}. Controlling when and where to signal may allow signalers to deceive receivers with chemical signals that seem otherwise difficult to fake¹²⁹. Alternatively, tactical signal delivery may arise via selection for signal efficiency^{15,130}. For example, male swordtails (*Xiphophorus birchmanni*) urinate more often in the presence of females and orient themselves upstream of females when courting, presumably to help deliver chemical signals¹³¹. Analogous non-behavioral traits can also facilitate signal delivery; some animals produce proteins that bind chemical signals (e.g., major urinary proteins in mice) to (1) slow evaporation of the molecule, thereby extending signal duration¹³² or (2) release the chemical only upon arrival to the sensory organ according to its local chemical environment (e.g., pH)¹³³.

Some sexual chemicals are delivered directly into the body without being detected by receiver's external sensory systems (allohormones; Box 1)¹³⁴. For example, males in some plethodontid salamanders open females' skin using hypertrophic teeth and then rub their mental gland on the wound to inject directly into the blood a pheromone that increases female receptivity⁷⁸. In addition to injection through skin using various methods^{135–137}, sexual chemicals can be delivered directly through insemination¹³⁸ or consumption via nuptial gifts¹³⁹. Importantly, chemical traits delivered directly into receivers' bodies are generally not considered signals, which are detected by receivers'

sensory systems^{134,140}. However, the line between these chemicals and conventional signals can be blurry, especially in closely related species that use the same class of molecules to interact with mates but differ in whether they deliver the chemicals to sensory systems or directly into the body⁷⁸. Regardless, chemicals that bypass sensory systems are important targets of sexual selection¹³⁴. Across various animal phyla, including commonly studied arthropods¹⁴¹ but also hermaphroditic annelids, platyhelminths, and mollusks^{135,136,142,143}, chemicals directly transferred to females prevent digestion or disposal of sperm, suppress future mating, and ultimately bias paternity. In an interesting twist, chemicals transferred to mates can subsequently be or modify chemical signals for competitors¹⁴⁴; for example, male moths mark females with an anti-aphrodisiac that deters other males¹⁴⁵ and inject females with substances that inhibit them from producing pheromones that attract males¹⁴⁶. Post-copulatory gamete competition^{135,147} and sexual conflict^{136,148} are usually suggested as sources of selection on these traits, but in some cases signal efficiency¹³⁷ and mate choice may also play a role¹³⁴.

Traits related to the detection of chemical signals. Animals detect chemical signals using a series of molecular, physiological, and behavioral traits that are often sexually dimorphic. Darwin hypothesized that sexually dimorphic sensory capabilities arise via sexual selection when males bear the primary burden of mate search^{4,149}. In the 150 years since, research on sexual selection has focused more on signals and attributes of receiver sensory systems that influence the evolution of signals. Nevertheless, sexual dimorphism has been reported in many taxa and for nearly all levels of chemosensory detection (Table 2), ranging from the behaviors involved in sampling chemical stimuli¹⁵⁰ to the neural circuits involved in processing chemical stimuli^{151,152}. Importantly, sexual dimorphism in sensory traits can arise from differences in the ecology or biology of males and females rather than competition for mates^{149,153,154}. However, empirical evidence, especially from arthropods, supports Darwin's hypothesis that sexual selection via scramble competition favors greater chemosensory capacity in males^{86,155–158}. Similar selection on detection of chemicals from potential mates may also be important in broadcast spawners, some of which release gametes after exposure to chemicals in the sexual fluids of mates or competitors¹⁵⁹ and have higher reproductive success when given the first opportunity for fertilization¹⁶⁰. Interestingly, sexual selection may also act on chemosensory capabilities via mate choice; in moths, females may choose high-quality mates by releasing minute quantities of pheromone only detectable by males with the most sensitive olfactory systems¹⁴⁹. Sexual selection on chemosensory detection traits is less studied than sexual selection on chemical signals but may be especially important in many animals that use chemical information during scramble competition for mates or fertilizations¹⁵⁷.

Conclusions

Decades of empirical and theoretical research have focused on sexual selection as a major evolutionary driver of animal biodiversity. Signaling traits have been at the center of this work, as they are diverse, often appear extreme, and can lead to speciation when divergent preferences generate assortative mating. However, sexual selection as a broad and versatile evolutionary force across higher taxonomic levels of animals remains surprisingly understudied as most studies on sexual selection^{12,13}, animal behavior⁵⁶, and chemical communication⁹⁴ focus on very few clades. Furthermore, most research on sexual selection has

focused on communication via vision and hearing, which most animal phyla lack. In this Perspective, we reviewed the evidence for sexual selection on signaling traits across Animalia as a whole, with particular emphasis on chemosensory traits. Our review illustrates two especially important and related points, which we discuss below.

First, the broad scope of theory around sexual selection and animal signals stands in sharp contrast to the limited higher-level taxonomic distribution of supporting empirical studies. Clearly, extensive evidence supports sexual selection as a powerful evolutionary force on signaling traits in many species within a few clades^{1,5,6}, especially some arthropods and chordates^{12,13,56}. After searching for evidence of sexual selection on chemosensory traits across all animal phyla, classes, and orders, we found studies that meet established criteria of sexual selection¹ in 10 of 34 animal phyla, and studies that report possible indications of sexual selection on chemosensory traits in an additional 13 phyla. Despite the clear potential for sexual selection on chemical signaling traits across diverse taxa, additional work is needed even in taxa for which current evidence meets established criteria of sexual selection¹. Foremost is a basic need for more direct tests of sexual selection in most taxa; many studies we found only scratched the surface of how chemosensory traits could affect mate choice or competition. Even when traits clearly affect mate choice or competition, the actual strength of sexual selection on them depends on various deterministic (e.g., operational sex ratio) and random processes that underlie variation in mating success¹⁶¹. Our review indicates sexual selection could play a common role in the evolution of chemical communication but highlights the need for research that better reflects the diversity of animals (see Box 2).

The need for research that better represents all animals raises our second major point: chemosensory traits are arguably the primary (potential) target of sexual selection on communication when considering Animalia as a whole. A basic implication of this point is that chemosensation should be a key focus of research on sexual selection. This will ensure we do not underestimate the role of sexual selection in Animalia or predicate concepts about the prevailing mechanisms or consequences of sexual selection on sensory systems that may not be representative of many animals. Unfortunately, chemoreception is also among the least studied channels of communication¹², due, in part, to the challenge of identifying the molecules that make up signals¹⁰¹ and the cryptic nature of most chemical signals¹⁶². Human biases further inhibit research on chemoreception¹⁶², and are exemplified by the superlatives used to characterize the traits that inspired the theory of sexual selection and continue to hold the attention of evolutionary biologists; what is an ‘extreme’ or ‘striking’ chemical signal? Emphasis on chemosensation is key to understanding sexual selection as a potentially universal and potent evolutionary force on animal communication.

Many interesting questions about sexual selection on animal communication remain unanswered^{20,163}. We suggest one of the most fundamental of these is whether sexual selection acts as a salient evolutionary force on communication across Animalia. Admittedly, determining when this question has been answered is challenging. Nevertheless, pursuing the answer will reveal if and how the mechanisms and consequences of sexual selection differ across animals. This information is critical to develop a fuller understanding of how Earth’s animal diversity arose and to conserve this diversity in the face of rapid global change¹⁶⁴.

Box 2 | Looking forward

Recommendations. We offer several recommendations that could help the study of sexual selection on communication to better span across Animalia.

1. *Increase taxonomic diversity in studies of sexual selection on communication.* Prioritizing taxa for future study could depend on the specific research questions being addressed, but we hope our literature review (Suppl. Data 1) will be a useful guide for identifying key knowledge gaps.
2. *Consider the many potential targets of sexual selection.* The molecular, physiological, and behavioral scaffolding underlying chemical communication can be particularly useful for studying sexual selection¹⁸³ when the identity of a signal remains unknown or when the mating behavior of a species is poorly understood.
3. *Leverage new and developing techniques.* New and developing technology will likely accelerate research on chemical signals. For example, metabolomics—the global analysis of small molecules—shows promise as a powerful tool to study the molecular basis of chemosensory interactions¹⁸⁴. Similarly, we expect other omic techniques (genomics, transcriptomics) will shed new light on the molecular and physiological processes underlying sexual selection on chemical communication.
4. *Expand the community of researchers studying sexual selection.* Achieving wider taxonomic representation is likely to rely, in large part, on researchers with specific taxonomic or technological expertise who currently focus on other research questions. We call for a broader community of scientists to study sexual selection on communication, and especially invite the attention of biologists studying animals that are not well represented in the field (see Figs. 2 and 3, Supplementary Data 1).

Future directions. Better representation across Animalia will support macroevolutionary studies that can test fundamental hypotheses about sexual selection. For example, Wiens and Tuschhoff²⁰ provide an insightful discussion on how macroevolutionary studies could help explain the diversity of sexually selected signals and weapons. Below, we outline a few additional examples:

1. *Sexual selection and diversification of chemosensory receptors.* Chemoreceptors are encoded by some of the fastest evolving and largest gene families in the metazoan genome¹⁸⁵ and in some species evolved under sexual selection^{186,187}. Although chemoreceptor repertoires are well-characterized primarily in vertebrates and insects¹⁸⁸, this list is likely to grow rapidly with the number of animal genomes sequenced^{189–194}, putting in reach an understanding of how sexual selection shapes receiver evolution at a molecular level but macroevolutionary scale.
2. *Sexual selection and nervous system evolution.* The brain is a key player in the process of sexual selection and, for example, complicates sexual decisions by integrating inputs related to nonsexual tasks¹⁹⁵. However, animals differ considerably in the complexity of their nervous systems, both among¹⁹⁶ and within phyla¹⁹⁷. How does the role of sexual selection on communication track the evolution of the nervous system in animals?
3. *Sexual selection and speciation.* The role of sexual selection in speciation has been the focus of a vibrant discussion for decades^{7–11}. However, empirical tests of speciation by sexual selection have focused largely on arthropods and chordates⁹, which are among the most taxonomically rich phyla¹⁹⁸. Greater taxonomic diversity in research on sexual selection will likely enrich discussions on the role of sexual selection in speciation.

Data availability

Our paper presents no new data. The results of the literature review are provided as Supplementary data.

Received: 3 May 2023; Accepted: 10 November 2023;

Published online: 20 November 2023

References

- Andersson, M. *Sexual Selection* (Princeton University Press, 1994).
- Girard, M. B. & Endler, J. A. Peacock spiders. *Curr. Biol.* **24**, R588–R590 (2014).
- Shuker, D. M. & Kvarnemo, C. The definition of sexual selection. *Behav. Ecol.* **32**, 781–794 (2021).
- Darwin, C. *The Descent of Man, and Selection in Relation to Sex* (Princeton University Press, 1871).
- Andersson, M. & Iwasa, Y. Sexual selection. *Trends Ecol. Evol.* **11**, 53–58 (1996).
- Andersson, M. & Simmons, L. W. Sexual selection and mate choice. *Trends Ecol. Evol.* **21**, 296–302 (2006).
- Lande, R. Models of speciation by sexual selection on polygenic traits. *Proc. Natl. Acad. Sci. USA* **78**, 3721–3725 (1981).
- West-Eberhard, M. J. Sexual selection, social competition, and speciation. *Q. Rev. Biol.* **58**, 155–183 (1983).
- Mendelson, T. C. & Safran, R. J. Speciation by sexual selection: 20 years of progress. *Trends Ecol. Evol.* **36**, 1153–1163 (2021).
- Schaefer, H. M. & Ruxton, G. D. Signal diversity, sexual selection, and speciation. *Annu. Rev. Ecol. Syst.* **46**, 573–592 (2015).
- Servedio, M. R. & Boughman, J. W. The role of sexual selection in local adaptation and speciation. *Annu. Rev. Ecol. Syst.* **48**, 85–109 (2017).
- Coleman, S. W. Taxonomic and sensory biases in the mate-choice literature: there are far too few studies of chemical and multimodal communication. *Acta Ethol.* **12**, 45–48 (2009).
- Zuk, M., Garcia-Gonzalez, F., Herberstein, M. E. & Simmons, L. W. Model systems, taxonomic bias, and sexual selection: beyond *Drosophila*. *Annu. Rev. Entomol.* **59**, 321–338 (2014).
- Ryan, M. J., Fox, J. H., Wilczynski, W. & Rand, A. S. Sexual selection for sensory exploitation in the frog *Physalaemus pustulosus*. *Nature* **343**, 66–67 (1990).
- Endler, J. A. Signals, signal conditions, and the direction of evolution. *Am. Nat.* **139**, S125–S153 (1992).
- Christy, J. H. Mimicry, mate choice, and the sensory trap hypothesis. *Am. Nat.* **146**, 171–181 (1995).
- Ryan, M. J. & Cummings, M. E. Perceptual biases and mate choice. *Annu. Rev. Ecol. Syst.* **44**, 437–459 (2013).
- Rodd, F. H., Hughes, K. A., Grether, G. F. & Baril, C. T. A possible non-sexual origin of mate preference: are male guppies mimicking fruit? *Proc. R. Soc. B Biol. Sci.* **269**, 475–481 (2002).
- Hare, R. M. & Simmons, L. W. Sexual selection and its evolutionary consequences in female animals. *Biol. Rev. Camb. Philos. Soc.* **94**, 929–956 (2019).
- Wiens, J. J. & Tuschhoff, E. Songs versus colours versus horns: what explains the diversity of sexually selected traits? *Biol. Rev. Camb. Philos. Soc.* **95**, 847–864 (2020).
- Nilsson, D.-E. The diversity of eyes and vision. *Annu. Rev. Vis. Sci.* **7**, 19–41 (2021).
- Webster, D. B. Epilogue to the conference on the evolutionary biology of hearing. In *The Evolutionary Biology of Hearing* (eds Webster, D. B. et al.) 787–793 (Springer, 1992).
- Illiff, A. J. et al. The nematode *C. elegans* senses airborne sound. *Neuron* **109**, 3633–3646. e3637 (2021).
- Wyatt, T. D. *Pheromones and Animal Behavior: Chemical signals and Signatures* (Cambridge University Press, 2014).
- Haldane, J. B. S. Animal communication and the origin of human language. *Sci. Prog.* **43**, 385–401 (1955).
- Hildebrand, J. G. Analysis of chemical signals by nervous systems. *Proc. Natl. Acad. Sci. USA* **92**, 67–74 (1995).
- Hegde, M. et al. Chemotaxis to the quorum-sensing signal AI-2 requires the Tsr chemoreceptor and the periplasmic LsrB AI-2-binding protein. *J. Bacteriol.* **193**, 768–773 (2011).
- Charlesworth, J. C., Beloe, C., Watters, C. & Burns, B. P. Quorum sensing in archaea: recent advances and emerging directions. In *Biocommunication of Archaea* (ed. Witzany, G.) 119–132 (Springer, Cham, 2017).
- Luporini, P., Vallesi, A., Miceli, C. & Bradshaw, R. Chemical signaling in ciliates. *J. Eukaryot. Microbiol.* **42**, 208–212 (1995).
- Versele, M., Lemaire, K. & Thevelein, J. M. Sex and sugar in yeast: two distinct GPCR systems. *EMBO Rep.* **2**, 574–579 (2001).
- Wicher, D. Functional and evolutionary aspects of chemoreceptors. *Front. Cell. Neurosci.* **6**, 48 (2012).
- Derby, C. D. Chemoreception in aquatic invertebrates. In *The senses: A Comprehensive Reference* (eds Fritzsche, B. & W. Meyerhof) Vol. 3, 65–84 (Elsevier, Academic Press, 2020).
- Strausfeld, N. J. & Hildebrand, J. G. Olfactory systems: common design, uncommon origins? *Curr. Opin. Neurobiol.* **9**, 634–639 (1999).
- Mollo, E. et al. Taste and smell: a unifying chemosensory theory. *Q. Rev. Biol.* **97**, 69–94 (2022).
- Sasson, D. A., Jacques, A. A. & Ryan, J. F. The ctenophore *Mnemiopsis leidyi* regulates egg production via conspecific communication. *BMC Ecol.* **18**, 1–10 (2018).
- Endler, J. A. Some general comments on the evolution and design of animal communication systems. *Philos. Trans. R. Soc. B Biol. Sci.* **340**, 215–225 (1993).
- Sarà, M. Sessile macrofauna and marine ecosystem. *Ital. J. Zool.* **53**, 329–337 (1986).
- Klepal, W., Barnes, H. & Munn, E. The morphology and histology of the cirripede penis. *J. Exp. Mar. Biol. Ecol.* **10**, 243–265 (1972).
- Gaston, K. J. Nighttime ecology: the “nocturnal problem” revisited. *Am. Nat.* **193**, 481–502 (2019).
- Hölker, F., Wolter, C., Perkin, E. K. & Tockner, K. Light pollution as a biodiversity threat. *Trends Ecol. Evol.* **25**, 681–682 (2010).
- Bennie, J. J., Duffy, J. P., Inger, R. & Gaston, K. J. Biogeography of time partitioning in mammals. *Proc. Natl. Acad. Sci. USA* **111**, 13727–13732 (2014).
- Grassle, J. F. & Maciolek, N. J. Deep-sea species richness: regional and local diversity estimates from quantitative bottom samples. *Am. Nat.* **139**, 313–341 (1992).
- Orgiazzi, A., Bardgett, R. D. & Barrios, E. *Global Soil Biodiversity Atlas* (European Commission, 2016).
- Warrant, E. Vision in the dimmest habitats on earth. *J. Comp. Physiol. A Neuroethol. Sens. Neural Behav. Physiol.* **190**, 765–789 (2004).
- Barton, R., Purvis, A. & Harvey, P. Evolutionary radiation of visual and olfactory brain systems in primates, bats and insectivores. *Philos. Trans. R. Soc. B Biol. Sci.* **348**, 381–392 (1995).
- Healy, S. & Guilford, T. Olfactory-bulb size and nocturnality in birds. *Evolution* **44**, 339–346 (1990).
- Wagner, H.-J. Sensory brain areas in three families of deep-sea fish (slicheads, eels and grenadiers): comparison of mesopelagic and demersal species. *Mar. Biol.* **141**, 807–817 (2002).
- Bradbury, J. W. & Vehrencamp, S. L. *Principles of Animal Communication* (Sinauer Associates, 1998).
- Ruggiero, M. A. et al. A higher level classification of all living organisms. *PLoS ONE* **10**, e0119248 (2015).
- Bone, L. W. Reproductive chemical communication of helminths. I. Platyhelminthes. *Int. J. Invert. Reprod.* **5**, 261–268 (1982).
- Bone, L. W. Reproductive chemical communication of helminths. II. Aschelminthes. *Int. J. Invert. Reprod.* **5**, 311–321 (1982).
- Grieves, L. A. et al. Olfactory camouflage and communication in birds. *Biol. Rev. Camb. Philos. Soc.* **97**, 1193–1209 (2022).
- Brown, R. E. & Macdonald, D. W. *Social Odours in Mammals* (Oxford University Press, 1985).
- Mayer, M. S. & McLaughlin, J. R. *Handbook of Insect Pheromones and Sex Attractions* (CRC Press, 1991).
- Dougherty, L. R. Designing mate choice experiments. *Biol. Rev. Camb. Philos. Soc.* **95**, 759–781 (2020).
- Rosenthal, M. F., Gertler, M., Hamilton, A. D., Prasad, S. & Andrade, M. C. Taxonomic bias in animal behaviour publications. *Anim. Behav.* **127**, 83–89 (2017).
- Westermann, B. & Beuerlein, K. Y-maze experiments on the chemotactic behaviour of the tetrabranchiate cephalopod *Nautilus pompilius* (Mollusca). *Mar. Biol.* **147**, 145–151 (2005).
- Sombke, A. & Müller, C. H. When SEM becomes a deceptive tool of analysis: the unexpected discovery of epidermal glands with stalked ducts on the ultimate legs of geophilomorph centipedes. *Front. Zool.* **18**, 1–19 (2021).
- Mendelson, T. C. & Shaw, K. L. The (mis) concept of species recognition. *Trends Ecol. Evol.* **27**, 421–427 (2012).
- Stacey, N. Hormonally derived pheromones in teleost fishes. In *Fish Pheromones and Related Cues* (eds Sorensen, P. W. & B. D. Wisenden) 33–88 (John Wiley & Sons, 2015).
- Sorensen, P. & Scott, A. The evolution of hormonal sex pheromones in teleost fish: poor correlation between the pattern of steroid release by goldfish and olfactory sensitivity suggests that these cues evolved as a result of chemical spying rather than signal specialization. *Acta Physiol. Scand.* **152**, 191–205 (1994).
- Appelt, C. W. & Sorensen, P. W. Female goldfish signal spawning readiness by altering when and where they release a urinary pheromone. *Anim. Behav.* **74**, 1329–1338 (2007).

63. Houck, L. et al. A new vertebrate courtship pheromone, PMF, affects female receptivity in a terrestrial salamander. *Anim. Behav.* **73**, 315–320 (2007).
64. Willaert, B. et al. Frog nuptial pads secrete mating season-specific proteins related to salamander pheromones. *J. Exp. Biol.* **216**, 4139–4143 (2013).
65. Beekman, M., Nieuwenhuis, B., Ortiz-Barrionos, D. & Evans, J. P. Sexual selection in hermaphrodites, sperm and broadcast spawners, plants and fungi. *Philos. Trans. R. Soc. B Biol. Sci.* **371**, 20150541 (2016).
66. Jackson, C. L. & Hartwell, L. H. Courtship in *S. cerevisiae*: both cell types choose mating partners by responding to the strongest pheromone signal. *Cell* **63**, 1039–1051 (1990).
67. Dunny, G. M., Brown, B. L. & Clewell, D. B. Induced cell aggregation and mating in *Streptococcus faecalis*: evidence for a bacterial sex pheromone. *Proc. Natl. Acad. Sci. USA* **75**, 3479–3483 (1978).
68. Gillard, J. et al. Metabolomics enables the structure elucidation of a diatom sex pheromone. *Angew. Chem. Int. Ed.* **52**, 854–857 (2013).
69. Frenkel, J., Vyveman, W. & Pohner, G. Pheromone signaling during sexual reproduction in algae. *Plant J.* **79**, 632–644 (2014).
70. Funch, P. & Kristensen, R. M. Cycliophora is a new phylum with affinities to Entoprocta and Ectoprocta. *Nature* **378**, 711–714 (1995).
71. Kristensen, R. M. Loricifera, a new phylum with Aschelminthes characters from the meiobenthos. *Z. für zoologische Systematik und Evolutionsforschung* **21**, 163–180 (1983).
72. Kristensen, R. & Funch, P. Micrognathozoa: a new class with complicated jaws like those of Rotifera and Gnathostomulida. *J. Morphol.* **246**, 1–49 (2000).
73. Sørensen, M.V. & Kristensen, R. M. Micrognathozoa. In *Gastrotricha and Gnathifera* (ed. Schmidt-Rhaesa, A.) Vol. 3, 197–216 (De Gruyter, 2014).
74. Schierwater, B. & DeSalle, R. Placozoa. *Curr. Biol.* **28**, R97–R98 (2018).
75. Raikova, E. V. Life cycle, cytology, and morphology of *Polypodium hydriforme*, a coelenterate parasite of the eggs of acipenseriform fishes. *J. Parasitol.* **80**, 1–22 (1994).
76. Smith, J. L. B. A living coelacanthid fish from South Africa. *Nature* **143**, 748–750 (1939).
77. Lampert, K. P. et al. Single-male paternity in coelacanth. *Nat. Commun.* **4**, 1–7 (2013).
78. Watts, R. A. et al. Stabilizing selection on behavior and morphology masks positive selection on the signal in a salamander pheromone signaling complex. *Mol. Biol. Evol.* **21**, 1032–1041 (2004).
79. Brant, C. O., Chung-Davidson, Y.-W., Li, K., Scott, A. M. & Li, W. Biosynthesis and release of pheromonal bile salts in mature male sea lamprey. *BMC Biochem.* **14**, 1–11 (2013).
80. Buchinger, T. J. et al. Increased pheromone signaling by small male sea lamprey has distinct effects on female mate search and courtship. *Behav. Ecol. Sociobiol.* **71**, 1–8 (2017).
81. Siefkes, M. J., Scott, A. P., Zielinski, B., Yun, S.-S. & Li, W. Male sea lampreys, *Petromyzon marinus* L., excrete a sex pheromone from gill epithelia. *Biol. Reprod.* **69**, 125–132 (2003).
82. Fissette, S. D. et al. Diel patterns of pheromone release by male sea lamprey. *Integr. Comp. Biol.* **61**, 1795–1810 (2021).
83. Fissette, S. D., Bussy, U., Huerta, B., Buchinger, T. J. & Li, W. Evidence that male sea lamprey increase pheromone release after perceiving a competitor. *J. Exp. Biol.* **223**, jeb226647 (2020).
84. Buchinger, T. J. et al. Intra- and interspecific variation in production of bile acids that act as sex pheromones in lampreys. *Physiol. Biochem. Zool.* **92**, 463–472 (2019).
85. Johansson, B. G. & Jones, T. M. The role of chemical communication in mate choice. *Biol. Rev. Camb. Philos. Soc.* **82**, 265–289 (2007).
86. Jayaweera, A. & Barry, K. L. Male antenna morphology and its effect on scramble competition in false garden mantids. *Sci. Nat.* **104**, 1–9 (2017).
87. Rollmann, S. M., Houck, L. D. & Feldhoff, R. C. Proteinaceous pheromone affecting female receptivity in a terrestrial salamander. *Science* **285**, 1907–1909 (1999).
88. Yoshida, M., Murata, M., Inaba, K. & Morisawa, M. A chemoattractant for ascidian spermatozoa is a sulfated steroid. *Proc. Natl. Acad. Sci. USA* **99**, 14831–14836 (2002).
89. Zeeck, E., Hardege, J., Bartels-Hardege, H. & Wesselmann, G. Sex pheromone in a marine polychaete: determination of the chemical structure. *J. Exp. Zool.* **246**, 285–292 (1988).
90. Li, K., Buchinger, T. J. & Li, W. Discovery and characterization of natural products that act as pheromones in fish. *Nat. Prod. Rep.* **35**, 501–513 (2018).
91. Mori, K. Significance of chirality in pheromone science. *Bioorg. Med. Chem.* **15**, 7505–7523 (2007).
92. Steiger, S., Schmitt, T. & Schaefer, H. M. The origin and dynamic evolution of chemical information transfer. *Proc. R. Soc. B Biol. Sci.* **278**, 970–979 (2011).
93. Kaae, R., Shorey, H. & Gaston, L. K. Pheromone concentration as a mechanism for reproductive isolation between two lepidopterous species. *Science* **179**, 487–488 (1973).
94. Symonds, M. R. & Elgar, M. A. The evolution of pheromone diversity. *Trends Ecol. Evol.* **23**, 220–228 (2008).
95. Löfstedt, C. Moth pheromone genetics and evolution. *Philos. Trans. R. Soc. B Biol. Sci.* **340**, 167–177 (1993).
96. De Pasqual, C., Groot, A. T., Mappes, J. & Burdfield-Steel, E. Evolutionary importance of intraspecific variation in sex pheromones. *Trends Ecol. Evol.* **36**, 848–859 (2021).
97. Steiger, S. & Stöckl, J. The role of sexual selection in the evolution of chemical signals in insects. *Insects* **5**, 423–438 (2014).
98. Eisner, T. & Meinwald, J. The chemistry of sexual selection. *Proc. Natl. Acad. Sci. USA* **92**, 50–55 (1995).
99. Nishida, R. Sequestration of defensive substances from plants by Lepidoptera. *Annu. Rev. Entomol.* **47**, 57–92 (2002).
100. Milinski, M. et al. Mate choice decisions of stickleback females predictably modified by MHC peptide ligands. *Proc. Natl. Acad. Sci. USA* **102**, 4414–4418 (2005).
101. Yohe, L. R. & Brand, P. Evolutionary ecology of chemosensation and its role in sensory drive. *Curr. Zool.* **64**, 525–533 (2018).
102. Herzner, G., Schmitt, T., Linsenmair, K. E. & Strohm, E. Prey recognition by females of the European bee wolf and its potential for a sensory trap. *Anim. Behav.* **70**, 1411–1418 (2005).
103. Rodríguez-Ruiz, G., López, P. & Martín, J. Possible reproductive benefits to female Carpetan rock lizards of pre-sensory bias towards chemical signals. *Biol. J. Linn. Soc.* **127**, 787–799 (2019).
104. Buchinger, T. J., Wang, H., Li, W. & Johnson, N. S. Evidence for a receiver bias underlying female preference for a male mating pheromone in sea lamprey. *Proc. R. Soc. B Biol. Sci.* **280**, 20131966 (2013).
105. Poling, K. R., Fraser, E. J. & Sorensen, P. W. The three steroidal components of the goldfish preovulatory pheromone signal evoke different behaviors in males. *Comp. Biochem. Physiol. B Biochem.* **129**, 645–651 (2001).
106. Sorensen, P., Pinillos, M. & Scott, A. Sexually mature male goldfish release large quantities of androstenedione into the water where it functions as a pheromone. *Gen. Comp. Endocrinol.* **140**, 164–175 (2005).
107. Ng, S. H. et al. Pheromone evolution and sexual behavior in *Drosophila* are shaped by male sensory exploitation of other males. *Proc. Natl. Acad. Sci. USA* **111**, 3056–3061 (2014).
108. Baeckens, S., Martín, J., García-Roa, R. & Van Damme, R. Sexual selection and the chemical signal design of lacertid lizards. *Zool. J. Linn. Soc.* **183**, 445–457 (2018).
109. Brückner, A. & Parker, J. Molecular evolution of gland cell types and chemical interactions in animals. *J. Exp. Biol.* **223**, jeb211938 (2020).
110. Pei, X.-J. et al. Modulation of fatty acid elongation in cockroaches sustains sexually dimorphic hydrocarbons and female attractiveness. *PLoS Biol.* **19**, e3001330 (2021).
111. Ma, P. W. & Ramaswamy, S. B. Biology and ultrastructure of sex pheromone-producing tissue. In *Insect Biochemistry and Molecular Biology* (eds Blomquist, G. & R. Vogt) 19–51 (Elsevier, 2003).
112. Barata, E. N. et al. Putative pheromones from the anal glands of male blennies attract females and enhance male reproductive success. *Anim. Behav.* **75**, 379–389 (2008).
113. Whittaker, D. J. & Hagelin, J. C. Female-based patterns and social function in avian chemical communication. *J. Chem. Ecol.* **47**, 43–62 (2021).
114. Bossuyt, F. et al. Multiple independent recruitment of sodefrin precursor-like factors in anuran sexually dimorphic glands. *Mol. Biol. Evol.* **36**, 1921–1930 (2019).
115. Mason, R. T. & Parker, M. R. Social behavior and pheromonal communication in reptiles. *J. Comp. Physiol. A Neuroethol. Sens. Neural Behav. Physiol.* **196**, 729–749 (2010).
116. Elliott, S., Tait, N. & Briscof, D. A pheromonal function for the crural glands of the onychophoran *Cephalofovea tomahmontis* (Onychophora: Peripatopsidae). *J. Zool.* **231**, 1–9 (1993).
117. Roe, P. & Norenburg, J. L. Morphology and taxonomic distribution of a newly discovered feature, postero-lateral glands, in pelagic nemertean. *Hydrobiologia* **456**, 133–144 (2001).
118. Schnier, J. et al. Ultrastructure of the epidermal gland system of *Tetranchyroderma suecicum* Boaden, 1960 (Gastrotricha: Macrodasysida) indicates a defensive function of its exudate. *Zoomorphology* **138**, 443–462 (2019).
119. Kearn, G. & Whittington, I. Sperm transfer in monogenean (platyhelminth) parasites. *Acta Parasitol.* **60**, 567–600 (2015).
120. Keller-Costa, T. et al. Muscular hypertrophy of urinary bladders in dominant tilapia facilitates the control of aggression through urinary signals. *Behaviour* **149**, 953–975 (2012).
121. Zizzari, Z. V. et al. Love at first sniff: a spermatophore-associated pheromone mediates partner attraction in a collembolan species. *Anim. Behav.* **124**, 221–227 (2017).
122. Haga, S. et al. The male mouse pheromone ESP1 enhances female sexual receptive behaviour through a specific vomeronasal receptor. *Nature* **466**, 118–122 (2010).

123. Johannesson, K. et al. Male discrimination of female mucous trails permits assortative mating in a marine snail species. *Evolution* **62**, 3178–3184 (2008).
124. Nisa Ramiro, C. et al. Chemosensory discrimination of male age by female *Psammotromus algirus* lizards based on femoral secretions and feces. *Ethology* **125**, 802–809 (2019).
125. Rajagopal, T., Archunan, G., Geraldine, P. & Balasundaram, C. Assessment of dominance hierarchy through urine scent marking and its chemical constituents in male blackbuck *Antelope cervicapra*, a critically endangered species. *Behav. Process.* **85**, 58–67 (2010).
126. Cartolano, M. C., Babcock, E. A. & McDonald, M. D. Evidence that Gulf toadfish use pulsatile urea excretion to communicate social status. *Physiol. Behav.* **227**, 113182 (2020).
127. Marneweck, C., Jürgens, A. & Shrader, A. Ritualised dung kicking by white rhino males amplifies olfactory signals but reduces odour duration. *J. Chem. Ecol.* **44**, 875–885 (2018).
128. Marneweck, C., Jürgens, A. & Shrader, A. M. The role of middens in white rhino olfactory communication. *Anim. Behav.* **140**, 7–18 (2018).
129. Christy, J. H. & Rittschof, D. Deception in visual and chemical communication in crustaceans. In *Chemical Communication in Crustaceans* (eds Breithaupt, T. & M. Thiel) 313–333 (Springer, 2010).
130. MacGillivray, T., Spezie, G. & Fusani, L. When less is more: coy display behaviours and the temporal dynamics of animal courtship. *Proc. R. Soc. B Biol. Sci.* **290**, 20231684 (2023).
131. Rosenthal, G. G., Fitzsimmons, J. N., Woods, K. U., Gerlach, G. & Fisher, H. S. Tactile release of a sexually-selected pheromone in a swordtail fish. *PLoS ONE* **6**, e16994 (2011).
132. Hurst, J., Robertson, D., Tolladay, U. & Beynon, R. Proteins in urine scent marks of male house mice extend the longevity of olfactory signals. *Anim. Behav.* **55**, 1289–1297 (1998).
133. Lazar, J., Rasmussen, L., Greenwood, D. R., Bang, I.-S. & Prestwich, G. D. Elephant albumin: a multipurpose pheromone shuttle. *Chem. Biol.* **11**, 1093–1100 (2004).
134. Koene, J. M. & Ter Maat, A. Allohormones: a class of bioactive substances favoured by sexual selection. *J. Comp. Physiol. A Neuroethol. Sens. Neural Behav. Physiol.* **187**, 323–326 (2001).
135. Chase, R. & Blanchard, K. C. The snail's love-dart delivers mucus to increase paternity. *Proc. R. Soc. B Biol. Sci.* **273**, 1471–1475 (2006).
136. Koene, J. M., Pförtner, T. & Michiels, N. K. Piercing the partner's skin influences sperm uptake in the earthworm *Lumbricus terrestris*. *Behav. Ecol. Sociobiol.* **59**, 243–249 (2005).
137. Schulte, L. M., Martel, A., Cruz-Elizalde, R., Ramírez-Bautista, A. & Bossuyt, F. Love bites: male frogs (Plectrohyla, Hylidae) use teeth scratching to deliver sodefrin precursor-like factors to females during amplexus. *Front. Zool.* **18**, 1–14 (2021).
138. Gillott, C. Male accessory gland secretions: modulators of female reproductive physiology and behavior. *Annu. Rev. Entomol.* **48**, 163–184 (2003).
139. Gwynne, D. T. Sexual conflict over nuptial gifts in insects. *Annu. Rev. Entomol.* **53**, 83–101 (2008).
140. Ruther, J. & Steidle, J. L. “Allohormones”: a new class of bioactive substances or old wine in new skins? *J. Comp. Physiol. A Neuroethol. Sens. Neural Behav. Physiol.* **188**, 161–162 (2002).
141. Wigby, S. et al. The *Drosophila* seminal proteome and its role in postcopulatory sexual selection. *Philos. Trans. R. Soc. B Biol. Sci.* **375**, 20200072 (2020).
142. Kimura, K., Shibuya, K. & Chiba, S. The mucus of a land snail love-dart suppresses subsequent matings in darted individuals. *Anim. Behav.* **85**, 631–635 (2013).
143. Patlar, B., Weber, M., Temizyürek, T. & Ramm, S. A. Seminal fluid-mediated manipulation of post-mating behavior in a simultaneous hermaphrodite. *Curr. Biol.* **30**, 143–149. e144 (2020).
144. Thomas, M. L. Detection of female mating status using chemical signals and cues. *Biol. Rev. Camb. Philos. Soc.* **86**, 1–13 (2011).
145. Hosseini, S. A. et al. Experimental evidence for chemical mate guarding in a moth. *Sci. Rep.* **6**, 1–6 (2016).
146. Kingan, T. G., Bodnar, W. M., Raina, A. K., Shabanowitz, J. & Hunt, D. F. The loss of female sex pheromone after mating in the corn earworm moth *Helioverpa zea*: identification of a male pheromonostatic peptide. *Proc. Natl. Acad. Sci. USA* **92**, 5082–5086 (1995).
147. Wigby, S. et al. Seminal fluid protein allocation and male reproductive success. *Curr. Biol.* **19**, 751–757 (2009).
148. Wigby, S. & Chapman, T. Sex peptide causes mating costs in female *Drosophila melanogaster*. *Curr. Biol.* **15**, 316–321 (2005).
149. Elgar, M. A., Johnson, T. L. & Symonds, M. R. Sexual selection and organs of sense: Darwin's neglected insight. *Anim. Biol.* **69**, 63–82 (2019).
150. Loudon, C. & Koehl, M. Sniffing by a silkworm moth: wing fanning enhances air penetration through and pheromone interception by antennae. *J. Exp. Biol.* **203**, 2977–2990 (2000).
151. Stowers, L. & Logan, D. W. Sexual dimorphism in olfactory signaling. *Curr. Opin. Neurobiol.* **20**, 770–775 (2010).
152. Williams, A. T., Verhulst, E. C. & Haverkamp, A. A unique sense of smell: development and evolution of a sexually dimorphic antennal lobe—a review. *Entomol. Exp. Appl.* **170**, 303–318 (2022).
153. Allen, C. E., Zwaan, B. J. & Brakefield, P. M. Evolution of sexual dimorphism in the Lepidoptera. *Annu. Rev. Entomol.* **56**, 445–464 (2011).
154. Shine, R. Ecological causes for the evolution of sexual dimorphism: a review of the evidence. *Q. Rev. Biol.* **64**, 419–461 (1989).
155. Hanks, L. M., Millar, J. G. & Paine, T. D. Body size influences mating success of the eucalyptus longhorned borer (Coleoptera: Cerambycidae). *J. Insect Behav.* **9**, 369–382 (1996).
156. Holwell, G., Barry, K. & Herberstein, M. Mate location, antennal morphology, and ecology in two praying mantids (Insecta: Mantodea). *Biol. J. Linn. Soc.* **91**, 307–313 (2007).
157. Lefebvre, F., Limousin, M. & Caubet, Y. Sexual dimorphism in the antennae of terrestrial isopods: a result of male contests or scramble competition? *Can. J. Zool.* **78**, 1987–1993 (2000).
158. Johnson, T. L., Symonds, M. R. & Elgar, M. A. Sexual selection on receptor organ traits: younger females attract males with longer antennae. *Sci. Nat.* **104**, 44 (2017).
159. Lin, C. Y., Tung, C. H., Yu, J. K. & Su, Y. H. Reproductive periodicity, spawning induction, and larval metamorphosis of the hemichordate acorn worm *Ptychodera flava*. *J. Exp. Zool. B Mol. Dev. Evol.* **326**, 47–60 (2016).
160. Marshall, D. & Evans, J. Does egg competition occur in marine broadcast-spawners? *J. Evol. Biol.* **18**, 1244–1252 (2005).
161. Jennions, M., Kokko, H. & Klug, H. The opportunity to be misled in studies of sexual selection. *J. Evol. Biol.* **25**, 591–598 (2012).
162. Caves, E. M., Nowicki, S. & Johnsen, S. Von Uexküll revisited: addressing human biases in the study of animal perception. *Integr. Comp. Biol.* **59**, 1451–1462 (2019).
163. Jones, A. G. & Ratterman, N. L. Mate choice and sexual selection: what have we learned since Darwin? *Proc. Natl. Acad. Sci. USA* **106**, 10001–10008 (2009).
164. Candolin, U. Mate choice in a changing world. *Biol. Rev. Camb. Philos. Soc.* **94**, 1246–1260 (2019).
165. Breithaupt, T. & Eger, P. Urine makes the difference: chemical communication in fighting crayfish made visible. *J. Exp. Biol.* **205**, 1221–1231 (2002).
166. Shibuya, K., Chiba, S. & Kimura, K. Sexual inactivation induced by the mucus that covers land snail love darts: sexual selection and evolution of allohormones in hermaphrodites. *J. Exp. Biol.* **225**, jeb238782 (2022).
167. Borne, F., Kasimatis, K. R. & Phillips, P. C. Quantifying male and female pheromone-based mate choice in *Caenorhabditis* nematodes using a novel microfluidic technique. *PLoS ONE* **12**, e0189679 (2017).
168. Hussain, Y. H., Guasto, J. S., Zimmer, R. K., Stocker, R. & Riffell, J. A. Sperm chemotaxis promotes individual fertilization success in sea urchins. *J. Exp. Biol.* **219**, 1458–1466 (2016).
169. Hussain, Y. H., Sadilek, M., Salad, S., Zimmer, R. K. & Riffell, J. A. Individual female differences in chemoattractant production change the scale of sea urchin gamete interactions. *Dev. Biol.* **422**, 186–197 (2017).
170. Koene, J. M. Tales of two snails: sexual selection and sexual conflict in *Lymnaea stagnalis* and *Helix aspersa*. *Integr. Comp. Biol.* **46**, 419–429 (2006).
171. Katoh, E., Johnson, M. & Breithaupt, T. Fighting behaviour and the role of urinary signals in dominance assessment of Norway lobsters, *Nephrops norvegicus*. *Behaviour* **145**, 1447–1464 (2008).
172. Bertin, A. & Cezilly, F. Sexual selection, antennae length and the mating advantage of large males in *Asellus aquaticus*. *J. Evol. Biol.* **16**, 491–500 (2003).
173. Chang, H. et al. Pheromone binding proteins enhance the sensitivity of olfactory receptors to sex pheromones in *Chilo suppressalis*. *Sci. Rep.* **5**, 13093 (2015).
174. Jönsson, M. et al. Sex-specific expression of pheromones and other signals in gravid starfish. *BMC Biol.* **20**, 1–18 (2022).
175. Datta, S. R. et al. The *Drosophila* pheromone *cVA* activates a sexually dimorphic neural circuit. *Nature* **452**, 473–477 (2008).
176. Hajdukova, M., Jindra, M., Herman, M. A. & Asahina, M. The nuclear receptor NHR-25 cooperates with the Wnt/ β -catenin asymmetry pathway to control differentiation of the T seam cell in *C. elegans*. *J. Cell Sci.* **122**, 3051–3060 (2009).
177. Maruska, K. P. & Fernald, R. D. Contextual chemosensory urine signaling in an African cichlid fish. *J. Exp. Biol.* **215**, 68–74 (2012).
178. Telford, M. J., Budd, G. E. & Philippe, H. Phylogenomic insights into animal evolution. *Curr. Biol.* **25**, R876–R887 (2015).
179. Johnson, N. S., Yun, S.-S., Thompson, H. T., Brant, C. O. & Li, W. A synthesized pheromone induces upstream movement in female sea lamprey and summons them into traps. *Proc. Natl. Acad. Sci. USA* **106**, 1021–1026 (2009).
180. Morris, R. Some aspects of the structure and cytology of the gills of *Lampetra fluviatilis*. *J. Cell Sci.* **3**, 473–485 (1957).

181. Ruxton, G. & Schaefer, H. Resolving current disagreements and ambiguities in the terminology of animal communication. *J. Evol. Biol.* **24**, 2574–2585 (2011).
182. Koene, J. M. & Ter Maat, A. The distinction between pheromones and all hormones. *J. Comp. Physiol. A Neuroethol. Sens. Neural Behav. Physiol.* **188**, 163–164 (2002).
183. Weiss, K., Herzner, G. & Strohm, E. Sexual selection and the evolution of male pheromone glands in philanthine wasps (Hymenoptera, Crabronidae). *BMC Evol. Biol.* **17**, 1–20 (2017).
184. Kuhlisch, C. & Pohnert, G. Metabolomics in chemical ecology. *Nat. Prod. Rep.* **32**, 937–955 (2015).
185. Nei, M., Niimura, Y. & Nozawa, M. The evolution of animal chemosensory receptor gene repertoires: roles of chance and necessity. *Nat. Rev. Genet.* **9**, 951–963 (2008).
186. Hickner, P. V. et al. Molecular signatures of sexual communication in the phlebotomine sand flies. *PLoS Negl. Trop. Dis.* **14**, e0008967 (2020).
187. Wyer, C. A., Cator, L. J. & Hollis, B. Release from sexual selection leads to rapid genome-wide evolution in *Aedes aegypti*. *Curr. Biol.* **33**, 1351–1357. e1355 (2023).
188. Touhara, K. & Vosshall, L. B. Sensing odorants and pheromones with chemosensory receptors. *Ann. Rev. Physiol.* **71**, 307–332 (2009).
189. Churcher, A. M. & Taylor, J. S. The antiquity of chordate odorant receptors is revealed by the discovery of orthologs in the cnidarian *Nematostella vectensis*. *Genome Biol. Evol.* **3**, 36–43 (2011).
190. Cummins, S. F. et al. Candidate chemoreceptor subfamilies differentially expressed in the chemosensory organs of the mollusc *Aplysia*. *BMC Biol.* **7**, 1–20 (2009).
191. Marquet, N. et al. Holothurians have a reduced GPCR and odorant receptor-like repertoire compared to other echinoderms. *Sci. Rep.* **10**, 1–16 (2020).
192. Roberts, R. E. et al. Identification of putative olfactory G-protein coupled receptors in Crown-of-Thorns starfish, *Acanthaster planci*. *BMC Genom.* **18**, 1–15 (2017).
193. Sania, R. E. et al. A new subfamily of ionotropic glutamate receptors unique to the echinoderms with putative sensory role. *Mol. Ecol.* **30**, 6642–6658 (2021).
194. Thomas, J. H. & Robertson, H. M. The Caenorhabditis chemoreceptor gene families. *BMC Biol.* **6**, 1–17 (2008).
195. Ryan, M. J. Darwin, sexual selection, and the brain. *Proc. Natl. Acad. Sci. USA.* **118**, e2008194118 (2021).
196. Arendt, D., Tosches, M. A. & Marlow, H. From nerve net to nerve ring, nerve cord and brain—evolution of the nervous system. *Nat. Rev. Neurosci.* **17**, 61–72 (2016).
197. Holland, L. Z. The origin and evolution of chordate nervous systems. *Philos. Trans. R. Soc. B Biol. Sci.* **370**, 20150048 (2015).
198. Mora, C., Tittensor, D. P., Adl, S., Simpson, A. G. & Worm, B. How many species are there on Earth and in the ocean? *PLoS Biol.* **9**, e1001127 (2011).

Acknowledgements

The authors were supported with funding from the Great Lakes Fishery Commission and the Great Lakes Fishery Trust. Thanks to Skye Fissette for reviewing several drafts of the paper and helping create Fig. 4, and to Leanne Grieves for providing the photo of a preen gland. Thomas Blankers and two anonymous reviewers provided insightful suggestions that greatly improved the manuscript.

Author contributions

The paper was conceived by T.J.B. and W.L., drafted by T.J.B., and revised by T.J.B. and W.L.

Competing interests

The authors declare no competing interests.

Additional information

Supplementary information The online version contains supplementary material available at <https://doi.org/10.1038/s42003-023-05572-w>.

Correspondence and requests for materials should be addressed to Tyler J. Buchinger.

Peer review information *Communications Biology* thanks Ignacio Escalante, Thomas Blankers and the other, anonymous, reviewer(s) for their contribution to the peer review of this work. Primary Handling Editor: Manuel Breuer.

Reprints and permission information is available at <http://www.nature.com/reprints>

Publisher's note Springer Nature remains neutral with regard to jurisdictional claims in published maps and institutional affiliations.



Open Access This article is licensed under a Creative Commons Attribution 4.0 International License, which permits use, sharing, adaptation, distribution and reproduction in any medium or format, as long as you give appropriate credit to the original author(s) and the source, provide a link to the Creative Commons licence, and indicate if changes were made. The images or other third party material in this article are included in the article's Creative Commons licence, unless indicated otherwise in a credit line to the material. If material is not included in the article's Creative Commons licence and your intended use is not permitted by statutory regulation or exceeds the permitted use, you will need to obtain permission directly from the copyright holder. To view a copy of this licence, visit <http://creativecommons.org/licenses/by/4.0/>.

© The Author(s) 2023