Lost in Translation: Adaptation of Mating Signals in Changing Environments

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Abstract Competition for mates is often intense and the ability of an individual to attract a mate is highly dependent on the traits that enable an animal to compete and communicate effectively with conspecifics. The animal's sensory system must be tuned to receive and process specific information and such information must be relayed clearly and efficiently. Signalling individuals must also assess their environment in order to produce a suitable signal, and possess the apparatus required to produce this signal. Traits that provide such signalling opportunities do so provided that the signalling behaviour or trait, sensory reception and surrounding environment facilitate both transmission and reception. If the surrounding environment is altered in any way, then this can compromise either signal transmission or reception or both, so communication is likely to break down. It is therefore important, and often essential, that animals have a plastic response to such changes in order to attract mates, avoid predation and find food resource in changing environmental conditions. Three 'critical signalling factors', signal (behaviour/trait), response (signal-induced behavioural response) and sensory systems should co-evolve to ensure reliable communication. This review discusses the interaction of sensory ecology and the environment in shaping signalling and decision-making within mating systems.

Keywords Sensory drive · Sensory bias · Behaviour · Evolution · Plasticity · Sexual selection · Communication

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Introduction

Animals communicate for a number of purposes and have developed a vast repertoire of signals in order to achieve this accurately. Because signals that are attractive or conspicuous to intended receivers are also susceptible to detection by predators, parasites and competitors, they frequently represent a trade-off between opposing selective directions. This constraint is apparent in many signalling systems [49, 59, 72, 113, 115, 195] but is further limited by another consideration, environmental stochasticity. The environmental conditions in which a signal is communicated will have consequences for the emission, transmission and reception of the signal which in turn can alter the behavioural responses of the receiver. An environmentally altered signal can therefore have important consequences at both the individual [217] and population [135, 184] levels by altering immediate individual behaviour and/or long-term evolution. It is thus essential that signals are tuned to the environment in which they are used, especially if such signals represent a part of mating behaviour.

In order for a signal to be effective, three 'critical signalling factors', the signal itself, the receiver's sensory system and the receiver's response, must be in tune with the environmental conditions that carry the signal [69]. If, in a changing environment, one or more of these factors is disrupted, the ability of a receiver to interpret the communication may become impaired or lost entirely. For example, if light environment is changed, visually based signals may become altered therefore affecting the reception and interpretation of the receiver, resulting in a changed, or absent, response. The consequences can be problematic if this signal limits or alters detection by potential mates or if the signal is intercepted instead by eavesdroppers such as predators or competitors. In such

cases it would be expected that selection should act to restore the efficacy of the signal in the new environment, through any of the critical signalling factors. This has indeed been shown in a variety of species [39, 59, 80, 87, 97, 135, 142, 145, 177]. Furthermore, the adaptive nature of each of the three critical signalling factors has been demonstrated individually [74, 88, 93, 94, 134, 185] providing evidence that selection drives evolution via such sensory functions.

Sensory Drive

The Sensory Drive hypothesis [64], stipulates that the three critical signalling factors, senses, signals and responses, will co-evolve and that signal transmission relies on several co-adapted traits which are influenced by differences in environmental conditions. The model predicts that changes in the signalling environment will influence the evolution of signalling traits, signalling behaviour and behaviour of receivers. This in turn will influence the evolution of habitat choice, the sensory system and brain, leading to multiple cycles of correlated selection on the senses, signals and signal responses. Although sensory drive can apply to any process that affects the outcome of an individual's fitness, predation [59], competition [76] and foraging behaviour [173, 191], it is most widely studied in the context of sexual selection. For example, males that create a signal best matched to stimulate a female's senses in a given environment will out-compete those that produce a poorer signal. Within the context of sexual selection, sensory drive has the potential to work via a number of mechanisms: neuronal processes, genetic regulation, behavioural plasticity and sensory systems. The field of sensory ecology teases apart these interactions and studies have demonstrated all parts of the process, although they have yet to demonstrate the process as a whole. Methods to date include phylogenetic analysis of traits and behaviours [8, 9], genetic studies on the linkage of preference and trait [88], field experiments [59] and molecular studies [30, 185]. Testable hypotheses include: (i) animals living in similar environments use similar signalling patterns and should evolve in a similar direction, (ii) habitat specificity should bias the direction of selection, (iii) successful communication in a given environment should be derived from the fewest number of evolutionary changes, (iv) animals should lose costly traits that are no longer suited to the signalling environment, and (v) sensory environmental change should lead to predictable gains and losses of signal, signal response and sensory traits.

Sensory drive is thought to occur within many different animal communication systems [72, 80, 87, 135, 142, 177, 198] and provides one explanation for differences in mate choice between [72, 87] and within [135] populations of the same species. For example, guppies use highly developed vision [207] to detect food, mates and predators, and it has been shown that changing signalling environment leads to evolution in signals, mate choice and behaviour [63, 64, 66–68, 94, 129]. A fundamental study demonstrated that populations subject to different light conditions in different locations are subject to different visual environments [63] and exhibit different mating preferences [72, 112] and evolutionary responses to predators [59, 60]. The importance of sensory drive should not be underestimated; it is thought that this process can lead to speciation through sexual selection in some systems [19, 20, 72, 135, 184]. Figure 1 shows a simplified version of the interactions involved.

An intriguing subject, aspects of the sensory drive theory are easily mis-interpreted. One such element is that linkage or pleiotropy must be present between trait and preference for sensory drive to be, or have been, operating. Indeed, such occurrences may take place over time; however, the absence of such factors does not necessarily indicate an absence of sensory drive which only requires a cause-effect relationship between the three critical signalling factors. All that is needed is correlational selection [24, 67]. Another is that sensory drive does not have to be mutually exclusive of other sexual selection processes, in fact it is an integral part of it [64, 70]. Furthermore, when considering the animal sensory system, care must be taken not to anthropomorphise characteristics and carefully consider differences between human and animal senses [12, 62]. For example, when investigating the visual environment, it is necessary to consider the spectral range that animals use, and how they sense it; as this is usually very different from humans. This is especially true of senses that we do not posses and therefore must work harder to understand. The importance of these aspects vary from system to system for example the presence of UV colouration is important in many species [13, 43, 100, 171].

Pre-existing Biases: A Possible Origin of Signals

The coupling of signals to their environment is futile if the signal is outside the sensory range of the receiver. The accurate detection and interpretation of information delivered by the signal are essential for successful communication. One way in which males can ensure reception of their sexual signals by females is by taking advantage of pre-existing sensory mechanisms within the female's sensory system. The generation of many sexual signals is thought to have originated from initial exploitation of female sensory biases [8, 9, 36, 70, 163, 164, 175, 177, 210]. The process of sensory bias posits that mating signals

Fig. 1 Outline of the sensory drive model adapted from Endler [66]. The model indicates the interactions between the major elements involved in signalling behaviour. The *large bubble arrows* indicate the interaction between signal, environment and sensory system, the *orange dashed bubble arrows* indicate the action of sensory exploitation (discussed later in the paper). The *black arrows* indicate the direct mechanisms of feedback and potential directions of signal evolution (Color figure online)
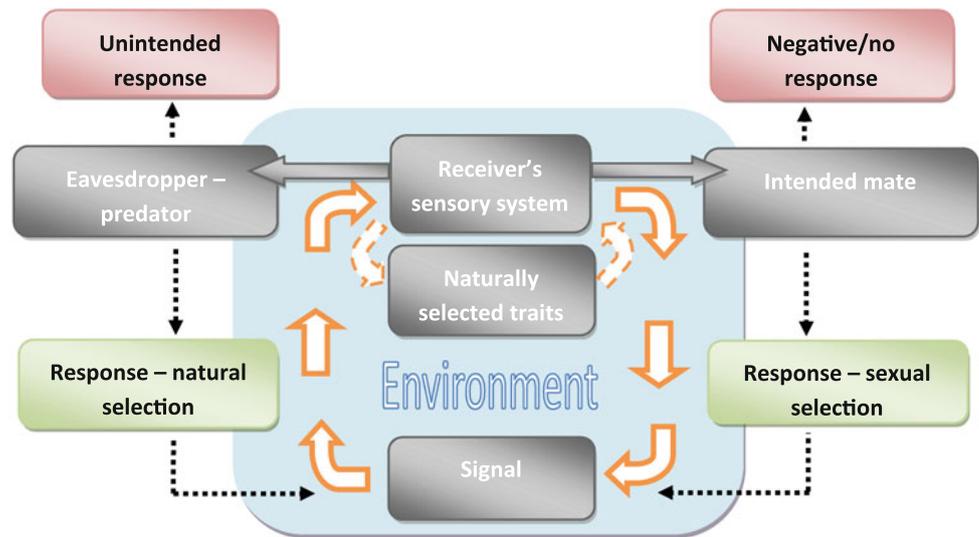
evolve as a by-product of naturally selected communication systems which are already pre-adapted to the environment.

The term 'sensory bias' is often used to cover a number of processes: sensory exploitation, sensory traps and pre-existing bias. The differences between these processes are subtle and often hard to determine but the distinction is important. The process of sensory exploitation predicts that sensory system properties affect perception and subsequent behaviour of an individual, sensory traps predict that existing neural processes are co-opted into a new context and pre-existing biases occur where existing properties in the sensory or cognitive pathways bias preferences for certain traits [70].

One of the earliest studies providing evidence for the existence of sensory bias in a behavioural context was Proctor [163, 164], who recorded male water mites mimicking the vibrations that females used to detect prey. Through manipulatory experiments Proctor [163] found that food deprived females would respond more readily to males using this behaviour indicating that the female's first motivation is for prey detection rather than mate detection. Furthermore, a phylogenetic analysis [164] indicated that hunting behaviour preceded the male use of vibratory cues providing further evidence of males exploiting innate female behaviours. Similarly, a female preference for orange food translates into a natural preference for orange mates through a tuned sensory system for this colour in guppies [80, 106, 173]. Colouration in this instance comes from carotenoids which are red and yellow pigments that most animals are unable to synthesise and therefore must get from their environment [59, 101]. It has been suggested that this is a sign of genetic quality [59, 128]. Interestingly, zebrafish show a similar bias towards red colouration despite no use of this colour in mate detection or

assessment [193] suggesting that a pre-existing preference for red may play a part in their evolutionary history, possibly resulting from detection of food. Other examples of sensory bias include the swordtail characin, *Corynopoma riisei* where males develop an opercular flag, which varies within populations with the abundance of prey, in order to mimic prey and act as a lure to females [5], a female preference for 'hooded' burrows for escaping predators, which is exploited by male fiddler crabs [37, 38] and complex calls in the Tungara frog, *Physalaemus pustulosus*, which have evolved over simple calls due to the nature of female's auditory senses [176].

Demonstrations that female preference pre-dates male sexual traits have been conducted using phylogenetic analysis, providing further evidence that sensory bias can indeed be looked upon as an origin of female preference for male signals in some species [8, 177]. Although no link has been reported between mate preference and food colour in some species such as killifish [88] and bowerbirds [17] there is some strong evidence to support this theory and these studies may require larger sample sizes and more extensive phylogenetic coverage to uncover such links. A thorough knowledge of a species' evolutionary ecology is also required as biases may originate from factors that are present in native habitats and not in more recent range expansions, or that are now absent from native habitats. This may be true of the latter example where satin bowerbirds feed on the blue fruit of the blue quondong tree whilst using blue as a preferred colour in mate choice.

The Decision to Produce a Signal

The first stage in the emission of a signal is the decision of how, when, and where to produce a signal that ensures the

best chance of detection by intended receivers. Sexual signals have generally evolved to be conspicuous to potential mates at given times, locations and positions; the horn of the beetle *Coprophanaeus lancifer*, is coloured to contrast with ambient forest light in order to maximise female perception at signalling times [198] and the signalling apparatus of the wolf spider, *Schizocosa ocreata*, contrasts sharply with background when viewed from the perspective of the female whilst remaining inconspicuous to predators [39]. It is important that signals are accurate to avoid unbalancing costs and benefits where inefficient signalling would increase potential predator/competition costs with lower mating benefit. Although signals are generally well adapted to specific environments animals must overcome environmental stochasticity in the short term in order to produce effective communication to ensure reproductive fitness, this is particularly true of those living in highly changeable environments [25, 153].

The decision to produce a signal at a particular time and place should be influenced by factors that potentially interfere with the signal such as habitat type, background interference, location, timing, type of signal and probability of detection by intended receivers and eavesdroppers. This initial decision requires the signaller to be aware of its environment and to be able to detect and react to changes that will potentially alter detectability by intended receivers, forming a complex problem for many species. For example, more dense habitats will produce different signal interference to open habitats [151, 212], signals emitted at height will disperse more and further than those on the ground [22] and certain visual signals will be more effective against different backgrounds. Additionally, chemical signals not only travel faster in higher temperatures but also fade faster [18, 167]. Adding to the complexity of this initial decision is the approximate position of the intended receiver [126], and similarly, any competition, predators or parasites. Furthermore, combinations of these factors are likely to change over minutes, hours, days and seasons. A decision process to ensure the most effective signal is produced given the environmental conditions would give an animal the best possible change of overcoming these issues.

The examples above represent just a few factors that animals should consider when producing a signal. How the initial decision is made however, is not well understood. Behaviour that suggests this decision process does exist has been reported in a wide range of animal taxa. For example, males of both Lawes' bird of paradise and bowerbirds leave their display courts on the ground to travel to the forest canopy where they use acoustic calls to attract females from further afield [86, 165], animals have been shown to alter the position of their courtship displays to ensure optimal lighting and visibility to potential mates

[73, 198] and detection of temporal gaps in the wind is used to improve reception of vibratory signals [145]. Further examples follow below.

The extraordinary ability of animals to solve novel problems is becoming well-known, and the ability to solve problems is part of daily life for most animals. There are some very effective ways of mitigating the effects of environmental change although both the long- and short-term mechanisms that facilitate such processes are poorly understood. For example, it has yet to be asked what are the mechanisms for detecting a change in environment and what is the decision process for enabling this change? Are these behaviours innate, are they learnt and do individuals carry out such decisions on a case by case basis? Are these traits a result of direct sensory reception of the environmental conditions, experience, or a lack of a detected response from the receiver? Experimental studies may be useful in detecting cues that initiate signalling decisions and monitoring environmental threshold values that trigger a simple signal adaptation such as increasing the rate of emission or amplitude of the signal. Although such studies may be viable in the lab, recreating these in nature will pose more of a problem. Suggestions have been made into the role of receiver responses as cues for altering signalling behaviour [107] although more work will provide clearer answers.

Signal Emission and Tuning to the Environment

After the initial decision to produce a signal has been made, an animal must have the energy and apparatus to emit a signal that is tuned to the environment. Signals can be generated via a number of pathways and each signal will be limited in the type and amount of information it can carry as well as the distance that it can travel. The diverse array of signals all serve the purpose of transmitting information, environmental conditions, the type of recipient, the information transmitted, distance to receiver and energetic cost all have important implications in signal emission.

The energetic and physiological requirements to produce a signal vary. The amount of energy required to produce different signals will be influenced by the amount of energy available to the animal. Habitat not only has direct effects on the effectiveness of a signal, but may also limit the type of signals that are physically possible for an animal to produce through indirect factors such as food availability or composition. For example, animals with low energy diets may be unable to produce signals requiring high energetic outputs [14, 137, 156]. Similarly, animals in challenging environmental conditions or high predation areas may be limited in the amount of energy and time

available for signal production and emission [156]. Furthermore, environmental variation may be directly correlated with the intensity of sexual selection and it is this that affects sexual signals. For example, birds breeding at higher elevations are subject to colder climates and shorter breeding seasons resulting in higher energetic costs linked to foraging and brood care in both parents [7]. This difference in life histories has created more intense sexual selection at lower elevations which in turn produces divergence in sexual signals across elevational gradients [192]. Other indirect effects include the need to remain inconspicuous; the whistle communication in killer whales is less complex in mammal eating species than in fish eating animals [172] possibly to avoid detection by mammalian prey.

The amount of energy required to emit a given signal and the amount of information a signal can carry are important considerations. For example, chemical signalling is one of the most primitive signals and requires less energy than producing either acoustic calls or behavioural courtships [22] but may be restricted in the amount of information it can carry. The importance of this however, varies between species; the amount of information required for a signal to be effective depends on the minimum value to elicit a response in the receiver which may only be a cue to determine the presence of a potential mate. A signal containing a low amount of information does not therefore have to be poor if the information is of high value; the quality rather than the amount of information emitted should minimise the occurrence of mistakes, increasing the chance that the receiver interprets the signal correctly. Selection should thus favour signallers that produce more efficient signals of high value, rather than high information. The evolution of more efficient signals relies on the balance of cost and benefit; a signal can only evolve under conditions where the benefits outweigh the costs (for both the emitter and intended receiver) and this is more likely if the energy requirement is decreased (potentially by decreasing information amount and increasing value).

In order to emit the required information, animals must have the correct apparatus given the environment and this apparatus must function efficiently in order to minimise the amount of energy required to emit a signal. Physiological structures that enable an animal to emit a signal are varied and are adapted to the type of substrate through which the signal must travel. For example, acoustic communication is produced through vibrating structures and must overcome environmental factors such as acoustic impedance boundaries, attenuation and background noise. This requires the use of specialised structures which amplify signals and closely couple them to the environment in order to propel them through the medium. Although the structures used to produce sounds use the same principles, they often differ in

structure. Both mammals and anurans use larynx to create sounds, however anurans (and some mammals such as gibbons) have developed a vocal sac in order to amplify their call (compensating for size) which is more effective than the larynx alone. Air in these vocal sacs has been found to closely match the acoustic impedance of the surrounding air allowing the sound to travel further [141]. Even with these adaptations only a small amount of energy produced by the frog is used to create the sound signal [174]. Additionally, the swim bladder has been co-opted to produce acoustic communication in some fish [170]. Different types of syrinx exist within birds to create acoustic signals and these are specialised to allow the production of different types of calls, such as the rapid song of some songbirds [99]. More adaptations can be seen in other animals; high intensity sounds are required to travel large distances and as such insects transmitting signals over distances have developed ways of creating signals using external structures such as foliage or modifications of the exoskeleton [54, 83]. Hairs and bristles assist emission of chemical signals in vertebrates [136, 152] and visual signals optimise the light wavelengths available to them [55, 65, 100].

The energy required to use and maintain such apparatus can be high and physiological trade-offs have been reported which compensate for this. For example, energy expenditure increases with light intensity in fly vision [157], animals that live in dark environments, have a reduced visual thalamocortical system (an area in the brain responding to visual stimulus) and an increased somatosensory system responding to stimuli in the skin such as touch [31]. Furthermore, developmental plasticity in the cortex of mammals [121] may enable them to adapt more readily to novel environments.

The environment can have very strong effects on the energetic and physiological requirements for signal emission. Not only can the environment dictate the energy required to produce a signal but can also limit the amount of energy available to an animal through diet and other challenges such as the energetic requirements of thermoregulation etc. A trade-off also exists in the amount of information and the quality of that information. A signal of low quality, high information will not be as efficient as that of high quality, low information. This balance is likely to be dictated by the information required by the receiver, the probability of interception by eavesdroppers, the energy required and the apparatus available.

Transmission and Environmental Effects

The effect of the environment on animal communication has been documented in many species [4, 11, 26, 27, 57, 146, 154, 178, 180]. Signalling environments can have

many different effects on the transmission of a signal and signals in both the terrestrial and aquatic environments are subject to limitations and as fluids are essentially governed by the same physical laws [50]. Environmental conditions can alter the structure and content of a signal having both direct (direct effects alter the chemical, physical or biological composition through interaction with the signal itself) and indirect impacts on the accuracy of communication through a number of factors such as background noise, habitat structure, lighting and climate; indirect effects alter signal generation, transmission and reception through factors, such as pollutants [6, 56] and diet [105, 106].

Animal signals are susceptible to distortion by environmental factors which will limit the type and efficacy of certain signals in a given location. Examples of this include the masking of acoustic communication in noisy environments [11, 85, 216], limitation of chemical detection in nutrient rich [201, 217] and chemically complex environments [148] and alteration of the light spectrum by the environment in visual communication [65, 73, 217]. In addition, the physical properties of a habitat (e.g. structure) can also hinder communication through various forces such as attenuation, reverberation and turbulence. Climate and location have many effects which include, within the terrestrial environment, wind [1, 46, 58, 145, 212], elevation [119], reverberation [190, 212], noise [11, 26, 108, 154, 180, 188], background movement [82, 161], light [51] and temperature [54, 206, 212] in the terrestrial and turbulence [131, 148], velocity [208], viscosity [131] and pH [111] in the aquatic.

The effect of these processes on animal signalling has been demonstrated in a variety of taxa. For example, temperature is known to affect chemical emission rates in insects [143], background interference affects weakly electric fish (that communicate using electrostatic pulses called electric organ discharges and are known to function in mate choice in some species) [44, 187] and echolocation in bats [4, 57]. The transmission properties of a signal are, however, often coupled to habitat type and there are some intriguing results in this field, best demonstrated by work on acoustic communication (for a review see [77]). Acoustic communication is found to be compromised by environmental factors in frogs [11, 196], primates [27, 78] and fish [204], although studies on avian communication most clearly indicate the relationship between habitat type and signal. A study by Wiley [211] investigated the relationship between habitat and call characteristics in 120 species of bird in the group and reported a correlation between habitat type (six habitats corresponding to forest and open habitat) and certain call structures, providing evidence that habitat structure can predict vocal communication in the group Oscine. Tobias et al. [200] studied song divergence between

closely related 'bamboo-specialist' bird species in two types of Amazonian forest and found that divergence was more strongly correlated with the transmission properties of the habitats than any other factor. These results have also been reported in white-crowned sparrows [52], grey-breasted wood-wren [53] and forest warblers [119]. In addition, Gish and Morton [97] investigated the characteristics of bird songs in native and non-native habitat; Carolina wren songs were played in two different habitats in order to determine the suitability of the song to their native habitats. Results showed that songs retained more of their original characteristics in native habitat. This highlights not only the difference in sound transmission between habitats but also song adaptation to a specific habitat and the potential for breakdown of the signal in mal-adapted environments. Morton [151] compared the sound propagation properties of three habitat types and discovered that they indeed differed, influencing the type of signals suitable for each habitat. Similar results were also found by Daniel and Blumstein [45]. Such differences in transmission qualities can impose divergent selection on signals between similar habitats (forests [200, 212] as well as 'opposite' habitat types (open vs. closed habitats [178]), mixing of signals is faster in open habitat than in forests [58], illustrating the importance that the transmission properties of a habitat have in shaping signalling behaviour.

The location within a habitat can also influence signal transmission for example in the aquatic environment, the type of sediment moderates turbulence and velocity [215] and sediment particle size has an effect on signal transmission with finer sediments facilitating signals over longer distances [149]. Signal generation can be further complicated by the environment affecting different parts of a signal differentially [48]. Signals that therefore require specific ecological conditions or specific microhabitats to transmit will be limited to use in either a specific microhabitat, position within the microhabitat or time of day. That animals do alter such aspects of signalling behaviour to overcome environmental constraints, has been shown.

Location

Location alone can mitigate many environmental factors if chosen carefully. For example, hyenas adapt scent marks depending on habitat to maximise detection by conspecifics [136] and male Bactrian camels use their humps to apply scent markings, increasing their signal range using the highest part of their body [209]. Animals using visually based signals are prone to interference from objects in the line of view and can only reflect the wavelengths that are available in a given place and time; therefore, location is particularly important in ensuring detection. Animals have been shown to alter the position of their courtship displays

to ensure optimal lighting and visibility to potential mates [73, 198]. A study by Nemeth et al. [155] investigated song-post height in antbirds, reporting that species were able to optimise the transmission of their song by choosing specific heights from which to sing.

Signal Timing

Call timing can be an adaptive response to environmental noise. Fuller et al. [92] found robins inhabiting urban areas would restrict their singing to periods of low anthropogenic noise in order to increase the transmission and accurate reception of their communication. Zelick and Narins [220] demonstrated that males of two neotropical treefrogs suppressed calls in response to bursts of noise which encompass the principal frequency components present in their vocalizations. Wind-speed and turbulence tend to be highly variable and animals signalling in such areas must be able to change behaviours in a short period of time. Treehoppers communicate using plant-borne vibrations which have the potential to be disrupted by external vibrations induced by the environment; McNett et al. [145] discovered that males use gap detection to time their signals to periods of low wind, limiting interference by high wind and enhancing reception by females. Incidentally, wind speed also affects the mate searching ability of the aphid parasitoid, *Aphidius nigripes*, where wind speed represents a trade off between the dispersion of chemical cues and male flying ability [138]. Thomas et al. [199] investigated signalling plasticity in the Australian field cricket, *Teleogryllus oceanicus* to discover that males increased their use of chemical cues during times of low group courtship song, a possible adaptation to compensate for the lack of amplitude from a group chorus, and Endler and Théry [73] investigated the courtship behaviours of three forest-dwelling birds showing that each species would alter its behaviour to coincide with optimal ambient light conditions that best show off their colouration. Timing of calls is very important in not only ensuring receiver response, but also in increasing conspicuousness of the signal to detection by predators. In some cases careful timing can maximise visibility to mates whilst minimising visibility to potential predators [61, 63, 73]. Time detection is a clever way of mitigating environmental effects but is not well understood.

Mode Switching and Multimodality

Multimodality is defined here as the use of a number of signal types (received via different sensory systems), either individually or simultaneously, within a single signalling event. Multimodality is known to be an important aspect in animal communication, that can either enhance reception of a signal when a number of signal types are used together [122, 202], increase the amount/type of information transmitted [158] or offer an alternative channel when one channel becomes ineffective [116]. The use of more than one type of signal, either singularly or simultaneously, is an effective way of avoiding environmental interference and coping with stochasticity to ensure accurate reception by intended receivers. This is not to suggest that one type of signal is necessarily used instead of others within a given individual, but refers to the principal sense used in a given situation. Mode-switching behaviours include changing between visual and olfactory senses [51], visual and seismic [213], acoustic and olfactory [199] and echolocation to visual [57]. For example, animals that must display in both the light and dark will frequently encounter conditions where some signals are no longer the most efficient form of communication. In order to cope with this many species will switch from visual to olfactory cues as in alpine newts [40, 51] and guppies [33]. Additionally, male sticklebacks substitute visual for chemical cues for long distance attraction of females [144] and males of the wolf spider (*S. ocreata*) switch between two types of signal, seismic and visual, depending on the substrate on which he is courting [102]; a behavioural response to environmental change whilst remaining inconspicuous to predators.

The use of different signalling channels simultaneously can be used to enhance signals or to increase the amount of information within a single event. The use of multiple signals has been seen to increase pollination attempts [122] and mitigate environmental stochasticity [117] in flowers, provide context specific signals in cowbirds [158] and increase female approach rate to male fire-belled toads [221]. Multimodality is undoubtedly an effective way of coping with environmental variation or change but this option is generally limited to those with very local small scale or clumped distributions; those species with larger territories are limited by the number of reliable signal types effective over larger ranges and more microhabitats. Limitations are also likely to occur due to energetic trade-offs in the apparatus required to emit more than one type of signal.

Bandwidth Selectivity

The masking of signals by background noise can pose a problem to many species. This masking can come from a number of sources including anthropogenic [26, 85, 189], conspecific [96, 197], heterospecific [23, 95, 132] and natural [16, 103]. Bandwidth selectivity, the use of signal components that are selected specifically to mitigate background noise, can play an important part in shaping animal communication. For example, frogs have avoided acoustic masking from low frequency abiotic noise with the use of high frequency vocalisations [16, 103], with similar results

recorded in birds [189]. In contrast primates have been shown to select low frequency calls for long distance propagation [147].

Visual signals have been shown to use components that contrast specifically with environmental noise. For example, behavioural displays in reptiles use movement components that differ from background vegetation movements [160–162]. The bright plumage of female eclectus parrots reflects wavelengths that contrast with those reflected by the background [110], this has also been reported in reef fish colouration [140], lizards [124] and bowerbird decoration use [71]. Electrically communicating fish have been shown to modulate the frequencies of their signal in times of interference [28]. Borean tree-hole frogs use water-filled tree holes to amplify their calls by tuning their vocalizations to the resonant frequency of the hole thereby increasing their chances of being heard by females. What's more the frogs are able to assess the holes according to how much water they contain and adjust their calls accordingly [123]. Other mechanisms for overcoming background noise include partitioning signal components in species that share the same spatial and temporal signalling space [132] and receiver sensory systems which are finely tuned to receive conspecific signals [181, 214].

Adaptation of Courtship Behaviour

Visually based behavioural signals are well researched and many effects of the environment including lighting, vegetation movement and background contrast have been studied. One such example is that of the head bobbing display of anoline lizards which is designed to attract females and serve in male competition. This display is often performed in areas of wind-blown vegetation which has the potential to disrupt the successful communication of the signal. Fleishman [82] investigated the mechanics of head bobbing and discovered that in order to be effective the display had to be conspicuous against the background and did so in several ways; the display was carried out with high velocity, high acceleration and high amplitude, all characteristics that differed to the background movement of vegetation. Additionally, the amplitude of this display is thought to maximally stimulate females' visual system from within the territory of the male and the speed of the movement is adjusted according to environment [160]. Similar results are found in the push-up and tail flicking displays of the Jacky dragon [161, 162]. Other examples of males adapting courtship displays to compensate for varying light conditions include male guppies. Male guppies have two distinct mating behaviours, sigmoid courtship display and sneaky (non-consensual) [98]. Chapman et al. [32] studied the relative frequency of these behaviours under varying lighting conditions and found that

under good visual conditions males carried out sigmoidal displays at a higher frequency than sneaky copulations and vice versa in poor visual conditions, indicating that males adapt aspects of their mating behaviour to compensate for the visual senses of the female in varying environments. This behaviour is also a way of reducing predation when predation pressure is correlated to ambient lighting intensity [61]. Males have also been shown to adapt mating distance from females in different light intensities to optimise signals to females [130]. Behavioural modification of structures or courts built has also been exhibited by some species in order to enhance visual contrast to increase conspicuousness to females, such as in the case of the bowerbirds [75] and golden-collared manakins [203]. This result demonstrates the importance of plasticity in signalling behaviour and ability of an animal to detect the environment and adapt accordingly.

The transmission properties of the aquatic environment also affect behaviourally based signal transmission. The transmission of light through water is dependent on a number of factors including depth, turbidity, mineral composition and submerged matter [127] which can in turn alter the perception of visual signals. Turbidity is one such factor that has been found to distort visual mating systems [217] and this has been found to break down systems to the extent that different colour signals are no longer distinguishable to receivers, causing hybridisation and limiting the promotion of diversity in some fish species [183]. Depth is another factor that has been found to affect signalling in the aquatic environment, particularly visual cues. As light travels deeper, the physical properties of the water change and different wavelengths are absorbed with increasing depth and water type [127]. For example, as water in clear lakes gets deeper it absorbs longer wavelengths in the red/orange spectrum and the prevailing light colours will be the shorter wavelengths, UV and blue. This, therefore, affects perception of colour in different depths, where the most conspicuous will be the opposite to those absorbed. It has been found that this absorption of wavelength can predict the colour of sexual signals in some fish species, most notably the cichlid which is thought to have speciated due to the partitioning of light in this way [135, 183].

Plasticity within sexual signalling is vital for many species; however there are some that lack this ability. The stability of a habitat may influence whether an animal is able to adapt uniform signalling behaviour; species that live in more stable habitats may not have evolved this flexibility and local environments may change in a novel way that exceeds the capacity for the animal to cope. For example, if an animal is required to make a decision on unfamiliar factors or if animals are physically unable to carry out the required behaviour it may be difficult for an animal to persist in an area. An example of the latter may be seen in

birds using acoustic signalling. Francis et al. [85] undertook a study of the effects of anthropogenic noise on communication in two subfamilies of flycatcher, the grey and ash-throated. With increased background noise grey flycatcher abundance declined whilst ash-throated flycatcher persisted but with an increase in call frequency to compensate. This adaptive response was not recorded in the grey flycatcher. Whether this response is an adaptation to environmental noise has been questioned however as an increase in frequency is not as effective at mitigating background noise as an increase in amplitude [11, 27, 154]. Additionally, many confounding variables in such studies render it difficult to determine the sole cause of changes in behaviour and why some species are able to adapt, whilst others are not.

The signal transmission properties of an environment can include both the physical composition of the transmission substrate or the physical properties of the surrounding habitat and both play an important part in determining the signalling pathway for many animals, especially those that must transmit a signal over large distances. Many animals cope with this well. However, it is less clear to what extent animals are able to change signal composition in order to overcome environmental effects. Some signal types that are immediately plastic, such as call amplitude, enable an individual to overcome immediate effects of transmission environment without altering the detection by, or response of, the receiver. Those species with more fixed signal types however, such as colour visual cues, are often unable to change the nature of their signal. This will promote evolution through the most evolutionary responsive factor which may be the sensory systems, or response of, the receiver.

Sensory Systems and Reception

Sensory systems match the profile of that which they are detecting (after the signal moves through the environment) [3, 114, 133, 169, 214]. The adaptation of senses to changing environments has been demonstrated in many species [74, 88, 93, 94, 134, 185]. Adaptation can include plasticity within the sensory system (a change within the physiology of a particular sense) or between sensory systems (switching from one sense to another) and can be dictated by genes, internal processes pathways, developmental strategy and environment. Furthermore responses can be indirect effects through hormonal or dietary effects [6, 105, 106]. An example is the effect of chemical pollutants on the olfactory ability of fish [15, 125] which can be due to the detection of chemical thresholds in noisy chemical environments [223] and/or physiological disruption of sensory systems [84].

Despite chemical signalling being one of the most common forms of communication in the animal kingdom,

few studies have looked at the plasticity of this system. It is known that the detection of chemical signals is susceptible to interference through a number of factors such as masking by other chemicals [81, 205], disruption of the internal (biological) signalling pathway [47] or interference with the sensor itself [159]. However, whether these systems are plastic has yet to be thoroughly investigated and studies generally focus on the behavioural consequences, rather than physiological mechanisms. Plasticity of chemoreceptors in *Drosophila melanogaster* has been demonstrated in relation to social environment [222] but whether this is also true of habitat is unknown.

A comprehensive example of sensory adaptation can be found in the visual system. The environment can influence visual systems in several ways such as perception, changes during development and genetic changes. Studies of plasticity within the visual sensory system have discovered several aspects of vision which alter in animals raised under different light conditions such as oil droplets [109], retinal filters [34, 35, 41, 42], lenses [120, 179], cone cells [186] and opsin expression [91] which may translate into changes in the perceived colour of mates. Tuning of the visual system can be achieved by several mechanisms including turning opsin genes off or on [21], shifting the wavelength absorption of a chromophore (by shifting between porphyropsins and rhodopsin types) and changing the amino acid complex of an opsin [21, 218, 219]. Furthermore, vision has been shown to change during development in many animals [10, 185] and be further tuned in adults [2] which may be implicated in the detection and assessment of mates [134].

Decision-Making and Responses

Decisions based on cues will certainly influence the direction of evolution. The outcomes of such decisions can be minimal on the individual level but could lead to divergence, hybridization [81] and even speciation [135, 184]. The driving factor of these processes is the altered perception of mates and/or interpretation of mating of signals that force selection in different directions. The absence of long-term, evolutionary, adaptation or short-term plasticity will inevitably lead to exclusion of the species from certain locations [85].

The behavioural responses of the receiver complete the signalling process and is a critical step in driving diversification through sensory drive. This is the point at which the signal emitter discovers whether the signal has been successful in obtaining a mating. There are three main responses that can occur from a sexual signal, assuming there is a potential mate present: an appropriate response, indicating that the signal has been received and understood, no response,

which may indicate that the signal has not been received or is irrelevant to the receiver, or an inappropriate response, which indicates that the signal has been mis-interpreted. These responses will all have consequences for the direction of evolution. For example, no response may mean complete breakdown of the mating system and possible exclusion of the species, a mis-interpreted response may result in hybridisation or poor quality mates, and the appropriate response can result in diversification and speciation.

For the most part, researchers have concentrated on female preference as the source of the behavioural response. A thorough example comes from Killifish in which females exhibit a preference for certain male morphs. The effects of a change in lighting environment on mate preference have been investigated by Fuller [87, 88, 93]. Fuller [87] showed the effects of light on female preference of male killifish colour morphs through the conspicuousness of the male trait in a given light environment [87]. Further investigation revealed that this response, both genetic and heritable [89], is key to explaining the relative abundance of colour morphs in habitats with certain water properties. Males also had higher levels of plasticity for these colour morphs (blue males in tea-stained water and red in clear water) respectively in line with predictions that males contrasting to background have higher reproductive success [87, 89]. Furthermore, visual sensitivity to UV and blue light varies amongst populations [90] indicating intraspecific plasticity of the visual senses which may be driving the female decision-making process. This process is also known to drive speciation in cichlids, where environmental conditions alter abundance of male nuptial colouration through increased female sensitivities to red and blue light dependent on photic environment which in turn influences mate choice responses [94, 129, 135, 184].

Differences caused by habitat have also promoted divergence in the calls of two subspecies of cricket frog which may prove a crucial component in the progression of speciation, especially considering the reliance of anurans on vocal communication in mate recognition [95]. Further examples include male warblers in India which maintain conspicuous colouration with respect to background reflectance in order to gain the best territories and influence female responses which are also thought to have played a role in species divergence in this group [139]. Female stickleback [19, 168, 182], guppies [60, 72], *Telmatherina sarasinorum* [104], southern pygmy perch [150] and cichlids [135, 184] have also been shown to exhibit preference in accordance with background contrast.

The above examples demonstrate altered but still appropriate responses to changed environment. Behavioural responses, however, can also include inappropriate responses and poor decisions, as well as badly timed or delayed responses. Delayed responses to odours have been reported in hermit crabs, where altered pH disrupts chemoreception [47], limited detection of sex-specific pheromones has been reported of snails in polluted water [194] and a copepod's chemical perception is disrupted in turbulence potentially inhibiting its ability to detect mating signals [131]. Inappropriate responses are at risk of being overlooked and can have extreme consequences as has been seen in species of zebrafish [79] and swordtail (*Xiphophorus birchmanni* and *Xiphophorus malinche*) [81]. Fisher et al. [81] investigated the effects of chemically disrupted habitats on the mate preferences of females and discovered that females are unable to determine con- from heterospecifics in such environments which has lead to a possible hybridization event.

Furthermore, the disturbance of the visual habitat has been reported to threaten the diversity of cichlids [183] reversing the diversification that sensory drive promoted through speciation in the first instance. This last example demonstrates the potential strength of the sensory drive process and highlights the importance of fully understanding the mechanisms behind it. In cases where animals are unable to identify conspecifics [81] or where environmental deterioration promotes dishonest [217] or altered [56] signalling the integrity of the mating system can be compromised. Eeva et al. [56] reported that environmental pollution may dull plumage colouration in the great tit having possible effects on mate choice decisions made by females. Wong et al. [217] discuss the opportunity for cheating amongst poor quality males in stickleback where honest signalling in three-spined sticklebacks is compromised by algal turbidity affecting visual conditions in the Baltic Sea. Under turbid conditions poor quality males are able to signal more frequently, something which would prove risky in clear water where they attract competition and aggression from honest, higher quality conspecifics. This interesting result has obvious impacts on the stability of such systems and repercussions for females that choose poor quality males which are more likely to cannibalise her young [29]. Additionally, the effects of altered light environment has been shown to alter the mating decisions in female *P. pustulosus* frogs, when light levels are increased females are less selective, a possible behavioural response to increased predation risk [166].

Conclusions

The link between signalling environment and signal efficacy has been shown in many species and the effects on mate choice are demonstrated. Pre-existing biases have been shown to form an important aspect of female choice models and can explain the origin of such preferences in some species demonstrating the importance of sensory

systems in shaping mating signals. The environment plays an important part in shaping the evolution of many mating signals and mating signal evolution is reliant on the coupling of sensory systems to their environment. Further considerations involving the receiver must also be taken into account: a signal must be timed to coincide with receiver presence, it must be received and interpreted accurately by the receiver, the signal must not be easily intercepted by 'eavesdroppers', the signal should be plastic in order to cope with changing environments, and signal generation should not be too costly relative to its benefits to the sender. Males have been shown to adapt all aspects of sexual signalling from courtship behaviour [32, 73, 98, 130] to colouration [87, 93] and even morphology [5] in order to gain female attention in changing environments and these are often within the constraints of predation pressure and mate competition [59]. Used in combination the structural properties of a habitat, climate and disturbance can be used to predict not only the optimal method of communication but also the potential selective pressures acting on communication and mating strategies. These predictions may be important in understanding the long-term effects of changing environments on the persistence of a species in a habitat and impacts on mate detection and choice.

Animals can adapt to environmental change in several ways, but the three critical signalling factors, the signal itself, the sensory system and the receiver response, must co-evolve in order to maintain the accuracy of the signal. Alteration of signal efficacy by the environment has been shown to have a range of effects on animal mating systems. A shift in light environment influences male colour pattern and the relative abundance of morphs [87], algal turbulence has been shown to alter behavioural mating strategies [217], sensory drive has been shown to lead to speciation [135] and background noise can limit the persistence of a species in a given habitat [85, 118]. Although many species have shown changes in response to variable environments in the long-term, rapidly changing environments may pose a threat to animals unable to adapt or evolve quickly enough to catch up. It is therefore important to understand not only the effects of environment but also the mechanisms by which species are able to cope with such stressors and potential effects on the direction of selection. In order to do this each step in the signalling process must be identified and investigated separately, starting with the initial decision to emit a signal.

The initial stage in the signalling process is the decision to create a signal and, as important as it is, it seems that this initial decision and the mechanisms behind it have been somewhat neglected in literature and need to be addressed. How the emitter interprets the surrounding environment has been shown to influence signalling behaviour, however the cues that initiate this process are largely unknown. Do sensory systems detect this change and if so is this through comparative processes, direct detection, thresholds, experience and learning, or do they use the response of the receiver to adjust their own behaviour? Such answers are important in helping us determine the likely impacts of environmental change on different species. A good starting point is the investigation into how the signal emitter interprets their environment rather than how the receivers sensory system interprets the signal.

Other areas that are in need of attention include the timeframes required for plasticity to restore signal efficacy in times of environmental change and the importance of learning in such processes. A related unknown is how rapidly populations can evolve to match new and changing environments. Phenotypic and evolutionary plasticity are particularly important given present times of rapid change, be it habitat destruction, climate change or pollution. Although physiology and/or evolutionary plasticity may allow adaptation in the longer term, learning (including experience, copying and imprinting) may bridge the gap between the initiation and completion of such changes depending on timeframes. And although sensory bias has been shown in a number of taxa, learning has yet to be ruled out as a driver.

Many aspects of sensory drive have been reported in different species and we have evidence suggesting that sensory functions do indeed play a crucial part in directing selection of signals. The evolutionary and phenotypic plasticity of male trait, female preference, and sensory systems have been shown independently and their link to environmental conditions proven. In order to take research one step forward the full process of sensory drive must be demonstrated and the co-evolution of the three critical signalling factors studied together. Although a daunting task, long-term artificial selection studies will be an effective way of demonstrating the process, piecing together the mechanics of sensory drive as a whole.

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