

Dynamics of multiple signalling systems: animal communication in a world in flux

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The ubiquity of multiple signalling is a long-standing puzzle in the study of animal communication: given the costs of producing and receiving signals, why use more than a single cue? Focusing on sexually selected signals, I argue that dynamic variation in selection pressures can often explain why multiple signals coexist. In contrast to earlier research, which has taken a largely static view of the world, new insights highlight how fluctuations in ecological and social environments, as well as non-equilibrium dynamics intrinsic to coevolutionary systems, can maintain both multiple redundant and non-redundant signals. Future challenges will include identifying the circumstances under which environmental fluctuations lead to multiple signalling, and the consequences of such fluctuations for speciation in multiple-signalling species.

The ubiquity of multiple signalling

During sexual and agonistic signalling, animals often use several cues to convey a message (see Glossary). The composite nature of a signal can be obvious, as in the strut display of the male greater sage grouse *Centrocercus urophasianus*, where mates are attracted by coordinated wing and tail movements combined with popping vocalizations [1] (Figure 1). However, signals that are usually regarded as single traits often comprise multiple components as well. For example, each patch in the colour pattern of a bird can be composed of several pigments conveying more or less independent information [2], and in the sexual display of the wolf spider *Schizocosa stridulans*, high speed cameras and laser vibrometry have revealed two distinct seismic components, produced simultaneously by the abdomen and pedipalp [3]. Signal components relying on infra- or ultrasound [4], infrared radiation [5] and ultra-violet reflectance [6] are also easily overlooked as they cannot be detected by the human senses.

But why engage in multi-component signalling instead of concentrating on a single cue? The question is intriguing given that signalling is often associated with considerable costs from time and energy loss as well as predation and disease risk [7]. For instance, in the wolf spiders, seismic signalling compromises the immune function of the signaller [8] and, when added to a visual display, increases the risk of predation for the signaller [9] and the receiver [10]. Until recently, adaptive explanations have mostly concen-

trated on static scenarios, where selection pressures are assumed to be consistent over time (Table 1a). Here, benefits of multiple signals can arise from overcoming constraints during either signal production or reception (Boxes 1 and 2). However, it is becoming clear that dynamic selection can also explain why more than a single signal is used to convey a message (Table 1b). Focusing on sexually selected signals, I review how fluctuating ecological and social environments, as well as oscillations inherent in coevolutionary processes between signaller and receiver, can lead to multiple signalling. The review reveals that dynamic selection might be a more widespread explanation

Glossary

Crossover: when reaction norms cross so that alternative genotypes are superior in different environments.

Cue: an informative trait, which might or might not have been selected as a signal.

Fisherian runaway process: sexual selection due to positive feedback between an arbitrary heritable (male) trait and a corresponding heritable (female) preference; arises from increased mating success of offspring bearing the traits ('sexy sons'), and genetic linkage between the preferred trait and the preference (e.g. in sandflies *Lutzomyia longipalpis*, preferred males produce attractive sons without any apparent good-genes benefits [62]).

Genotype-by-environment interaction (GEI): occurs when environmental change has a different effect on different genotypes. Non-parallel reaction norms reveal GEI, with crossing reaction norms characterising strong GEI. Signal reliability can be undermined by both strong and weak GEI [13,14].

Good-genes models: sexual selection models based on a heritable (female) preference for a heritable (male) trait that reflects high genetic quality (i.e. condition acquisition ability).

Lek paradox: why does female preference for a specific male indicator of indirect benefits persist when such a preference is predicted to erode the genetic variance underlying the indicator and, as a consequence, the benefit of the preference?

Multimodal signal: a multiple signal with at least two components in different modalities.

Multiple (multicomponent or complex) signal: a composite signal that comprises two or more components, each with signal properties.

Rare male effect: negative frequency-dependent selection promoting rare (male) phenotypes as a result of (female) mate preferences.

Reaction norm: a function that describes the response of a single genotype to a gradient in the environment; usually visualized as a line connecting the phenotypic expression of a genotype in two environments.

Redundant signal: signal that repeats information already present in another signal. A signal can be redundant to another without the converse being the case; nevertheless, two signals are often described as 'redundant' when the least informative only repeats information in the other.

Sexually antagonistic coevolution: coevolution owing to adaptation and counteradaptation in sexual conflict over the optimum value of a fitness-related trait.

Signal: a structure or action of an organism (the signaller) that is selected for its effects on the behaviour of another organism (the receiver) via its sensory-nervous system in a fashion that is adaptive to the signaller and (usually) also to the receiver.

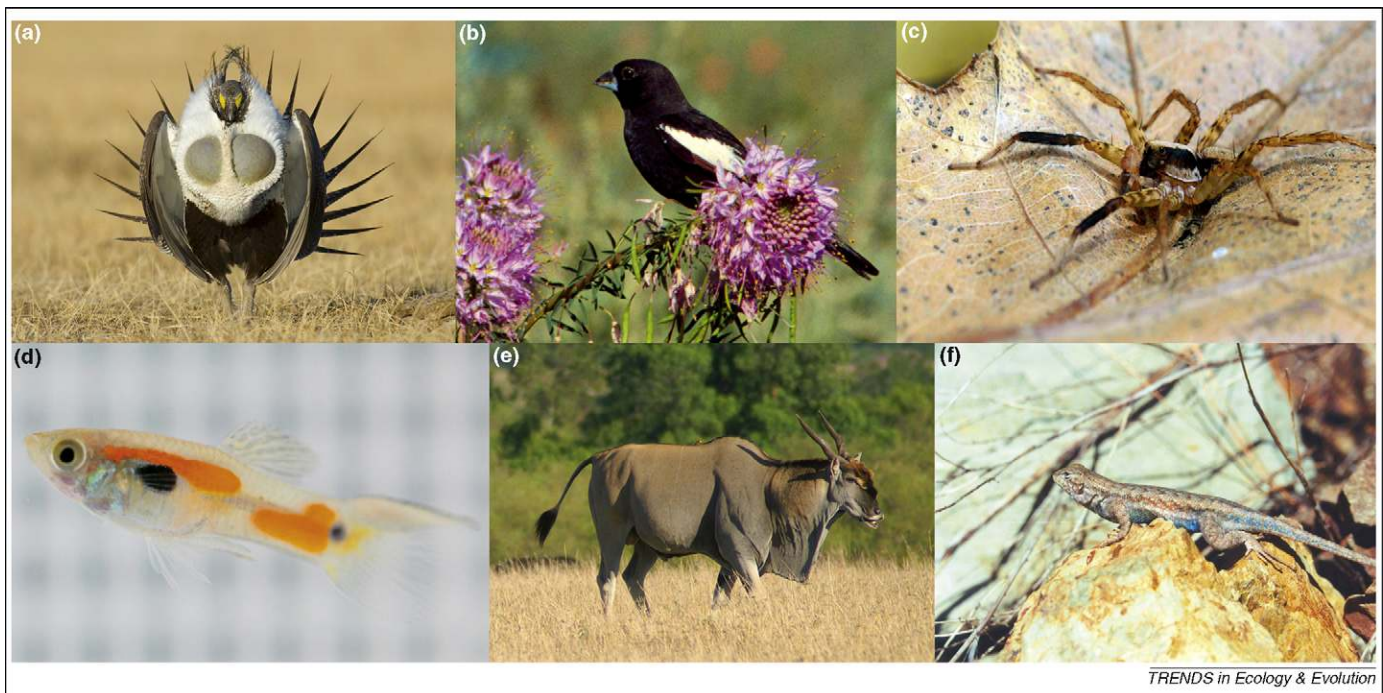


Figure 1. Examples of organisms using multiple signalling systems. (a) The strut display of the male greater sage-grouse includes both visual and vocal elements [1]; (b) the nesting success of the male lark bunting is indicated by multi-faceted coloration and other morphological traits [18]; (c) the male wolf spider uses seismic as well as visual components in courtship [10]; (d) the male guppy attracts females by intricate colour patterns [48]; (e) the eland bull *Tragelaphus oryx* broadcasts fighting ability both visually and by knee-clicking [85]; and (f) the male sagebrush lizard uses posture, headbob displays as well as chemical cues in signalling to conspecifics [80]. Photos courtesy of Neil Losin (a); Alexis Chaine (b); Eileen A. Hebets (c); Anna Price (d); and Ahrash Bissell (f); photo (e) taken by the author.

for multiple signalling than previously appreciated. Clarifying how dynamic selection operates on multiple signals therefore offers an exciting new focus for studies in animal communication, with fundamental implications for understanding the maintenance of genetic variance in sexually selected signals, as well as speciation.

Why do environmental fluctuations matter for signal selection?

Animals are often exposed to drastic changes in both their ecological and social environment, including fluctuations in resource abundance, predation pressure, disease transmission risk, habitat structure, and inter- and intraspecific competition. The consequences of environmental variability have been a key subject in other areas of evolutionary biology for decades; however, the implications for sexually selected signalling have only come into focus more recently [11]. Although a single signal can remain reliable in a fluctuating environment if it is sufficiently flexible to track changes in the message to be conveyed (Figure 2a,b), recent studies have identified several ways in which single signals can become unrepresentative of signaller quality following environmental changes. Here, I suggest that temporal and spatial variability in the environment can often explain why multiple sexually selected signals coexist ('fluctuating environments' hypothesis). In the following sections, I will outline three scenarios in which multiple signalling can be adaptive in response to environmental fluctuations.

Scenario 1: Static signals, but fluctuating signaller quality

Sexually selected signals encompass both agonistic signals to sexual rivals, and sexual signals to mates. Agonistic

signals convey information about fighting ability whereas sexual signals convey information about mate quality (Box 3). Environmental shifts can have profound effects on both these signaller qualities [12], and in such cases, signal expression needs to be flexible in order to reflect the changes. However, whereas some signals remain flexible through life (e.g. many behavioural traits), others are innate or fixed during early development (e.g. many morphological traits). Fixed signals become particularly misleading when environmental changes have different effects on the quality of different genotypes (i.e. when genotype-by-environment interaction (GEI) occurs [13,14]). When environmental change thus compromises the correlation between a fixed signal and signaller quality, a new signal can evolve from a cue which is a better indicator of quality in the new environment (Figure 2c).

As an example of how environmental change can render a fixed signal unreliable, consider the horns of male bovids, which Darwin suggested might be partly selected as an intersexual signal of quality to females [15]. In the sheep *Ovis aries*, male horn length has been found to indicate high lifetime reproductive success only in stable, benign climates; in contrast, under severe conditions, where survival matters more than breeding success, horn length becomes negatively related to lifetime reproductive success [16]. Horn length thus becomes an unreliable indicator of overall mate quality. In such cases, where a static signal is primarily determined by condition during a particular developmental stage and does not reflect signaller quality across all contexts encountered later in life, selection can favour additional signals to reflect current condition. For example, when assessing mates, female crickets *Gryllus campestris* take into account not only male call frequency, which reflects exoskeletal size

Table 1. Evolutionary hypotheses and proximate functions of multiple signalling systems

Hypothesis	Description	Redundancy in information encoded (isolated vs. combined components) ¹	Redundancy in information perceived (isolated vs. combined components) ^{1,2}	Relationship between components perceived ²	Example
(a) Static selection regimes					
<i>Multiple messages</i>	Each component reflects distinct information	A resp. B vs. (A + B)	A resp. B vs. (A + B)	Independence	[85]
<i>Emergent message</i>	Information resides in the combination of signal components	A resp. B vs. C	A resp. B vs. C	Emergence	[86]
<i>Backup</i>	Backups compensate for coding errors	~A resp. ~A vs. A	~A resp. ~A vs. A	Equivalence	[72]
<i>Alerting signal</i>	One component is an 'attention grabber'	A resp. 0 vs. A	0 resp. 0 vs. A	Modulation	[73]
<i>Receiver psychology</i>	Multiple cues enhance discriminability or learning	A resp. A vs. A	a resp. a vs. A	Enhancement	[74]
<i>Sensory overload</i>	Manipulation of receivers by exploiting reduced ability to process multiple stimuli	A resp. 0 vs. A	A resp. 0 vs. 0	Dominance	Pending
(b) Dynamic selection regimes					
<i>Fluctuating environments</i>	Fluctuations in ecological or social conditions affect signal information content, transmission or receiver interests	Context-dependent	Context-dependent	Context-dependent	[18]
<i>Sexually antagonistic coevolution</i>	Diverging interests of the sexes over signal honesty result in non-equilibrium coexistence of multiple signals	Context-dependent	Context-dependent	Context-dependent	Possibly [87]
<i>Rare male effect</i>	Negative frequency-dependent selection arising from the 'rare male' effect maintains multiple sexual signals	Context-dependent	Context-dependent	Context-dependent	[48]

¹ The letters A, B and C indicate distinct messages, with small letters indicating part of the information content; 0 denotes no information; 'resp.', respectively. ² Modified from Ref. [61].

and thus condition during juvenile development, but also chirp rate which indicates current condition [17].

Is the reliability of some signal types more susceptible to environmental fluctuations than others? When receivers assess signals of fighting ability or non-genetic ('direct') benefits provided by mates, they are typically interested in signaller condition over a shorter timeframe than when assessing signals of heritable genetic ('indirect') benefits, which rather depend on an individual's lifetime performance. Environmental fluctuations might therefore have a particularly strong effect on the reliability of the first two types of signals. For example, in the multiple-signalling lark bunting *Calamospiza melanocorys*, drastic fluctuations have been discovered in how well individual signals reflect the direct benefits provided by males [18]. In this socially monogamous songbird, the suite of male size and plumage traits which predicts mate quality depends on the adversity of the environment and thus varies dramatically from year to year. Corresponding to these changes in signal content, the signal preferences of individual females are flexible over time, tracking the traits that are currently superior fitness indicators [18]. As a result, several male traits are under positive selection in certain years only, with some of these, such as body size and various colour

patterns, even coming under negative selection in different years. This shows that the sexual signals of the lark bunting are maintained by fluctuating selection, although further work is needed to investigate exactly how fixed each signal is within individual males.

It should not be assumed that animals can always signal adaptively in any environment encountered. Whether effective signals will evolve and persist depends on the evolvability of both the signal and the receiver preference, as well as on how frequently the signal provides a selective advantage to the signaller. Thus in erratic environments, where some conditions are only rarely encountered, even multiple-signalling animals might be unable to convey a message. For example, in the blue tit *Parus caeruleus*, where multiple colour signals are known to be strongly dependent on the environment [19], neither direct nor indirect benefits associated with the signals have been detected [20]. Here it is possible that none of the signals used are adaptive in the environment studied.

Scenario 2: Converging signal expression in good or poor environments

In scenario 1, single signals, which were phenotypically fixed, were undermined by changes in the quality of the

Box 1. Multiple signals as equilibrium solutions

So far, multiple signalling systems have largely been considered within a theoretical framework assuming static selective regimes [61,63], and empirical studies over the past decades have provided many examples where both multiple redundant and non-redundant signals are seen as equilibrium solutions.

Focusing on signal content, the 'multiple messages' hypothesis proposes that the signal information value is increased most cost-effectively by adding novel, non-redundant components [64]. Support for this idea has been reported from a broad range of taxonomic groups, particularly in studies of sexual and agonistic communication where receivers seek information on several distinct aspects of mate quality and fighting ability, respectively [26,65].

According to the 'emergent message' hypothesis [66], the information relevant to receivers emerges from the interactions between signal components, and animals with higher cognitive ability are indeed known to integrate separate signal elements in their assessment of both sexual and agonistic signals. For example, when male songbirds produce a trill, they experience a tradeoff between the trill rate and frequency bandwidth [67]; vocal performance therefore depends on both these traits jointly [67], and in evaluating trills, receivers of both sexes have been shown to take this into account [68,69].

The 'backup' hypothesis maintains that multiple redundant signals compensate for errors during information coding [70]. In general, artificial neural networks show backup signals to be most robust when multimodal [71]; however, unimodal and repeated signals can also act as backups. For example, in the waggle dance of the honey bee *Apis mellifera*, the direction of each waggle run indicates the location of a food source with error, and receivers average the angle of multiple runs to improve their estimate of the location [72].

Multiple signals can also improve signal efficacy rather than content. Attention grabbers can improve signal detection by alerting receivers to other, more informative, signal components, as stated by the 'alerting signal' hypothesis [60]. For example, in the Bornean ranid frog *Staurois guttatus*, advertisement calls cause conspecifics to orientate towards a subsequent foot-flagging display [73].

Finally, the 'receiver psychology' hypothesis suggests that redundant signal components enhance the accuracy and speed of receivers in discrimination and learning tasks [60]. For instance, in domestic fowl *Gallus gallus*, the reaction time of the hens to the food-alerting signal of the cock ('tid-biting') decreases when the hens are exposed to both the vocalization and the rhythmic head movements of the cock [74]. Facilitated learning might explain why aposematic signals are often multimodal [75]; hence the combination of visual and auditory components accelerates the speed with which domestic fowl learn to discriminate against unpalatable food items [76].

signaller; in scenario 2, signaller quality is fixed but phenotypic changes in signal expression renders single signals uninformative. Hence some flexible signals are sensitive to variation in signaller quality over a limited range of environments only. Specifically, where signal reliability is assured by condition-dependent differences between individuals in their ability to bear signal costs [21], the magnitude of these costs is likely to depend on the environment. Consequentially, informative variation in signal expression can disappear in both unfavourable environments, where the signal becomes too costly for any individual to express, and in favourable environments, where all individuals can afford to express the signal fully [22]. Under such circumstances, the variance in quality among signallers becomes cryptic [23], selecting for alternative condition-dependent signals, with higher sensitivity in the current context (Figure 2d).

Flexibility in expression, which renders a signal vulnerable to signal size convergence, is common in behavioural

Box 2. Sensory processing of multiple stimuli

New insights into the neural mechanisms behind multimodal stimulus integration are shedding new light on how neural constraints impact on the evolution of multiple signals. Specifically, the discovery that crossmodal integration occurs at several cognitive levels agrees well with the diversity of evolutionary explanations for multiple signals (Table 1). Previously crossmodal stimulus integration in mammals was believed to be confined to higher-level processing in the association cortex, the area which generates a meaningful representation of the world and allows abstract thought; however, evidence now shows that sensory convergence also occurs during early processing in the primary sensory cortices [77]. Early sensory convergence is characterized primarily by temporal coordination across modalities [77]. For example, when rhesus macaques *Macaca mulatta* process vocalizations from conspecifics, whether neurons in the auditory cortex respond to combined auditory and visual components by suppression or enhancement depends on whether the stimulus onsets are separated by more or less than 0.2 s, respectively [78]. Such simple neural mechanisms can favour simultaneous emission of multiple redundant signals to facilitate discrimination.

Another intriguing idea is that the neural suppression of incongruent multimodal stimuli might be exploited by signallers to conceal information when the interest of signaller and receiver diverge ('sensory overload' hypothesis) [63]. There are several examples of multimodal stimuli hampering information transfer. In male noctuid moths *Spodoptera littoralis*, exposure to female pheromones inhibits the response of the tympanic nerve to echolocation signals from bats, thereby increasing predation risk [79]. Also, in the sagebrush lizard *Sceloporus graciosus*, responsiveness to visual headbob displays and, in particular, to chemical signalling is reduced when these signals are combined [80]. However, empirical evidence that signallers benefits from manipulating receivers by sensory overloading is still wanting.

signals but can also be seen in sexually selected morphological signals. For example, in the black grouse *Tetrao tetrix*, tail length and eye comb colouration, which are both sexually selected, are more sensitive to stressful conditions than are body mass and wing length, which are naturally selected [24]. It is not only the ecological environment, but also the social context which can affect signal expression. For instance, in fowl *Gallus gallus*, males respond to their current dominance status by adjusting multiple sexual traits, including comb size, a condition-dependent signal, and vigilance, a potential-mate choice cue [25]. Moreover, the environment can affect the informative variation in signal size by influencing transmission rather than expression [26]. For instance, in the wolf spider *Schizocosa ocreata*, a 'drumming' courtship signal produced by leg tapping is inhibited on substrates which are not conducive to vibration, whereas a largely redundant visual display is obstructed in environments with visual noise or low light [27]. This example illustrates how multimodal signalling is particularly efficient in securing transmission across environments, because different environments often impede transmission disproportionately in specific modalities.

Scenario 3: Different receiver interests in different environments

As well as responding to fluctuations in signal content, receiver preferences might themselves be directly affected by environmental changes and thereby act as drivers of signal evolution. Receivers can thus prefer different

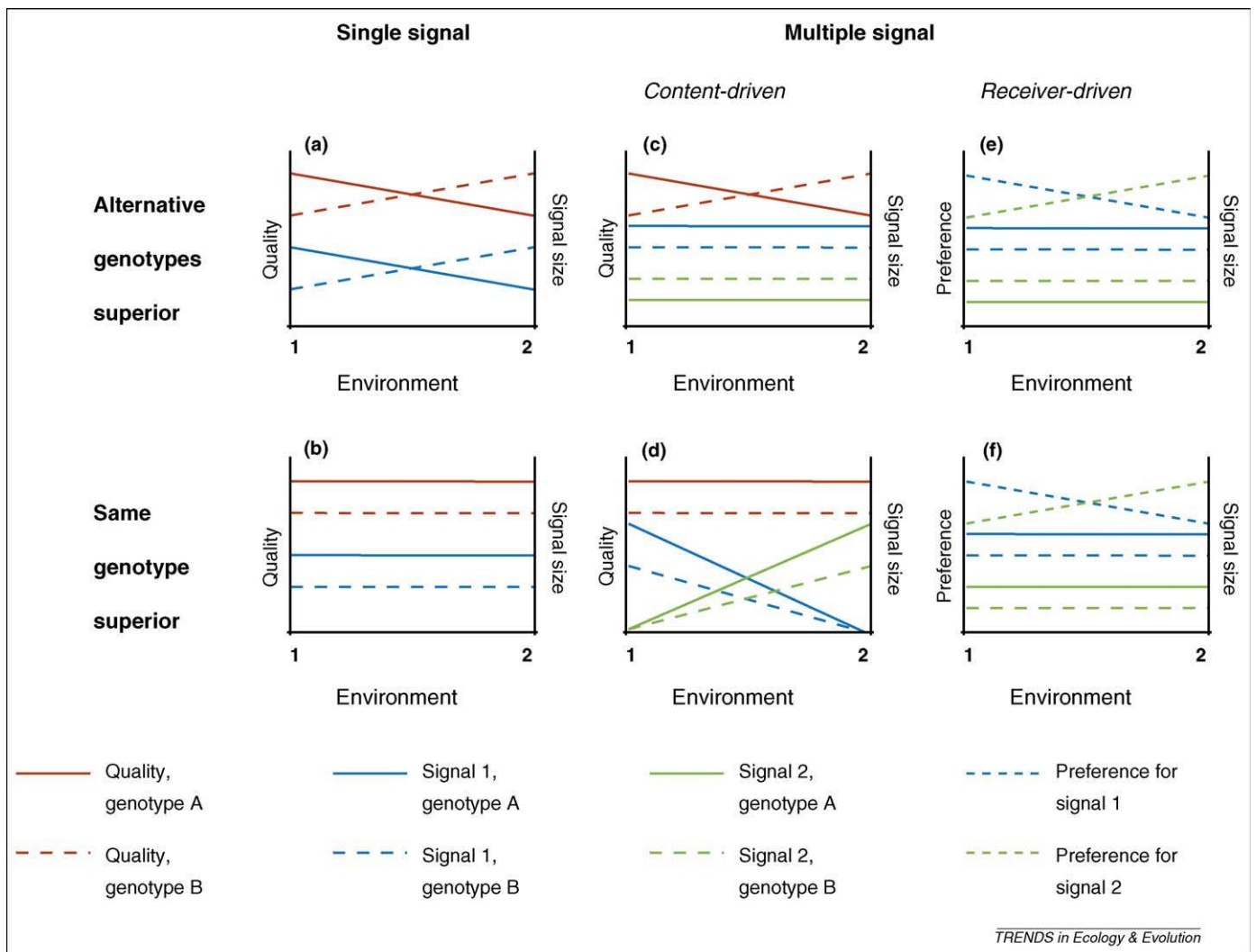


Figure 2. Signalling of individual quality across environments. (a) A single signal stays reliable across environments if it tracks any changes occurring in signaller quality; (b) hence a phenotypically fixed signal is reliable only when signaller quality remains constant. (c) Where different genotypes are superior in different environments, but signals are fixed, multiple signals are needed to reflect individual quality across contexts (scenario 1 in main text). (d) For flexible signals, reliability can be undermined in environments where signal expression converges, either because conditions are good and full signal expression is affordable to all, or because conditions are poor and signalling is too costly for all. In these cases, multiple flexible signals which differ in their sensitivity to environmental conditions, are required to reflect signaller quality across contexts (scenario 2 in main text). (e,f) Multiple signals can also coexist because signal preferences of receivers are affected directly by environmental changes. This can happen either because signals differ in their accuracy or assessment costs, or because the signaller attributes of interest to receivers differ between contexts. Such changes in receiver preferences might (e) or might not (f) lead to selection on different signaller genotypes (scenario 3 in main text).

signals in different contexts, either because signals vary in their accuracy or assessment costs [28], or because the signaller attribute of interest to the receiver depends on the environment (Figure 2e,f). Thus there is a growing realization that receiver preferences, like signals, are often condition-dependent [29], and since condition is strongly influenced by the ecological environment, condition-dependent preferences can target different traits in different environments. Receiver preferences, like signal expression, also sometimes depend on social rather than ecological contexts [30–32]. For example, in the sand goby *Pomatoschistus minutes*, a small fish with paternal care, males attract females by courtship displays and well-built nests [33]; however, females only show an additional preference for large males in the context of intense male competition, where large body size might prevent a male from being expelled from his nests [34].

Receiver genotypes do not always respond similarly to environmental changes. Thus receiver preference functions are basically reaction norms which denote the environment-specific responses of distinct receiver genotypes to the range of signal values encountered [35]. For instance, in wax moths *Achroia grisella*, ecological cross-over of reaction norms occurs not only in male calls [36], but also in the female preferences for these calls [37]. Such simultaneous strong GEI in receiver preferences as well as signal expression can result in complex selection dynamics, which can have a key role in maintaining the genetic variance in multiple signals.

Intrinsic coevolutionary dynamics favouring multiple signals

The evidence reviewed above shows how dynamic selection generated by environmental fluctuations can lead to multiple signalling. However, even in the absence of

Box 3. Sexually selected signals and their condition-dependence

Sexually selected signals include both agonistic signals to sexual rivals and sexual signals to mates. Sexual signals convey either indirect benefits, arising from genes passed on to offspring, or direct benefits, which include resource provisioning, and low risks of predation and disease transmission. Signals of indirect benefits reflect heritable genetic quality in the form of compatibility genes [81], viability genes or attractiveness genes [82], where viability genes and attractiveness genes can be seen as extremes in a continuum [83]. Many sexual and agonistic signals are believed to be condition-dependent, with their reliability arising either from mechanical constraints associated with signal production, or from individual differences in the cost paid, or benefits gained, from signalling [21]. Condition can be determined by both intrinsic (often polygenic) and extrinsic factors. Whereas condition-dependent signals of indirect benefits require a link between condition and heritable genetic quality, in the case of signals of direct benefits and agonistic signals, covariation between signal expression and condition can be entirely environmental in origin.

environmental variability, oscillations in selection gradients have the capacity to maintain multiple signals owing to dynamic processes which are intrinsic to the coevolution between signaller and receiver.

Sexually antagonistic coevolution

Similar to the focus on static selection regimes in empirical studies of multiple signals, theoretical models of these systems have traditionally proposed equilibrium solutions, implicitly assuming environmental constancy. The findings of early models emphasized how costs oppose the evolution of redundant signals for the same underlying quality [38,39], and rather pointed to the Fisherian runaway process [40] and selection for independent good genes indicators [41,42] to explain the existence of multiple sexual signals. However, recent insights from non-equilibrium models show how multiple redundant sexual signals can be maintained through sexually antagonistic coevolution without relying on low costs ('sexually antagonistic coevolution' hypothesis) [43]. Sexually antagonistic coevolution can be triggered by sexual conflicts between females seeking honest information about male quality, and males seeking to manipulate females by signal exaggeration [44,45]. When both sexes are allowed to respond optimally by introducing adaptive dynamics to a standard good genes-model of condition-dependent signalling, multiple redundant signals can coexist even if the signal preferences entail significant costs [43]. For instance, assuming only two distinct viability components, the models explain the evolution of up to 20 ornaments and corresponding preferences. This discovery demonstrates that multiple sexual signals can coexist owing to fluctuations in selection, which are inherent in the coevolution between signals and their preferences.

The rare male effect

In species where females prefer rare males as mates, multiple signals can be maintained by negative frequency-dependent selection ('rare male effect' hypothesis) [46]. For example in green swordtails *Xiphophorus helleri*, females prefer rare males based on the frequency of two sexually selected traits, sword size and body size [47].

Likewise, in guppies *Poecilia reticulata*, the selection gradients acting on the multiple ornaments oscillate as females prefer currently rare male phenotypes [48]. The adaptive significance of the rarity preference remains enigmatic. In guppies, it is possible that offspring survival is improved because of reduced predation on rare morphs [49], which would make the rarity preference a consequence, rather than a cause, of multiple signalling in this case.

Conserving genetic variance in multiple signals

The wide scope for context-dependent selection to act on signal evolution emphasises the need to analyse selection patterns over a sufficiently long time-frame in the wild to cover the relevant ecological and social scenarios [50]. From a quantitative genetic perspective, this is particularly important in order to understand the genetic basis for the sexual signals indicating heritable genetic benefits. Here, two central puzzles are: (1) 'the lek paradox': why is the additive genetic variance observed in sexual signals for indirect benefits not eroded by directional selection? [51,52], and (2) how can multiple sexual signals advertise genetic benefits when the genetic covariance structure underlying the signals often drastically limit the amount of independent genetic variation available for selection in each individual signal?

Resolving the lek paradox

Short-term studies can result in an erroneous impression of strong directional selection acting on a single indicator of indirect benefits. This poses the lek paradox as an apparent conundrum: why aren't the advantageous alleles advertised driven to fixation with the result that the signal becomes obsolete? Here long-term studies can be crucial because they can capture fluctuations in selection gradients, which reveal selection to be weak on average, but act upon several traits. Particularly when GEI is strong (i.e. different genotypes are superior in different environments), selection can fluctuate drastically and thereby prevent erosion of genetic variation in signal traits.

Identifying independent genetic variance in multiple sexual signals

Where multiple sexual signals are known to co-occur, explaining how the corresponding multiple receiver preferences can all provide indirect benefits is often challenging. First, the genetic variance in a signal is typically only partly correlated with signaller quality, and hence only partly meaningful to the receiver. Furthermore, the genetic covariance structure underlying the multiple signals can also radically reduce the proportion of the meaningful genetic variance in each signal which is available for selection [35]. This is because the information provided by individual signals overlap, which reduces the selective advantage of responding to multiple signals. Thus empirical studies have sometimes reported insufficient independent genetic variance in multiple signals to explain the adaptiveness of multiple female preferences by condition-dependent signalling of male quality [53]. However, where studies fail to encompass the natural range of environments faced by a species, context-dependent signal expression remains potentially powerful in identifying additional

meaningful genetic variance [13]. Hence, signals might only be sensitive to variation in condition of the signaller in a limited range of environments. In particular, some signals might only express their condition-dependence under more severe conditions than experienced in a benign laboratory environment [54]. Like field studies, laboratory experiments must therefore include multiple representative environments if the genetic consequences of context-dependent selection are to be accounted for.

Spatially dynamic selection on multiple signals and speciation

Multiple-signalling species are likely to be more prone to speciation because they are more flexible in their response to context-dependent selection on communication [26]. Spatially dynamic selection thus has strong potential to cause population divergence when different signals are adaptive locally, and the alternative signals are exposed to genetic drift or negative selection. Several recent studies have documented an association between multiple signalling and high speciation rates [55,56]; and specifically in antbirds (Thamnophilidae), signal complexity has been shown to demonstrate the strongest link with taxonomic richness at the subspecies level where speciation is incipient [56]. That multiple signalling can facilitate reproductive isolation at the prezygotic stage is also consistent with findings showing that mate preferences often diverge in several signals between sister taxa, at both the subspecies and species level [57–59]. Here the fact that multiple signalling can enhance signal discrimination and learning [60] might be relevant in promoting assortative mating, which reduces gene flow. Still, there is a lack of studies specifically investigating the role of environmental variability on speciation rates among multiple-signalling species.

Conclusion

The evolution of multiple signals through dynamic selection merits distinction from static evolutionary hypotheses because of the fundamentally different implications for the maintenance of genetic variance and the operation of sexual selection. However, dynamic hypotheses are not easily subsumed within the established theoretical framework for explaining the adaptive value of multiple signals. This framework is based on the redundancy of signal components (Table 1a), but under dynamic selection, signal redundancy is context-dependent (Table 1b). This difference furthermore underscores the limitation of the common methodological approach where receiver responses to signal components in isolation are compared with responses to the multi-component signal [61]: if receiver reactions are context-dependent, such studies do not clarify the adaptive value of the system unless they are carried out in multiple environments [47]. I therefore advocate the explicit recognition of dynamic selection in formal hypotheses, which will hopefully encourage field studies and laboratory experiments to be designed appropriately for the detection of context-dependence (Box 4). Indeed, the possibility that context-dependence of signal content and receiver preferences is widespread calls for multiple signalling systems, which have previously been ascribed to static selection regimes by default, to be revisited.

Box 4. Future studies

Analysing multiple signals as the outcome of dynamic, rather than static, selective regimes opens up several new exciting areas for research. Three central questions are:

When do environmental fluctuations select for multiple signals and when do they rather undermine signal reliability altogether?

We know little about how often and how regularly environments need to be experienced in order to maintain a context-dependent signal, and its preference, in a population. Even less is known about the evolutionary origin of multiple signals. We need quantitative genetic analyses that address these questions. However, relevant analyses require a good understanding of the natural history of the study systems. Thus, there is a need to incorporate the frequency and duration of environmental shifts, as well as their timing in relation to the organisms' life history [13]. The interdependence of selection gradients in multivariate traits also means that identifying and including the full range of signals used is important [84].

What is the relationship between phenotypic plasticity in signal expression and selection for multiple signals in variable environments?

Signal expression can be largely determined by the genotype or show pronounced phenotypic plasticity in response to environmental conditions, either during development or throughout life. Because signal plasticity might or might not be adaptive in terms of conveying a given message, the relationship between signal plasticity and selection for multiple signals is not obvious *a priori*. Comparative studies can clarify these relationships. We might expect different evolutionary patterns to occur in sexual signals for indirect and direct benefits, and again in agonistic signals, since the purpose of a signal is likely to influence whether receivers pay attention to indicators of long-term or short-term condition. Hence, average condition across contexts might best reflect indirect genetic benefits, and this could select for permanent, costly signals in order to prevent opportunistic cheating by low quality individuals. In contrast, current condition might be a better predictor of direct benefits and competitive ability, and this could select for signal flexibility.

What are the links between multiple signalling, speciation and environmental variability?

Do speciation rates depend on the number of signals diverging? What is the relative power of ecological and sexual selection in explaining the link between multiple signalling and species richness? Can condition-dependent receiver preferences for alternative signals lead to assortative mating and speciation? Are multiple-signalling species generally better at adjusting to climatic changes owing to more diverse and flexible communication systems? Will they respond by increasing their speciation rates?

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