

Review



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Evolutionary biology

Evolutionary novelty in communication between the sexes

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The diversity of signalling traits within and across taxa is vast and striking, prompting us to consider how novelty evolves in the context of animal communication. Sexual selection contributes to diversification, and here we endeavour to understand the initial conditions that facilitate the maintenance or elimination of new sexual signals and receiver features. New sender and receiver variants can occur through mutation, plasticity, hybridization and cultural innovation, and the initial conditions of the sender, the receiver and the environment then dictate whether a novel cue becomes a signal. New features may arise in the sender, the receiver or both simultaneously. We contend that it may be easier than assumed to evolve new sexual signals because sexual signals may be arbitrary, sexual conflict is common and receivers are capable of perceiving much more of the world than just existing sexual signals. Additionally, changes in the signalling environment can approximate both signal and receiver changes through a change in transmission characteristics of a given environment or the use of new environments. The Anthropocene has led to wide-scale disruption of the environment and may thus generate opportunity to directly observe the evolution of new signals to address questions that are beyond the reach of phylogenetic approaches.

1. Introduction

Animals have evolved an astonishing variety of communication systems, spanning many signalling modalities, contexts and levels of complexity [1]. *Novelty* in animal communication is often striking (figure 1) and is characterized by abrupt or discontinuous change including new mechanisms of *signal* production, detection or perception (e.g. the use of a new organ and/or stimulation of a different sensory organ). How is communication sustained when such changes occur? Here, we describe alternative scenarios for the evolutionary origins of novelty in communication and analyse how initial conditions of the *sender*, *receiver* and the environment influence the evolutionary consequences (table 1). We focus on intersexual communication—mating signals, mating preferences and mate choice—because it provides countless opportunities for novelty to proliferate. Environmental selection on signals and receiver mechanisms, preferences for arbitrary traits and sexual conflict generate fitness surfaces that are dynamic over time and space [13–15], likely making mating signals, mating preferences and mate choice especially prone to novelty. Nevertheless, some of these characteristics are common components of other types of signalling, so the scenarios described may generalize beyond mating contexts.

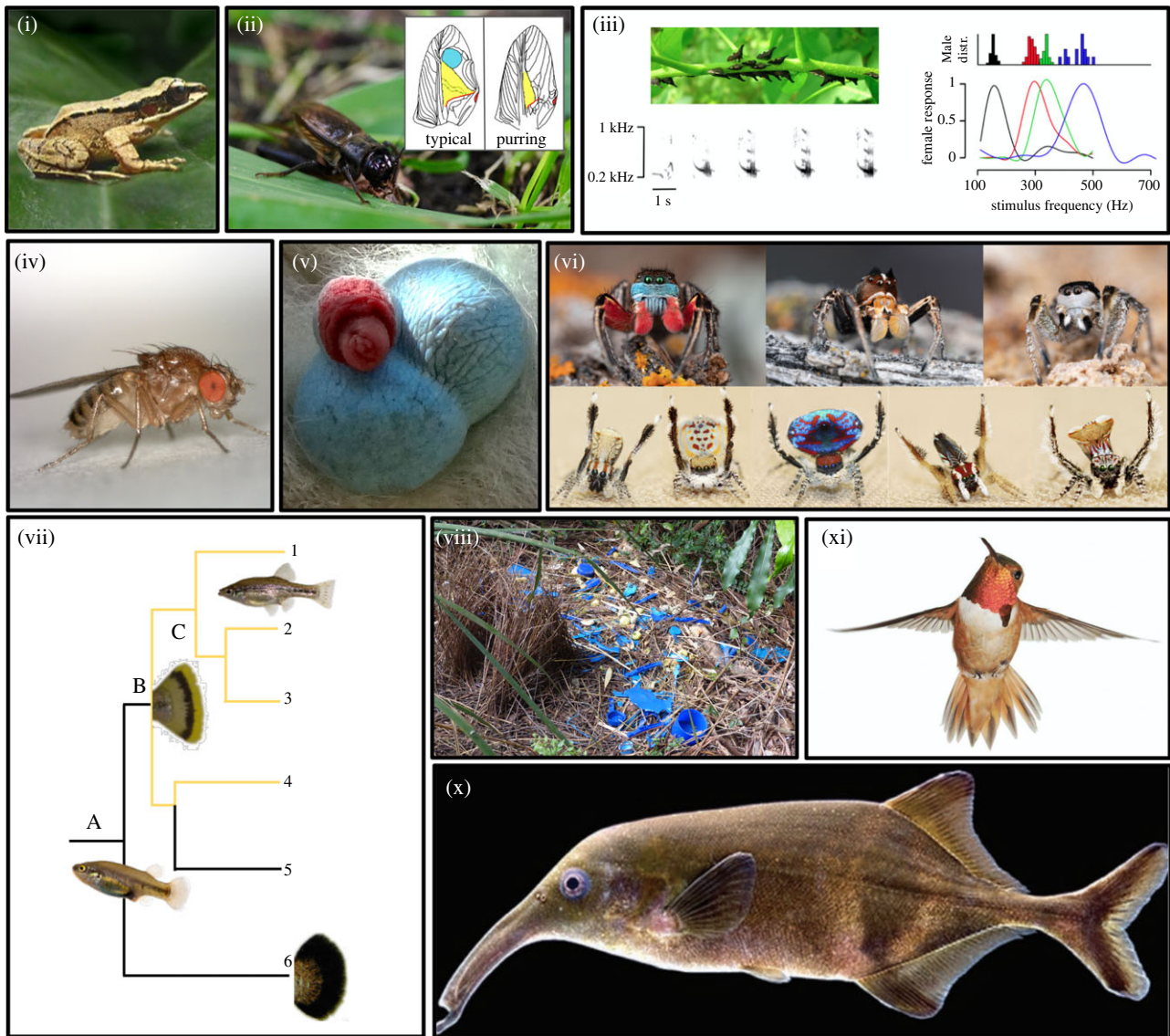


Figure 1. Novelty in animal signals and receiver features: (i) *Odorrana tormota* evolved ultrasonic calling songs, while ancestral species' songs are audible [2]; picture credit: A.S. Feng (<https://phys.org/news/2008-05-female-concave-eared-frogs-ultrasonic.html>); (ii) recently evolved morphs of the Pacific field cricket (*Teleogryllus oceanicus*) produce new sexual signals using modified wing morphology ([3]; picture credit: E.D. Broder); (iii) coevolution between male signals and female preference functions across the *Enchenopa binotata* complex [4]; picture credit: R.L. Rodríguez; (iv) in *Drosophila*, temperature impacts sender signalling behaviour but has minimal effects on female preferences [5]; picture credit: Hannah Davis/CC BY-SA (<https://creativecommons.org/licenses/by-sa/4.0/>); (v) vervet monkeys use blue scrotal colour in sexual communication, which differs among species [6]; picture credit: Bjørn Christian Tørrissen/CC BY-SA (<https://creativecommons.org/licenses/by-sa/3.0/>); (vi) visual signal variation in closely related *Habronattus* (top; picture credit Marshal Hedin) and *Maratus* (bottom; picture credit Madeline Girard) jumping spiders [7]; (vii) A. Origin of female foraging bias for male terminal yellow bands. B. Origin of terminal yellow band in males. C. Origin of female resistance to foraging costs in goodeid fishes [8]; picture credit: Wolfgang Gessl; (viii) satin bower birds (*Ptilinorhynchus nuchalis*) incorporate discarded blue items like pens, clothespins and bottlecaps into their displays [9,10]; picture credit: Gail Hampshire CC BY 2.0; (ix) frequency characteristics of vocal songs (produced via the syrinx) and feather sounds (produce via aeroelastic flutter) are similar across the 'bee' hummingbird clade ([11]; picture credit: Anand Varma); (x) electric mating signals have evolved independently in multiple lineages including elephant fish (*Paramormyrops* spp.) [12]; picture credit: C. Hopkins (<https://www.nature.com/articles/467159a>).

In this review, we first describe contemporary examples of novelty in a mating context (figure 1; electronic supplementary material, table S1) and the mechanisms underlying the origin of such traits. We suggest that novel signal components and receiver features arise easily. Then, we reimagine the classic framework (e.g. [1]) of whether change occurs first in the signal or the receiver. We use a schematic (figure 2) to unpack four scenarios by which the interactions among the sender, the receiver and the environment facilitate the maintenance or elimination of novel animal communication features. Even in the case of no change occurring in the sender or the receiver, environmental change (figure 2, scenario 4) may approximate the scenarios of change in either signals or

receivers (figure 2, scenarios 1–3). We conclude with four open questions about novelty in animal communication.

2. Conceptualizing novelty in mating

Novelty can be conceptualized in terms of how new variants originate [16], or in terms of new functional and evolutionary consequences of those variants [17–19]. New variants in communication can arise through changes in senders, receivers and the environment in any combination. Novelty in signals includes changes in production (how signals are made), in signal properties (the distribution of energy in signals) or in the transmission features of the environment (how signals

Table 1. Key terms. Terms are italicized the first time they appear in the text.

<i>Associative learning</i> : the development of a new behavioural response to a stimulus as a consequence of its pairing with positive or negative stimuli or experiences
<i>Bias</i> : reaction by a receiver that did not evolve in the context of the signal
<i>Co-opt</i> : an existing trait evolves to have a new function
<i>Cue</i> : trait that provides incidental information to a receiver
<i>Disruption</i> : (in communication) a change in the environment that distorts or masks the production, transmission, detection or reception of an existing mating signal
<i>Novelty</i> : (in communication) abrupt or discontinuous change in signal component or receiver feature, including new mechanisms of signal production, detection or perception (e.g. the use of a new organ, and/or stimulation of new perceptual mechanisms)
<i>Receiver</i> : an individual that attends to and evaluates signals
<i>Response</i> : reaction from a receiver that is prompted by a signal
<i>Sender</i> : individual producing and transmitting a signal or cue
<i>Signal</i> : trait that evolved to provide information to a receiver that benefits the sender

are modified during transmission). Receivers may change in sensory transduction (which organs are used to detect signal energy and their sensitivity spectrum with respect to signals), integration (how the central nervous system integrates responses from the periphery) and evaluation (how signals are interpreted); all of these changes are hereafter referred to as receiver features.

Contemporary examples will help to illustrate the striking novelty in mating communication. Because many examples of change in senders exist, we focus this paragraph on senders. New sender variants can arise when signal production changes and structures that did not previously serve a communicative function evolve or are *co-opted* to produce new signals. For example, club-winged manakins (*Machaeropterus deliciosus*) and hummingbirds (*Stellula calliope*) evolved novel acoustic signals (sonations) via modification of feather morphology ([11,20]; figure 1(ix)). These new sounds are produced using a mechanism that differs from the more widespread vocalizations produced in the syrinx, yet the song frequencies produced by both mechanisms overlap [21,22]. Similarly, in ghost crabs (*Ocy-pode quadrata*), co-opted gastric stridulation produces an acoustic signal that overlaps with sounds produced through claw stridulation [23]. Alternatively, structures currently used in communication can be refined to produce a signal with different attributes, such as changes in the aforementioned syrinx, which have produced much of the diversity found in song birds [24]. Changes to an existing structure can lead to radically new sender variants (novelty) by shifting the signal parameter space relative to the ancestral signal. For example, dramatic shifts to the ultrasonic range evolved in *Odorrana* frogs; calling songs in ancestral species are in the audible range (100–6000 Hz), while in *Odorrana tormota*, calling songs are in the ultrasonic range (greater than 20 000 Hz) ([2,25]; figure 1(i)). Such shifts in the signal parameter space could include changes

in signalling modalities (e.g. from visual to vibration [26]; or from airborne to substrate-borne sound [27,28]). Similarly, new sender variants may also dramatically expand or contract the variation in parameter space. For example, ancestral Pacific field cricket (*Teleogryllus oceanicus*) calls are highly tonal in the 5 kHz range, while recently evolved ‘purring’ crickets (*Teleogryllus oceanicus*) use distinct wing morphology to produce broadband songs with peak frequencies spanning approximately 2–30 kHz ([3]; figure 1(ii)).

3. Novelty arises easily through many mechanisms

Novelty in senders and receivers can originate in a surprising diversity of ways, including through mutation (e.g. gene duplication), hybridization and cultural innovation (figure 2). New mutations can arise that change signal and receiver phenotypes [29,30] usually by directly changing metabolic networks, regulatory circuits or macromolecules [31] or through the recruitment or co-option of genes [32]. Hybridization can similarly generate novel signals [33–35] or signal combinations [36,37] through transgressive segregation [38] or new epistatic interactions [39].

Importantly, novelty can also arise very quickly without genetic change and could be incorporated into the genome at a later time, for instance via genetic accommodation [16]. Both signal expression and receiver preference often depend on the environment in which animals develop [40] and may be especially affected by early learning or imprinting (reviewed in [41]). Developmental plasticity, for instance, produces novel phenotypes when environments change, exposing hidden genetic variation to the novel selection regimes [16,42,43]. Developmental plasticity caused dramatic changes in receivers in cross-fostering experiments, for example [44,45]. Culturally transmitted signals and receiver features also change rapidly; meaningful differences in the attractiveness of conspecific songs arose recently in the white-throated sparrow (*Zonotrichia albicollis*) as a result of cultural evolution of bird song over only 20 years [46]. *Associative learning* may provide an even more general source of change in mating signals, mate preferences and mate choice; all that is required here is that an arbitrary stimulus be paired with a sexual reward. For example, rats and quail can both be trained to exhibit sexual arousal in conjunction with arbitrary inanimate objects present during sexual interactions [47,48]. Any stimulus that is associated with a positive sexual experience could thereby become a sexual signal. Finally, even without learning, changes in the availability of signal-building resources in the environment may result in novel signals. For example, orchid bees (*Euglossa viridissima*) incorporate compounds from herbicides in courtship chemical *cues* [49].

Novelty in animal communication is readily detectable at a macroevolutionary scale, and phylogenetic comparative methods (pioneered by Maddison & Maddison [50] and Felsenstein [51]) are useful for reconstructing changes in traits like signals or receiver features along the branches of an evolutionary tree. We often detect signal novelty because it is restricted to particular taxa and absent from close relatives (e.g. bowers in pufferfish (*Torquigener* spp.) [52] and bowerbirds (*Ptilinorhynchus nuchalis*) [9], electric pulses in gymnotiforms and mormyriiform fishes [53]; figure 1). Characterizing new receiver variants requires behavioural and/or physiological

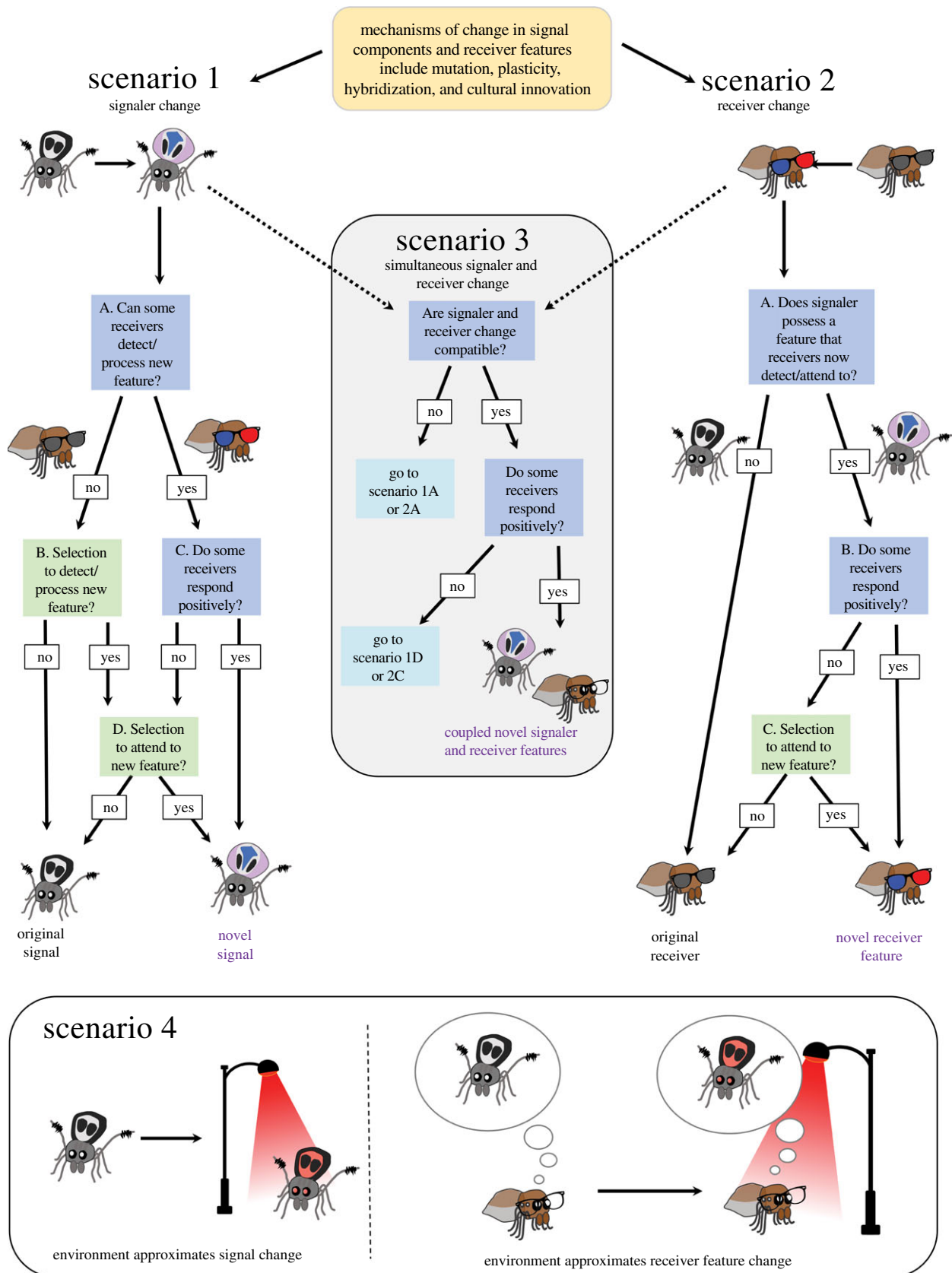


Figure 2. Simplified schematic showing alternative scenarios by which novelty may evolve in mating communication. Our example is a generalized peacock Jumping spider (*Maratus* spp.) mating system where drab females choose males based on many traits including abdomen colouration. Change is initiated by mechanisms including mutation, hybridization, plasticity and cultural innovation. If change is in a signal component only, scenario 1 follows. If change is in a receiver feature only, scenario 2 unfolds. Change may be simultaneously initiated in both sender and receiver and if compatible, scenario 3 follows. Scenario 4 occurs when environmental change approximates signal change (left) or receiver change (right). In this example, there is a change in the light environment. Blue boxes indicate proximate considerations, while green indicate ultimate considerations. Glasses on the receivers represent receiver features (i.e. sunglasses indicating monochromatic and 3D red/blue glasses indicating colour vision). There are some simplifications here. For instance, in all scenarios, new signal components and receiver features may not be costly and could be maintained in the genome and later co-opted for a communication function. Additionally, new traits are subject to costs and benefits, including those unrelated to mating communication, and we should expect them to persist only when net benefits outweigh costs.

work, but is also tractable at a macroevolutionary scale. For example, terminal yellow bands were a new sexual signal in male goodeid fishes that initially elicited a prey-approach response from females [8]. The authors went on to show a new receiver response in the lineage with yellow bands: females decoupled their sexual response from their prey-approach response (figure 1(vii)). Phylogenetic comparative methods likely underestimate the extent to which novel communication phenotypes arise, however. Longitudinal studies of mating signals and preferences, and experimental tests of responses to new signals, suggest that cultural transmission or rapid evolution can lead to loss or spread of novelty over just a few generations [46,54,55]. Such traits are expected to be gained and lost along individual branches of a phylogeny without leaving a trace in terms of interspecific variation in communication. Since mating traits and preferences have the potential to change assortative mating and population structure [56], such undetected changes in communication may have longer-reaching consequences for local adaptation and hybridization.

4. Novelty and the maintenance of communication

Here, we focus on the immediate evolutionary context that facilitates the maintenance or elimination of new features of communication when new variants arise (figure 2). To keep the framework simple, we consider situations in which a single sender sends a signal and a single receiver responds, rather than situations in which receivers also send signals (i.e. duetting). This rationale should nevertheless be applicable to more complex cases. We suggest that the characteristics of the sender and the receiver, and the environmental conditions present when the novelty arises, dictate whether and how coevolution between sender and receiver progresses. It is important to note here that the pre-existing characteristics of sender and receiver have been shaped by historic evolution, including forces outside of the context of communication (e.g. abiotic and biotic selection, drift); such characteristics (e.g. cues, receiver *biases*) can be co-opted for communication function via the processes we describe. Novelty in animal communication may involve initial changes in both the sender and the receiver, only the sender, only the receiver or neither (in which case the environment may approximate sender or receiver change (see below); figure 2 [1]). We use these four scenarios to frame our analysis, but we recognize that there is some overlap. For example, for both scenarios 1 and 2, there is one path in which receivers can already detect the new signal—whether we refer to this as sender first or receiver first depends on our starting point and is less important than understanding the possible evolutionary paths to novelty.

In the case of novelty occurring first in a signal component (figure 2, scenario 1), the immediate evolutionary dynamics depend on the environment and receivers. A novel signal is unlikely to be maintained if it is undetectable to receivers, detectable but unattractive to receivers or costly in that given environment (e.g. because of predation and food limitations). However, even if initially undetectable or unattractive, there may be selection for receivers to start attending to a novel signal component (e.g. if it reduces search costs; figure 2, scenario 1). On the other hand, it may be that receivers can already detect novel signal components when they arise, even if the signal changes are abrupt and discontinuous (figure 2,

scenario 1 boxes A,C). Some receivers may respond positively if they have perceptual biases (so-called hidden preferences) [57–61] or general biases for novelty.

Perceptual biases in receivers are ubiquitous. Receivers generally perceive and attend to many more aspects of their surroundings than the signals of potential mates (e.g. they navigate the world attending to indications of the presence of food, natural enemies, etc.), and their sensory systems are more broadly tuned than only to courtship signals [62,63]. A novel signal will be favoured if it is detectable and elicits a favourable response as a consequence of latent biases. Importantly, although sensory systems are broadly tuned, receiver responses may be negative (e.g. if the new signal mimics something receivers have been selected to avoid, like a predator). And, novel signals may trigger biases in receivers even if they are initially harmful to receivers if they elicit responses that are beneficial to senders. However, responding to novel signals may instead bring about benefits (e.g. increased salience [58,64,65]). Good-eid fish (figure 1(vii)) are an example of the potential for receivers to evolve context-dependent responses following the evolution of a novel signal. Here, the terminal yellow band (TYB) of courting males mimics an insect larva, causing naive females to lose weight as they chase after male tails in lieu of prey. Females that have coevolved with the TYB, however, exhibit a more sophisticated response, attending to TYBs only in the context of mating [8]. Similarly, swordtail fish (*Xiphophorus birchmanni*) exhibit decoupled responses to body size and fin elongation once the latter evolves [66]. When novel signals evolve, receiver responses may thus be refined and further diversified, rather than eliminated [27,67–69].

Along with perceptual biases, a general bias for novelty can also cause novel signal components to be initially attractive. There are widespread mechanisms that allow new or rare signals to be salient such as comparative evaluation (mate assessment via comparison to other possible mates rather than assigning each mate an individual score [14]), which sometimes favours rare phenotypes [70], and release from habituation (receivers typically begin to tune out stimuli that repeatedly trigger the same sensor, but new signals may circumvent that [71]). So-called novelty or ‘rare-male’ effects, where unusual phenotypes are more attractive, are also widespread. Choosers often exhibit the Coolidge effect, preferring unfamiliar mates [72]. In addition to being easier to detect, novel signals may be easier to recognize and distinguish in memory [14,73]. It is important to note that even though many receivers likely have general biases for novelty, the expression of those biases still depends on their being presented in an appropriate context. This is suggested by studies of female starlings (*Sturnus vulgaris*) [74,75], which only respond to novel song elements as enhancements of already attractive long-bout songs. Similarly, female túngara frogs (*Engystomops pustulosus*) prefer songs with any of a vast array of novel acoustic ornaments, but only when paired with the species-typical ‘whine’ call [76].

Once receivers attend to a novel signal component, provided that they also respond positively to it, the component and its processing evolve through the cue-to-signal pathway [77]. Receiver features, including novel receiver features (see scenario 2 below), exert selection on signal components, favouring signal variants that match receiver features. The widespread presence of ritualized signals that arose as cues, e.g. from grooming movements [1,78], suggests that this pathway for novelty is not uncommon or constrained. In figure 2—scenario 1, we have focused on the role of the

receiver in whether a novel signal component persists, but this path to novelty is also dependent on the broader environmental context. Specifically, if the cost of possessing the novel signal component or responding to it outweighs the benefits (e.g. by attracting predators, inhibiting mobility and impeding foraging), the new signal will not evolve.

If novelty arises first in a receiver feature (figure 2, scenario 2), the immediate evolutionary dynamics depend strongly on the properties of the signal. When novel receiver features arise, if the existing signal lacks an aspect to which receivers are now attentive the ancestral signal will persist (figure 2, scenario 2). However, if the novel receiver feature is not costly, it could be maintained in the genome, generating a hidden preference [58,59]. On the other hand, when novel receiver features arise, senders may already have a trait that the novel receiver feature can now detect. If so, receivers may immediately respond positively to the newly perceptible sender trait, which could then be refined into a signal (figure 2, scenario 2 [58]). As with novel signal components, when novelty arises only in a receiver feature, it will be subject to selection both within and outside the context of communication; there must be a net benefit for individuals possessing the novel receiver feature in order for it to be incorporated into a communication system. In the existing literature, we often know less about the receiver than the sender (electronic supplementary material, table S1), perhaps because the behavioural and physiological data required to answer questions about the receiver change are absent. But phylogenetic comparative methods have revealed several cases in which receivers appear to lead in the evolution of novelty: female *Xiphophorus* preference for swords predates the evolution of swords [79], and trichromacy (colour vision) evolved in old world monkeys before colourful male mating signals arose (e.g. red fur and skin) [80].

When there is a simultaneous novel change in both senders and receivers (figure 2, scenario 3), the evolutionary dynamics depend on whether or not the changes are compatible (i.e. in the same direction and modality). If changes are not compatible, the scenario would simply be equivalent to scenario 1 or 2 (figure 2). By contrast, simultaneous, congruent changes in both the sender and the receiver are surprisingly common. Communication systems can change rapidly if receivers respond favourably to signal changes (figure 2, scenario 3). In a number and diversity of cases, mating signals and mate preferences change near simultaneously via apparent pleiotropy, close physical linkage or associated with polyploidy (e.g. [81–88]). A similar pattern may arise when juveniles learn or imprint on their parents' signals and preferences [41]. Broader causes of plasticity (e.g. social interactions) have also been predicted to have the ability to generate signal-preference codivergence [89,90], and even non-social sources of phenotypic variation can result in striking signal-preference matching covariance (e.g. host plant developmental environments [91]). We recognize that the differences among scenarios 1, 2 and 3 depend on the starting point. On a phylogenetic scale, most examples of novelty in communication will appear to have evolved via scenario 3, resulting in coupled signaller and receiver traits. However, the initial path to novelty may begin with the sender, the receiver or both, and without the opportunity to directly watch this process play out, we may miss this nuance. These details are important for exploring the initial microevolutionary patterns facilitating novel mating signals and may be best studied using

detailed investigations of organisms currently undergoing dynamic change in mating communication.

Finally, even if there is no change in signal components or receiver features (figure 2, scenario 4), novel communication can still occur through changes in the dynamics of the communication environment. We expand on this idea in the next section.

5. Disruptions through environmental effects

Environmental variation may catalyse the evolution of novel signals and responses to those signals through genetic accommodation and coevolution. When production and transmission are *disrupted* by changes in the environment, this would approximate a change in the sender, while a change in the environment impacting detection would approximate a new feature in the receiver (figure 2, scenario 4). To illustrate these points, we focus on temperature as an example. Temperature could impact sender behaviour and have minimal to no effect on receivers (figure 2, approximating scenario 1). For example, in some flies, temperature impacts sender signalling behavior but has minimal effects on female preferences for signals [5]. Temperature could also theoretically impact receivers and not senders (figure 2, approximating scenario 2). While we could not identify studies that showed this exact pattern, it has been demonstrated repeatedly that some components of signalling are temperature invariant, but are subject to varying receiver preferences across temperatures [92,93]. Additionally, temperature has been demonstrated to affect receiver sensory abilities [94,95], suggesting the possibility of this pattern. Temperature could also have effects on both senders and receivers (figure 2, approximating scenario 3) in ways that are equivalent (i.e. 'temperature coupling' [96,97]) or not [92,98].

While the above examples measure immediate adult responses to temperature, developmental exposure to environmental variation may also affect signals and receiver features through developmental plasticity [99]. In *Bicyclus anynana*, rearing temperature affects the development of sender behaviour (pheromone production, eyespot and colouration patterns [100,101]) and receiver mate choice behaviours [102,103]. Developmental plasticity can promote the evolution of novelty through several mechanisms, including, for example, genetic accommodation and expansion of targets for selection [40]. Importantly, even non-adaptive plasticity can facilitate a rapid evolutionary change by increasing the strength of selection, as has been demonstrated in guppies (*Poecilia reticulata*) [104].

A contemporary anthropogenic change may offer opportunity for the evolution of novelty in animal communication through changes to the abiotic (e.g. transmission properties and signal detection, and human-manufactured objects) and biotic (community composition, eavesdropping natural enemies and species distributions) environments as described above. Changes in the biotic and abiotic environments can also clearly alter the way natural selection acts on both sexual signals and receiver features [105,106]. Widespread habitat fragmentation, for example, alters the distributions and abundance of predators and parasitoids [107]. Changes in the predator community and eavesdropping natural enemies can then exert selection on sexual signals (e.g. a silent male morph evolved in response to selection from an introduced acoustic eavesdropper [108,109]) and receiver features (e.g. female guppies shift preferences in the presence of a predator [110]).

Consider signal transmission and detection, which are dependent on the abiotic environment through which senders transfer signals [1,111–113]. Most signal types are transmitted through the environment, and the environment can attenuate, amplify, filter and otherwise distort signals in a variety of ways. Human alteration of the environment (artificial light, acoustic anthropogenic noise and chemical pollutants [105,106]) has accelerated disruption to communication systems, potentially generating opportunity for the evolution of new signals [114]. Following the environmental change, we expect natural selection to favour signals that effectively transmit through the changed environment (e.g. through sensory drive [115]) and thus could favour the evolution of novelty in many instances. If a newly evolved cue cannot be transmitted through a particular environment, it likely will not be maintained. Numerous examples have been identified where anthropogenic effects mask signals, thus constraining the signal properties available to receivers [98,106,116–126] and sender and/or receiver behaviour itself [127–131]. For example, in turbulent water, female cichlids can no longer use male colouration to choose mates [126], and in polluted water with high concentrations of humic acid, female swordtails (*Xiphophorus birchmanni*) no longer preferred conspecific male chemical cues to congener species [125]. Alternatively, the changed environments (e.g. habitat change) could relax constraints on signal evolution and reveal different aspects of signals to selection, allowing for the evolution of novelty in communication. Though not directly linked to human impacts, microhabitat specialization on oak litter habitats is hypothesized to have relaxed restrictions on signal form in the wolf spider *Schizocosa floridana*, allowing a novel signal component, the tonal ‘chirp’, to evolve in this particular microhabitat [132,133]. ‘Sensory drive’ mechanisms driven by the environmental change such as these are expected to have wide ranging impacts on the evolution of novel signals. The impacts of environmental change will, in part, depend on how widespread and predictable the change is. Anthropogenic land-use change tends to homogenize environments across multiple scales including sensory environments [106,134–137]. Widespread, homogeneous alterations of the sensory environments driven by anthropogenic change are thus expected to lead to widespread changes in senders and receivers, although strong constraints may exist for some taxa [120,138].

Finally, human-manufactured objects have also created new environments to be exploited (metal and glass used as anchor points for webs of orb-weaving spiders (*Araneus diadematus*) [136]) and even new signals themselves (objects such as pens and clothespins used as bower bird ornaments or incorporation of compounds for herbicides in orchid bee courtship chemical cues [49]). Human-manufactured chemicals that are released into the environment also appear to affect receiver preferences; synthetic oestrogen affects female [139,140] and male preferences [141]. It is important to ascertain at what level (i.e. production, transmission or detection) and to what extent the environment disrupts signals as it has important implications for potential origins of novelty.

6. Conclusion

Understanding how biological diversity comes to be requires appreciation of evolutionary novelty, and novelty is readily detectable in mating communication (figure 1; electronic supplementary material, table S1). We argue above that novelty

may arise easily, and we discuss how initial conditions of the sender, receiver and environment dictate how coevolution between the sender and the receiver progresses and whether a new cue becomes a signal. Our review reveals four open questions that require further investigation. Finding the answers to these questions is inherently multidisciplinary and will require studies integrating genetics, development, physiology, neurobiology, behaviour and phylogenetics. First, how widespread are each of the scenarios we outlined (figure 2), and does the evolutionary outcome differ depending on the scenario? While there are many compelling contemporary examples of novelty in mating communication (electronic supplementary material, table S1), for most of these there remain open questions, particularly regarding receivers. We will need more detailed behavioural and physiological work on receivers in systems that have documented a signal change, particularly in a robust phylogenetic context. We would gain a great insight by carefully identifying and documenting sender and receiver behaviours in study systems that are currently experiencing change in signal and/or receiver features (e.g. purring crickets [3]; see also question four). Second, which systems and which types of signals (e.g. courtship signals and warning colouration) are more resistant to novelty in animal communication? Theory predicts that some types of communication (e.g. warning and aggressive signals) may be more stable, but these types of signalling systems are also incredibly variable [142]. Additionally, how often is novelty in mating and courtship signals favoured *per se*? Future work needs to examine how the type of signalling system influences how (and what type of) novelty arises, the stability of the communication system to novelty and the evolutionary trajectory of novel signals for different communication systems. Third, it seems especially challenging to explain seemingly abrupt, discontinuous changes; e.g. new mechanisms of signal production or detection like new organs. Are the mechanisms most often involved in gradual versus abrupt changes in communication the same or different? We know that drift and selection are always important, but perhaps discontinuous change is associated with particular mechanisms (i.e. mutation, hybridization and pleiotropy). Fourth, how important is the environmental change in catalysing novelty in animal communication and under what circumstances do novel traits/novel responses follow from ecological change? One way to approach this question is to ask whether and what type of environmental change accompanies the emergence of novel communication features, but this is difficult to determine when looking back on past evolutionary change. The Anthropocene may offer increased opportunity to directly observe sender and receiver responses to the environmental change (the less detectable ephemeral ‘blips’ along branches of a phylogeny), allowing us to ask detailed behavioural and mechanistic questions that were heretofore inaccessible using phylogenetic approaches.

Data accessibility. This article has no additional data.

Authors' contributions. E.D.B. and R.M.T. conceived of the topic, invited the coauthors and led the writing. All authors met regularly to discuss ideas and contribute to the writing. All authors made substantial intellectual contributions, wrote sections of the manuscript and edited throughout. The authors have read and approved the manuscript, and agree to be held accountable for all aspects of the work.

Competing interests. We declare we have no competing interests.

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