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Sensory ecology, receiver biases and sexual selection

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During courtship, signals are sent between the sexes, and received signals contain information that forms the basis of decision making. Much is known about signal content, but less is known about signal design – what makes signals work efficiently? A consideration of design not only gives new insights into the evolution of signals (including novelty), but also allows the development of specific and testable predictions about the direction of evolution. Recently there has been increased interest in signal design, but this has resulted in some apparently divergent views in the literature.

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Growing interest in signal design efficiency has produced some diverse and divergent views in the literature because various authors have emphasized different and partially overlapping components of the evolution of signals and signal recognition, giving them different names. Models include pattern recognition and general assessment programs¹ (PRP and GAP), sensory traps^{2,3} (ST), pre-existing bias^{4–7}

(PB), sensory drive^{8,9} (SD), sensory exploitation^{10,11} (SE), receiver psychology^{12,13} (RP), hidden preference¹⁴ (HP) and perceptual drive¹⁵ (PD). The classical sexual selection models^{16–19} [Fisher process (FP), good genes and/or handicap and/or indirect benefits (GG) and direct benefits (DB)], differ in their aims; they emphasize signal content rather than design efficiency. Each model encompasses a different part of the

process of signal evolution. We will place them in perspective by considering the factors and processes that affect each stage of communication (Box 1) and the sequence of evolutionary steps involved (Box 2).

During mate choice, the receiver must detect, perceive, assess (extract information) and act upon the signal. Signal evolution is biased and constrained by how these receiver processes can work, as well as by the biophysics of signal generation, emission and transmission (Box 1). Environmental conditions can affect signal reception and perception, and signalling behaviour determines the range of these conditions during communication. The functional relationships between these factors mean that changes in one will cause evolutionary changes in the others (Box 2). Known and predictable properties of the environment, signals and neural systems will bias the direction of evolution at each stage⁹. We call the resulting process sensory drive (SD), and it provides a conceptual framework for all the models (Box 2).

Models

Sensory drive

The SD model emphasizes the evolutionary processes and interactions, and the ecological determinants of signals and sensory systems (Box 2). For example, environmental factors can affect signals, signalling site choice and timing^{20–23}. The model also emphasizes that there are many

Box 1. Stages in communication between a sender and a receiver and the factors and processes which can bias the evolution of communication systems

There are nine stages in communication between signal generation and decisions based on the signal by the receiver (modified from Ref. 34). Natural and sexual selection can operate independently and differently at each stage, and these processes can bias the direction of evolution of signals, senses, signalling behaviour and decisions. Genetic and developmental biases and constraints can also affect the direction and rate of evolution, but are not discussed here.

(a) Generation and emission of the signal by the signaller: signal structure

Some signals might be less costly to emit than others or degrade more slowly, even if emitted at the same total intensity. This is a function of the biophysics and biochemistry of emission and the match between the emitting organ and the environment^{9,34,35,49}. The decision whether or not to signal, or how complex or loud the signal can be at any one time, will be a function of the energetic and psychological state of the signaller, as well as the local predation rate.

(b) Transmission: environmental properties

The signalling environment predictably attenuates and degrades signals. Choice or modification of the signalling microenvironment can minimize these effects^{9,20,21}, as in mole crickets⁵⁰. Predation avoidance can also be aided by choice of particular signalling microenvironments^{20,21}.

(c) Reception: sense organ structure and environmental parameters at the sense organ boundary

Background noise and organ–environment interactions affect the efficiency of signal collection and coupling to the receptor cells^{34,37,38,40,51}.

(d) Transduction: signal collection and transducing properties of the receptors

The structure of receptors and the degree and rate of physiological adaptation to previous signals affects collection and transduction efficiency and quality^{34,37,38,40,51}.

(e) Coding: signal design and content

The ways signals are initially processed and coded in the sense organs for subsequent processing by the brain sets limits on what sorts of signals can be received and the types of information they can transmit^{34,37–39}, but can result in unexpected biases towards new signals¹⁵.

(f) Perception: recognition that the signal is present and estimating its parameters

Mechanisms of signal processing, sense-specific brain regions (e.g. tectum in fish) and regional separate processing of different parts of the signal might affect signal alerting and attendance, and how signals are perceived⁵².

(g) Classification: recognizing, discriminating between and classifying perceived signals

Pattern recognition and classification can bias recognition of some signal structures over others^{1,3,12,14}. Signal structure can affect the ease of classification depending upon the evolution of deception⁵³, as well as passive interference or jamming from other males³⁴.

(h) Assessment: interpreting signal and extracting critical information

Assessment and decoding of signal content involves cognition and other higher brain processes¹. Signal design will affect what types of information can be extracted and the ease of assessment. Signal extraction and assessment will also be affected by the evolution of deception⁵³ and mating resistance²⁵.

(i) Decision: deciding, on the basis of the assessment, what to do in response to the signal^{1,16–19}

Alternatives to a direct response include waiting for more signals and comparison with other signals in short- or long-term memory.

cycles of evolutionary interactions (Box 2 and Fig. 1vi).

Curiously, some authors^{24,25} associate the SD model and its components with evolutionary static levels of preference. This is incorrect²⁶; populations vary in sensory properties, which consequently cause the biases. Neural systems continually evolve in response to changing environments and, even if they were static, nonlinearities in neural systems mean shifting preferences for multiple traits^{17,27}. Even simple open ended preferences^{4,28} (e.g. increasing preference for larger size, volume, frequency, brightness etc.) will result in continual changes in sexual selection systems. The rate of change in the SD model and its components will depend upon the rates and directions of selection in each link^{9,26}.

Receiver bias models

There are three related models that emphasize evolution arising from biases generated within the sensory system and

brain of the signal receiver (Box 2, steps 2–4): pre-existing bias, sensory exploitation and sensory traps. The PB model is the most general one and includes the other two. However, all three differ in emphasis. Pre-existing bias emphasizes the evolution of novel traits as a result of inherent biases in the sensory system and brain; SE emphasizes the evolutionary modification of existing male traits in response to the female sensory system; and ST emphasizes co-option (i.e. switching) of sensory functions from contexts that were formerly unrelated to sexual selection. All of these aspects have been discussed in the literature relating to each model^{2–11}.

Pre-existing bias. In the PB model, biases in sensory or cognitive systems (Box 1c–i) result in preferences for particular traits or trait combinations, and these preferences favour male traits that match them^{5–7}. Thus, PB corresponds to evolutionary steps 2 and 3 of the SD model (Box 2), and is affected by selection explicitly from factors

in stages c–i of Box 1. These biases could have evolved in contexts other than sexual selection (Box 2, steps 1, 5 and 7), or in the context of different sexually selected traits. The biases could also have evolved by processes other than natural selection, such as genetic drift and recurrent mutation^{5–7}. The PB model suggests that the same bias can result in different male traits being selected in different lineages that share the same bias, and that such biases act concomitantly with additional selective or other evolutionary processes that can also influence the direction and strength of sexual selection^{5–7}. Basolo^{5–7} proposed four criteria needed to show that a male trait has evolved as a result of a pre-existing bias:

- The species has the trait, a preference for that trait and the trait is used in mate choice.
- The trait is absent (or in a primitive form) in ancestors.
- Preference for the trait is ancestral (Fig. 1i).
- There is a bias in the sensory system or brain that accurately and specifically predicts the direction of preferences.

Sensory exploitation. In the SE model, sensory system properties affect perception and hence female preferences. The male traits that are most successful in stimulating the female sensory system are favoured, leading to similarities between signals and preferences^{10,11}. Therefore, SE corresponds to steps 2–3 of the SD model (Box 2), and is affected by selection explicitly from factors in stages c–e of Box 1. In its original form^{10,11,24}, the evolution of the sensory system was not emphasized (Fig. 1i) but, more recently²⁹, this has been explicitly included (Fig. 1ii). The SE model was the first with an explicit phylogenetic component¹¹, and assumptions about event sequences allow some specific and clever tests of the SE model and the more general PB one^{29–31} (Fig. 1). The SE model is a subset of the PB model, in that PB explicitly includes higher brain processes (Box 1f–i) and emphasizes preferences for traits that have not yet evolved. The SE model includes cases in which the preference evolves for reasons unrelated to sexual selection on the trait under study. These were implicit before but are now explicitly included (M.J. Ryan, pers. commun.).

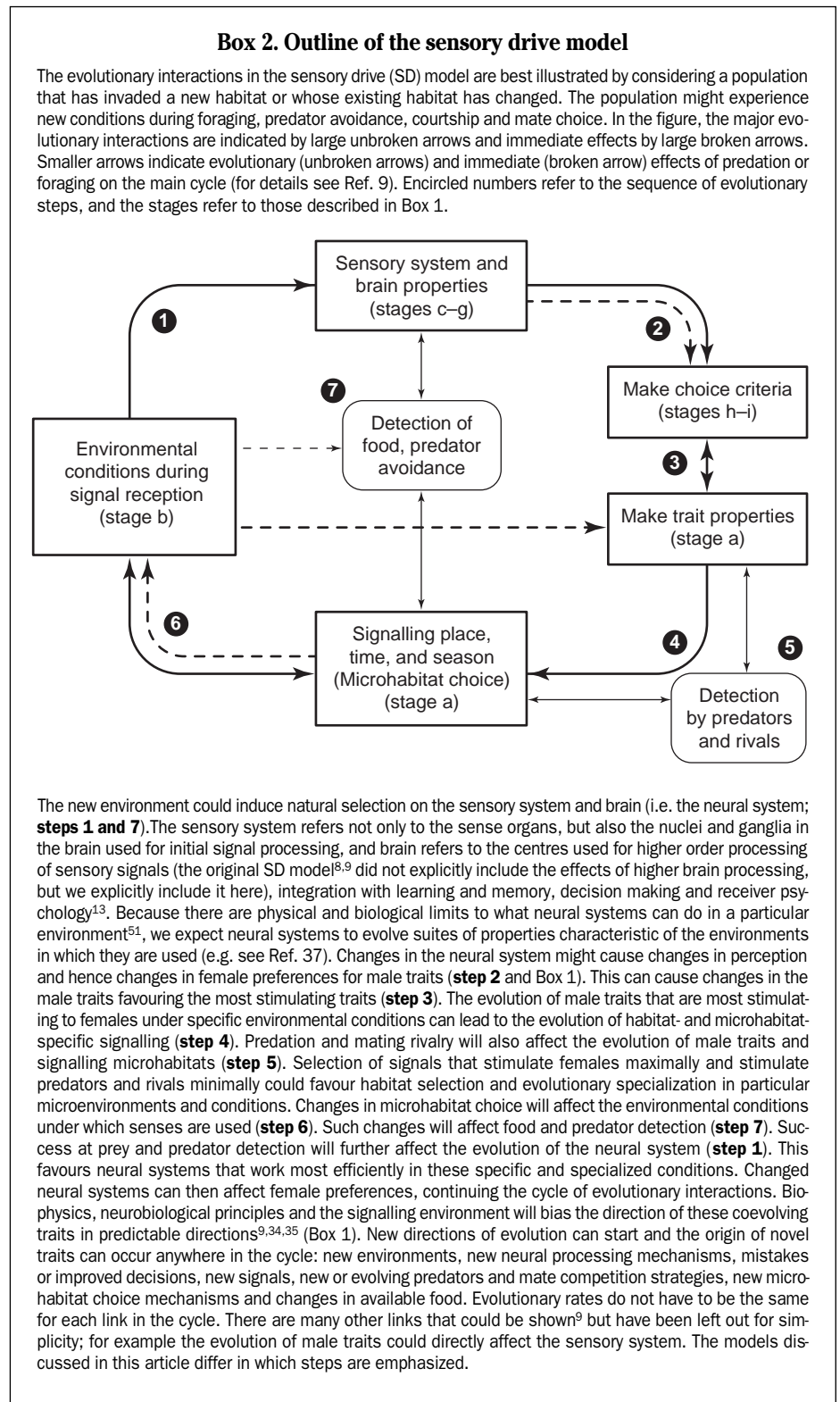
Sensory traps. The idea of STs is similar to SE and PB but emphasizes neural responses to signals that evolved in contexts other than sexual selection^{2,3,32} (steps 2, 3, 5 and 7 in Box 2). For example, male crabs (*Uca beebei*) sometimes build mud pillars at their burrow entrances. Claw waving and other movements are the primary

female choice criteria, followed by pillar presence (J. Christy, pers. commun.). Females move on the surface between male burrows when searching for a mate. Crabs that move away from their burrows are at a relatively greater risk of predation than are crabs that remain at burrows. The presence of pillars apparently exploits the general tendency of crabs, when moving on the surface, to orient towards and hide behind vertical objects such as pneumatophores^{3,32}. Females that have a pillar nearby can also be less vigilant and thus have more time to assess the male building the pillar. Mating with him is also more likely because he will be closer. This example shows that it is invalid to assume that selection of a response occurs only because it is elicited by a particular sexual signal³. The ST model requires only an out-of-context response – the signal must resemble the model stimulus (e.g. a pneumatophore) enough to work. It emphasizes co-option of higher neural processing systems (Box 1f–i) that cause incidental mate preferences, whereas the SE model emphasizes exploitation of sensory factors (Box 1c–e). Water mites have co-opted the prey recognition response to stimulate females³³ and thus are an example of a ST, whereas Túngara frogs have modified song frequency to maximally stimulate the hearing system^{10,29} and are an example of SE.

The evolution of the sensory system and brain are affected by all aspects of a species' ecology, including finding prey, detecting and avoiding predators, and mate choice (Box 2). Because the evolution of preferences under the ST model is primarily determined by factors other than sexual selection, diversity of signals and preferences should primarily be determined by ecological factors (J. Christy, pers. commun.). This ecological input was not included in the SE model (although it could be) but was a major part of the original SD model^{8,9,34–36}. Except for work on visual ecology in fishes and bees^{37–40}, the evolutionary link between environment and sensory systems (Box 2, step 1) is virtually unexplored. The link between male traits and the preferred signalling environment (Box 2, step 4) is also poorly known^{9,20,21,35}.

Hidden preferences

Hidden preference models are based upon neural networks^{14,15,17,27,41,42}. As with the ST model, HP models are mostly concerned with evolutionary biases caused by sensory properties that evolved outside the context of sexual communication. By explicitly modelling generic coding properties of sense organs (Box 1e), in conjunction with learning and discrimination, they yield results that are not accessible in the verbal models. Networks with given

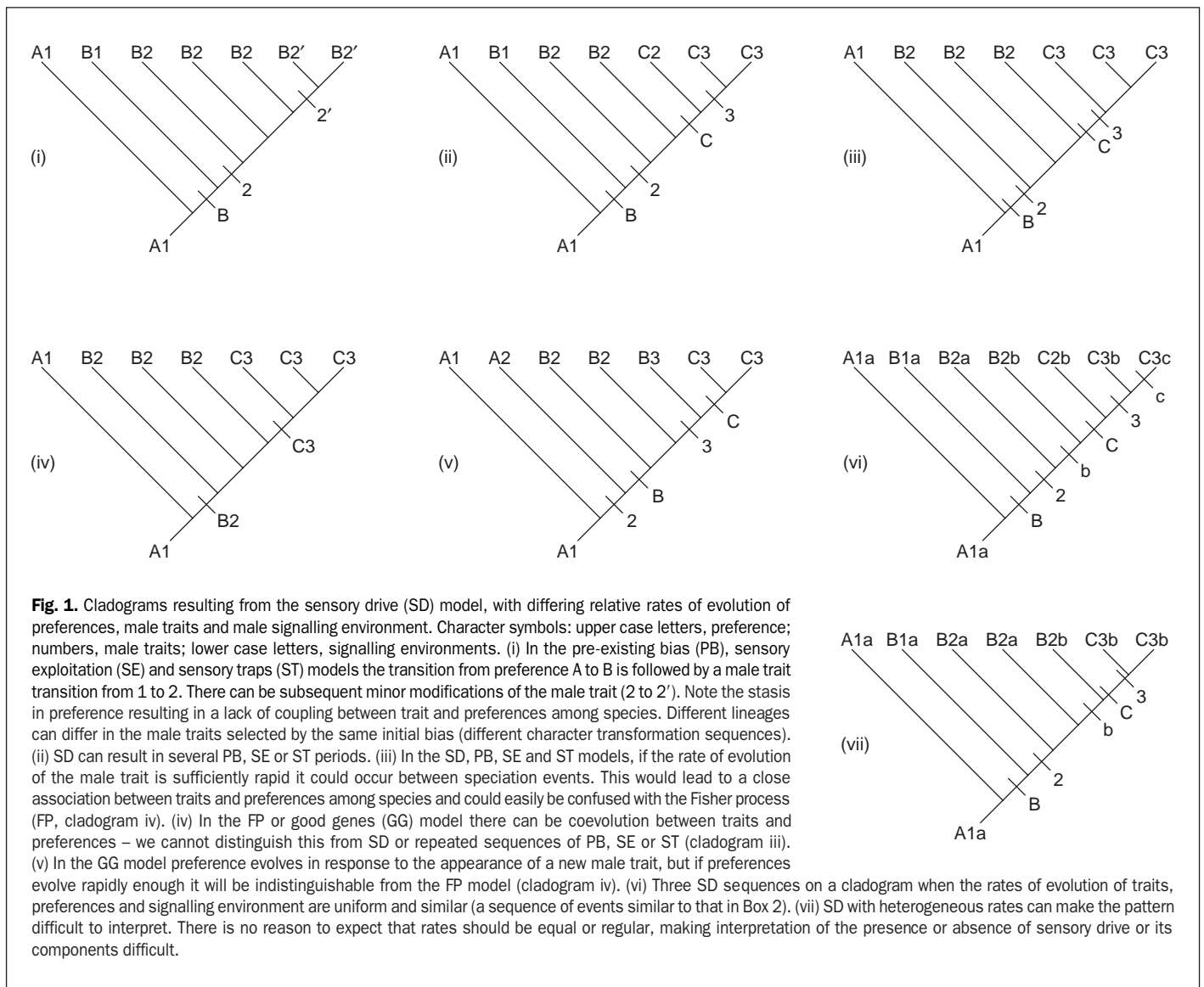


signal-coding properties are trained with target signals that have particular properties. Training includes both learning and evolutionary changes, which result in better recognition and discrimination of the target signal compared with non- or negative signals. There are four main results^{14,15,17,27,41,42}:

- Preferences can have any form – they do not have to be open-ended or necessarily linear or even continuous functions of the signal.

- After training, the network will recognize not only the target, but also other signals which fortuitously stimulate the evolved coding system, even though the system has had no evolutionary experience with the signals. This is a mechanism for SD and the new preferences can be termed hidden preferences (HPs).

- The same target can result in completely different HPs, depending upon how the coding for the target evolved. Different populations (networks) training on the



same target will evolve divergent HPs; SD will diverge among populations experiencing the same environments. This is a mechanism for generating biodiversity.

- Two relevant signals, producing different responses, might diverge in form even though they are processed through the same network. Attractive signals do not need to share common properties, and this could induce very uneven rates of evolution of traits and preferences.

The HP models have been criticized⁴³ because they are oversimplified, linear rather than two-dimensional, and because they might not explain all aspects of signals, such as symmetry (but see Ref. 27). However, this criticism misses the point that even the simplest neural-network model can yield preferences for completely new traits after evolving to recognize very different ones. The criticism of simplicity is actually a compliment – the generality of unexpected biases towards new traits is more likely to occur and be more extensive as the number of dimensions and the

complexity of the connections increase¹⁵. The point of HP models is to capture some fundamental properties common to all sensory systems, rather than to model any specific system, although specific models would be very interesting.

Receiver psychology and perceptual drive

Guilford and Dawkins^{12,13} emphasized that the evolution of signals and preferences is also influenced by higher brain processes (Box 1g–i) and termed these processes receiver psychology (RP). The evolutionary bias caused by RP has been termed perceptual drive (PD)¹⁵. These processes have been known in ethology for a long time^{1,2,15,44–46}, but have only recently been applied to sexual selection theory^{2,4,15,28,47}. For example, supernormal signal response functions and/or peak shifts might favour elaboration, and habituation could favour novel stimuli. The summation of signals, each of which is insufficient by itself to elicit a response, could favour complexity and novel signal

combinations. Old behavioural components used in new ways can also yield new evolutionary directions^{1,2,47}.

Types of bias

A common theme in all SD models is that existing characteristics of the receiver's sensory system or psychology (Box 1c–i) will bias the direction of evolution by affecting which new courtship signals will be most successful. There are five kinds of biases included in these models^{5–7,29} (modified from J. Christy, pers. commun.):

- (1) Biases resulting from properties that once had a particular function that is now lost.
- (2) Biases that are incidental and even non-functional consequences of how organisms are built.
- (3) Biases that have a function outside the context of sexual communication.
- (4) Biases that have a function in sexual communication but are so fundamental to the sensory system or brain that they bias further evolution.

(5) Biases that had no previous function but were established by mutation and not selected against.

The models differ in which biases they emphasize: the SD, SE and PB models emphasize all five, although ST primarily emphasizes 3 and possibly 4, HP primarily 2, and RP and PD 2–4. Consequently, HP, RP and PD models concentrate on the mechanisms producing the bias, whereas PB, SE and ST models concentrate on the evolutionary results of the bias. All can bias the direction of evolution (Box 2). The first three and the fifth biases can cause evolution of preferences even in the absence of heritability of the male signal, because the preference evolves for other reasons (Box 2, steps 5 and 7); this avoids the lek paradox (i.e. why should preferences evolve if there is no gain from choice²¹⁶). Once the preferences are expressed in a sexual selection context, their subsequent evolution will depend upon their fitness costs and benefits in the new and old contexts.

Biases, the order of character evolution, and coupling

The SE and PB models were originally presented as an alternative to both the FP (Fisher process) and the GG (good genes/handicap/indirect benefits) models of sexual selection because the former models produce different sequences of characters in a phylogeny³¹. In the SD, SE, PB and ST models, the preference arises first, followed by the male trait (Fig. 1ii). In the FP model, the trait and preference coevolve (Fig. 1iv), and in the GG and DB (direct benefits) ones the good (or indicating) male trait arises first, followed by the preference (Fig. 1v). There are, therefore, three types of model (SD, FP, and GG and DB). In the GG model the preference might evolve rapidly enough to produce a pattern resembling coevolution³¹.

Unfortunately, there are four implicit assumptions that will cause problems of interpretation of trait sequences in cladograms:

- The rate of evolution of traits is faster than that of the preferences (and vice versa for the GG model).
- The evolutionary effect of the preferences on the traits is greater than the trait on the preference (and vice versa for the GG model).
- Both trait and preference rates are homogeneous throughout the clade.
- There is at least one speciation event between each preference and trait character-transition.

None of these assumptions is necessarily true, so a lack of the best expected pattern (Fig. 1) is not a rejection of a model.

The high correlation between traits and preferences among species and in the cladogram has been called coupling³¹.

There might be no coupling in any SD model, although there is in the FP one⁴⁸, and it can occur in the GG and DB models if preferences evolve quickly³¹. However, the four assumptions make it difficult to distinguish between the models. We cannot assume the evolutionary rates of preferences to be equal or instantaneous (in the FP model) or slower (in the GG model) or that there is interspersed speciation over the entire clade. We can only distinguish the types of model if these assumptions are true and if one of the patterns happens to occur. If rates are very unequal, rapid relative to speciation and heterogeneous in the clade, then we could have no idea what has happened, even if only one of these three processes actually occurred throughout the clade (Fig. 1). Consequently, we must be cautious in interpreting phylogenetic evidence.

Coupling³¹ must not be confused with a genetic correlation between traits and preferences (as in Ref. 24). A genetic correlation can arise or decay independently in each species depending upon multivariate selection conditions^{18,28}, and coupling might occur for the FP, GG and SD models depending upon the relative rates (Fig. 1vii). It is possible to redefine FP, GG and SD purely on the basis of relative rates, but this would ignore the strength of these models in providing mechanisms for evolution.

Relationship to other sexual selection models

The processes preceding assessment (Box 1a–g) are related to natural selection for communication efficiency (signal design), whereas assessment and decision mechanisms (Box 1h–i) function with signal content and are related to the selective processes in conventional sexual selection models. Processes affecting signal design and content are not alternatives but operate concurrently; the same traits could be affected by both types of selection^{12,34–36}. This must be true because assessment depends upon successful signal reception and perception.

Burley¹ made the first clear distinction between signal design and content in a discussion of signal evolution: signals might be processed by a PRP (pattern recognition program), which receives and classifies the signal (Box 1c–g), and then by a GAP (general assessment program), which extracts the signal content and makes decisions on the basis of the content (Box 1h–i). These programs are typical of behavioural systems in that they will respond more strongly to some kinds of signal structure than others, regardless of whether or not the animal has experienced them before. Such responses will bias the direction of the evolution of male traits (Box 2, steps 2 and 3); novel signals that happen to be

recognized by the PRP will be responded to in preprogrammed ways, and might therefore increase in frequency¹. Burley suggested that PRPs are less predictable than GAPs because they are species-specific and signals are often arbitrary, but this depends upon what is meant by predictable. General assessment programs are more predictable in the sense that they are likely to be similar across species; they deal with strategic fitness decisions common to many species (Box 1i). However, the FP, GG or DB models (the substance of GAPs) are relatively vague about predicting the actual form of signals^{9,15}. This is because these models only make predictions about signal content, so they cannot predict why a male has blue and green plumage and sings with a particular set of frequencies. This is a matter of degree. They can predict that males should use brighter plumage and sing more loudly if these are associated with fitness. Pattern recognition programs are more predictable than GAPs because they can be predicted in detail from environmental, biophysical and neurobiological principles^{9,20,34,35,38} (Box 1a–g). The difference is that PRPs predict an absolute scale of variation in traits, whereas GAPs predict only relative differences among signals. More importantly, both PRPs and GAPs have context-dependent rules, complex properties and can respond to novel as well as older signals.

Sensory-drive models are sometimes regarded as alternatives to adaptive mate choice (i.e. the GG and DB models) and Fisherian models (i.e. the FP model) but this is not realistic^{9,36}. Sensory drive can run simultaneously with both the FP and GG models^{5,7,9,11,36}. The full model (Box 2) involves selection by predators and selection for environments that maximize communication, minimize predation and interference and maximize feeding. Females choosing males whose signals work in this way are actually selecting offspring with higher viability (Box 2, steps 4–6). Even in the absence of the indirect benefits¹⁶ of microhabitat selection, SD models are adaptive in the same way as DB models are^{16,18}. There are direct benefits to efficient communication because females will spend less time searching for males and in courtship, consequently reducing predation vulnerability and increasing time for foraging^{9,34–36}.

The distinctions between the various models depend upon varying emphasis on different components of sensory drive (Boxes 1 and 2). The distinctions intergrade and result from various perspectives rather than biological principles. It would be more productive in future to integrate subsequent studies into the broader picture (Box 2) and make more effort to incorporate ecological factors in these processes.

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