28 Laurance, W.F. *et al.* **Rain forest fragmentation and the dynamics of Amazonian tree communities,** *Ecology* (in press)

29 Laurance, W.F. *et al.* (1997) **Biomass collapse in Amazonian forest fragments,** *Science* 278, 1117–1118

30 Laurance, W.F., Laurance, S.G. and Delamonica, P. **Tropical forest fragmentation and greenhouse gas emissions,** *For. Ecol. Manage.* (in press)

31 Brown, P. (1998) **Forest fires: setting the world ablaze,** *The Guardian,* London 20 March

32 Borges, B. (1997) **Brazil considers logging national forests,** *Environment News Service* (Washington DC) 29 October

33 Anon. (1997) **A rain forest imperiled,** *The New York Times* (Editorial) 15 October

34 Meggers, B.J. (1994) **Archeological evidence for the impact of mega-Niño events on Amazonia during the past two millennia,** *Clim. Change* 28, 321–338

35 Fearnside, P.M. and Leal-Filho, N. **Soil and development in Amazonia: lessons from the Biological Dynamics of Forest Fragments Project,** in *Lessons from Amazonia: The Ecology and Conservation of a Fragmented Forest* (Bierregaard, R.O., Jr *et al.*, eds), Yale University Press (in press)

36 Phillips, O.L. and Gentry, A.H. (1994) **Increasing turnover through time in tropical forests,** *Science* 261, 954–958

37 Mahlman, J.D. (1997) **Uncertainties in projections of human-caused climate warming,** *Science* 278, 1416–1417

38 Intergovernmental Panel on Climate Change (IPCC) (1996) *Climate Change 1995. Impacts, Adaptations and Mitigation of Climate Change: Scientific Technical Analyses*, Cambridge University Press.

39 Nepstad, D.C. *et al.* (1994) **The role of deep roots in the hydrological and carbon cycles of Amazonian forests and pastures,** *Nature* 372, 666–669

40 Salati, E. and Vose, P.B. (1984) **Amazon basin: a system in equilibrium,** *Science* 225, 129–138

41 Fearnside, P.M. (1995) **Hydroelectric dams in the Brazilian Amazon as sources of "greenhouse" gases,** *Environ. Conserv.* 22, 7–19

42 Christie, M. (1997) **Yanomami Indians appeal for help against invaders,** *Reuters News Service* 31 August

43 Soltani, A., and Osborne, T. (1997) *Arteries for Global Trade, Consequences for Amazonia*, Amazon Watch (Malibu, California)

44 Holmes, B. (1996) **The low-impact road,** *New Sci.* 151(2048), 43

45 Robinson, J. and Redford, K., eds (1991) *Neotropical Wildlife Use and Conservation*, The University of Chicago Press

46 Terborgh, J. (1992) **Maintenance of diversity in tropical forests,** *Biotropica* 24, 283–292

47 Batmanian, G. (1998) **President Cardoso announces plan to conserve 10% of Brazil's forests,** in *Rain Forest Pilot Program Update* (Vol. 6 No. 1), pp. 1 and 4, The World Bank (Washington, DC)

48 Anon. (1998) **Brazil announces Amazon protection plan,** *United Press International* 29 April

49 Schomberg, W. (1998) **Brazil introduces new law to protect environment,** *Reuters News Service* 13 February

50 Schomberg, W. (1998) **Brazil seeks to limit settler damage to rainforest,** *Reuters News Service* 19 March

51 Anon. (1998) **House approves debt relief for tropical forest conservation,** *Associated Press* 19 March

52 Grace, J. *et al.* (1994) **Carbon dioxide uptake by an undisturbed tropical rain forest in southwest Amazonia, 1992 to 1993,** *Science* 270, 778–780

53 Malhi, Y. *et al.* **Carbon dioxide transfer over a central Amazonian rain forest,** *J. Geophys. Res.* (in press)

54 Enting, I.G., Trudinger, C.M. and Francey, R.J. (1995) **A synthesis invasion of the concentration of delta-C-13 of atmospheric CO_2,** *Tellus* 47B, 35–53

Sensory ecology, receiver biases and sexual selection

John A. Endler

Alexandra L. Basolo

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.

John Endler is at the Dept of Ecology, Evolution and Marine Biology, University of California, Santa Barbara, CA 93106, USA (endler@lifesci.ucsb.edu); Alexandra Basolo is at the Nebraska Behavior Biology Group, School of Biological Sciences, University of Nebraska-Lincoln, Lincoln, NE 68583, USA (basolo@niko.unl.edu).

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 programs[1] (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 preference[14] (HP) and perceptual drive[15] (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 stage[9]. 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

415

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 crickets[50]. 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 signals[15].

(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 perceived[52].

(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 deception[53], as well as passive interference or jamming from other males[34].

(h) Assessment: interpreting signal and extracting critical information
Assessment and decoding of signal content involves cognition and other higher brain processes[1]. 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 deception[53] and mating resistance[25].

(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 incorrect[26]; 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 recently[29], this has been explicitly included (Fig. 1ii). The SE model was the first with an explicit phylogenetic component[11], 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.).
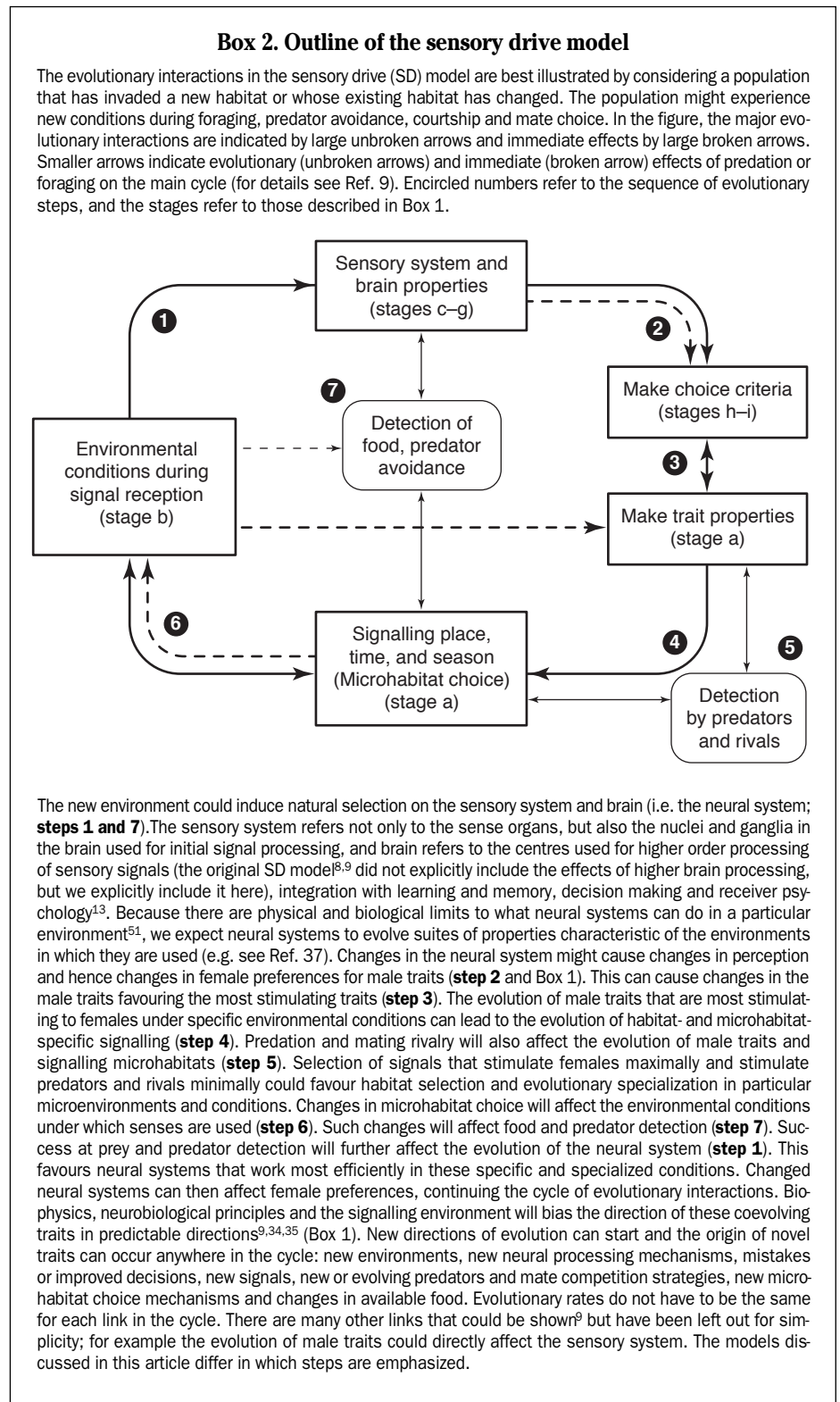
Sensory traps. The idea of STs is similar to SE and PB but emphasizes neural responses to signals that evolved in contexts other than sexual selection[2,3,32] (steps 2, 3, 5 and 7 in Box 2). For example, male crabs (*Uca beebei*) sometimes build mud pillars at their burrow entrances. Claw waving and 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 signal[3]. 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 females[33] 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

Box 2. Outline of the sensory drive model

The evolutionary interactions in the sensory drive (SD) model are best illustrated by considering a population that has invaded a new habitat or whose existing habitat has changed. The population might experience new conditions during foraging, predator avoidance, courtship and mate choice. In the figure, the major evolutionary interactions are indicated by large unbroken arrows and immediate effects by large broken arrows. Smaller arrows indicate evolutionary (unbroken arrows) and immediate (broken arrow) effects of predation or foraging on the main cycle (for details see Ref. 9). Encircled numbers refer to the sequence of evolutionary steps, and the stages refer to those described in Box 1.

The new environment could induce natural selection on the sensory system and brain (i.e. the neural system; **steps 1 and 7**). The sensory system refers not only to the sense organs, but also the nuclei and ganglia in the brain used for initial signal processing, and brain refers to the centres used for higher order processing of sensory signals (the original SD model[8,9] did not explicitly include the effects of higher brain processing, but we explicitly include it here), integration with learning and memory, decision making and receiver psychology[13]. Because there are physical and biological limits to what neural systems can do in a particular environment[51], we expect neural systems to evolve suites of properties characteristic of the environments in which they are used (e.g. see Ref. 37). Changes in the neural system might cause changes in perception and hence changes in female preferences for male traits (**step 2** and Box 1). This can cause changes in the male traits favouring the most stimulating traits (**step 3**). The evolution of male traits that are most stimulating to females under specific environmental conditions can lead to the evolution of habitat- and microhabitat-specific signalling (**step 4**). Predation and mating rivalry will also affect the evolution of male traits and signalling microhabitats (**step 5**). Selection of signals that stimulate females maximally and stimulate predators and rivals minimally could favour habitat selection and evolutionary specialization in particular microenvironments and conditions. Changes in microhabitat choice will affect the environmental conditions under which senses are used (**step 6**). Such changes will affect food and predator detection (**step 7**). Success at prey and predator detection will further affect the evolution of the neural system (**step 1**). This favours neural systems that work most efficiently in these specific and specialized conditions. Changed neural systems can then affect female preferences, continuing the cycle of evolutionary interactions. Biophysics, neurobiological principles and the signalling environment will bias the direction of these coevolving traits in predictable directions[9,34,35] (Box 1). New directions of evolution can start and the origin of novel traits can occur anywhere in the cycle: new environments, new neural processing mechanisms, mistakes or improved decisions, new signals, new or evolving predators and mate competition strategies, new microhabitat choice mechanisms and changes in available food. Evolutionary rates do not have to be the same for each link in the cycle. There are many other links that could be shown[9] but have been left out for simplicity; for example the evolution of male traits could directly affect the sensory system. The models discussed in this article differ in which steps are emphasized.
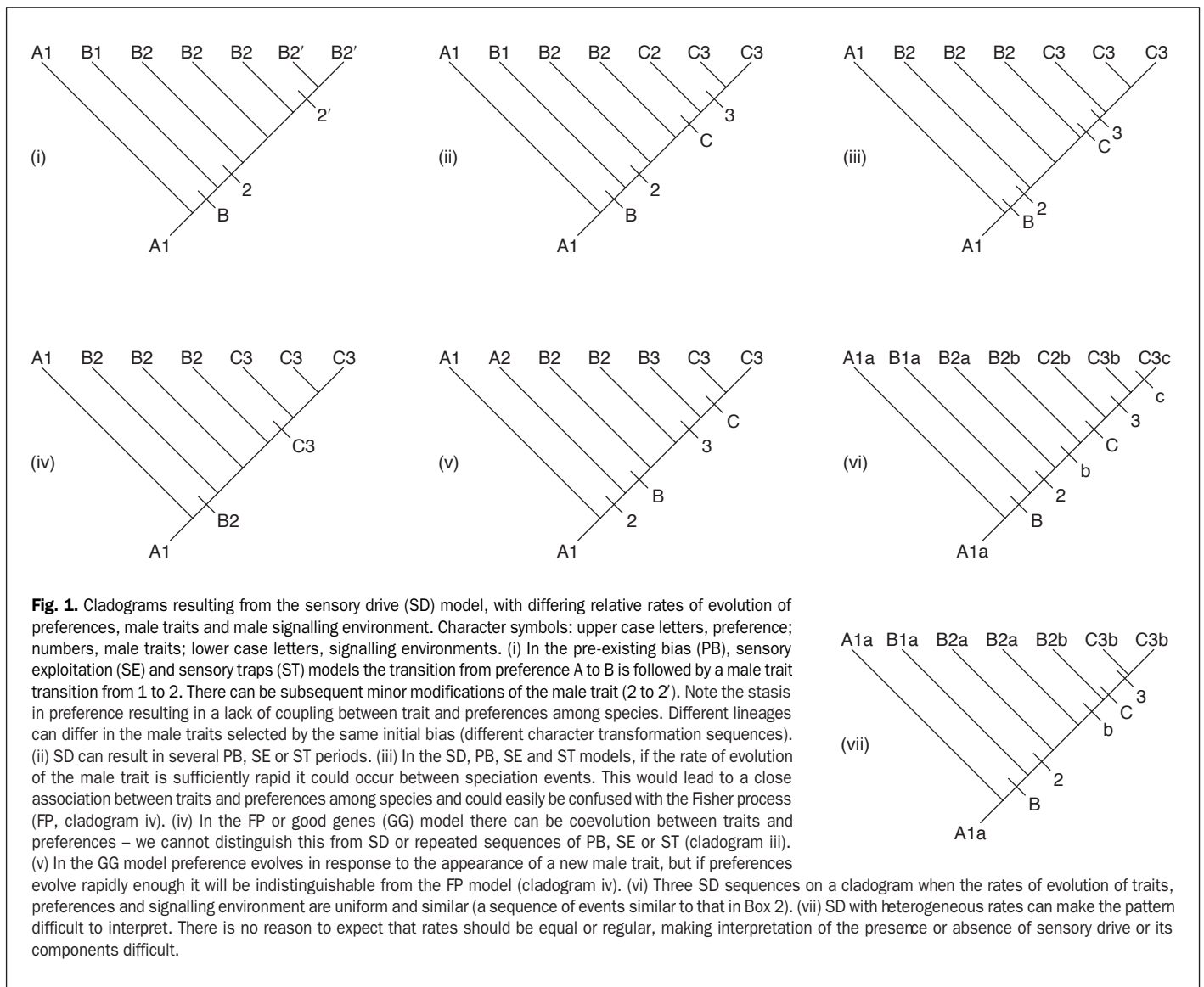
signal-coding properties are trained with target signals that have particular properties. Training includes both learning and evolutionary changes, which result in better recognition and discrimination of the target signal compared with non- or negative signals. There are four main results[14,15,17,27,41,42]:

• 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

Fig. 1. Cladograms resulting from the sensory drive (SD) model, with differing relative rates of evolution of preferences, male traits and male signalling environment. Character symbols: upper case letters, preference; numbers, male traits; lower case letters, signalling environments. (i) In the pre-existing bias (PB), sensory exploitation (SE) and sensory traps (ST) models the transition from preference A to B is followed by a male trait transition from 1 to 2. There can be subsequent minor modifications of the male trait (2 to 2′). Note the stasis in preference resulting in a lack of coupling between trait and preferences among species. Different lineages can differ in the male traits selected by the same initial bias (different character transformation sequences). (ii) SD can result in several PB, SE or ST periods. (iii) In the SD, PB, SE and ST models, if the rate of evolution of the male trait is sufficiently rapid it could occur between speciation events. This would lead to a close association between traits and preferences among species and could easily be confused with the Fisher process (FP, cladogram iv). (iv) In the FP or good genes (GG) model there can be coevolution between traits and preferences – we cannot distinguish this from SD or repeated sequences of PB, SE or ST (cladogram iii). (v) In the GG model preference evolves in response to the appearance of a new male trait, but if preferences evolve rapidly enough it will be indistinguishable from the FP model (cladogram iv). (vi) Three SD sequences on a cladogram when the rates of evolution of traits, preferences and signalling environment are uniform and similar (a sequence of events similar to that in Box 2). (vii) SD with heterogeneous rates can make the pattern difficult to interpret. There is no reason to expect that rates should be equal or regular, making interpretation of the presence or absence of sensory drive or its components difficult.

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 criticized[43] 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 increase[15]. 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 choice?[16]). 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 phylogeny[31]. 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 coevolution[31].

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 coupling[31].

There might be no coupling in any SD model, although there is in the FP one[48], and it can occur in the GG and DB models if preferences evolve quickly[31]. 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.

Coupling[31] 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.

Burley[1] 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 frequency[1]. 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 benefits[16] 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.

PERSPECTIVES

References
1 Burley, N. (1985) **The organization of behavior and the evolution of sexually selected traits,** in *Avian Monogamy* (Gowaty, P.A. and Mock, D.W., eds), pp. 22–44, American Ornithologists' Union Publication 37

2 West-Eberhard, M-J. (1984) **Sexual selection, competitive communication, and species-specific signals in insects,** in *Insect Communication* (Lewis, T., ed.), pp. 283–324, Academic Press

3 Christy, J.H. (1995) **Mimicry, mate choice, and the sensory trap hypothesis,** *Am. Nat.* 146, 171–181

4 Kirkpatrick, M. (1987) **Sexual selection by female choice in polygynous animals,** *Annu. Rev. Ecol. Syst.* 18, 43–70

5 Basolo, A.L. (1990) **Female preference predates the evolution of the sword in swordtail fish,** *Science* 250, 808–810

6 Basolo, A.L. (1995) **A further examination of a pre-existing bias favouring a sword in the genus *Xiphophorus*,** *Anim. Behav.* 50, 365–375

7 Basolo, A.L. (1995) **Phylogenetic evidence for the role of a pre-existing bias in sexual selection,** *Proc. R. Soc. London Ser. B* 259, 307–311

8 Endler, J.A. and McLellan, T. (1988) **The processes of evolution: towards a newer synthesis,** *Annu. Rev. Ecol. Syst.* 19, 395–421

9 Endler, J.A. (1992) **Signals, signal conditions, and the direction of evolution,** *Am. Nat.* 139 (Suppl.), S125–S153

10 Ryan, M.J. and Rand, A.S. (1990) **The sensory basis of sexual selection for complex calls in the Túngara frog, *Physalaemus pustulosus* (sexual selection for sensory exploitation),** *Evolution* 44, 305–314

11 Ryan, M.J. (1990) **Sexual selection, sensory systems and sensory exploitation,** *Oxf. Surv. Evol. Biol.* 7, 157–195

12 Guilford, T. and Dawkins, M.S. (1991) **Receiver psychology and the evolution of animal signals,** *Anim. Behav.* 42, 1–14

13 Guilford, T. and Dawkins, M.S. (1993) **Receiver psychology and the design of animal signals,** *Trends Neurosci.* 16, 430–436

14 Enquist, M. and Arak, A. (1993) **Selection of exaggerated male traits by female aesthetic senses,** *Nature* 361, 446–448

15 Hurd, P.L., Wachtmeister, C.A. and Enquist, M. (1995) **Darwin's principle of antithesis revisited – a role for perceptual biases in the evolution of intraspecific signals,** *Proc. R. Soc. London Ser. B* 259, 201–205

16 Kirkpatrick, M. and Ryan, M.J. (1991) **The evolution of mating preferences and the paradox of the lek,** *Nature* 350, 33–38

17 Johnstone, R.A. (1995) **Sexual selection, honest advertisement and the handicap principle: reviewing the evidence,** *Biol. Rev.* 70, 1–65

18 Kirkpatrick, M. (1996) **Good genes and direct selection in the evolution of mating preferences,** *Evolution* 50, 2125–2140

19 Andersson, M. and Iwasa, Y. (1996) **Sexual selection,** *Trends Ecol. Evol.* 11, 53–58

20 Endler, J.A. (1991) **Variation in the appearance of guppy color patterns to guppies and their predators under different visual conditions,** *Vision Res.* 31, 587–608

21 Endler, J.A. and Théry, M. (1996) **Interacting effects of lek placement, display behavior, ambient light and color patterns in three neotropical forest-dwelling birds,** *Am. Nat.* 148, 421–452

22 Ryan, M.J. and Wilczynski, W. (1991) **Evolution of intraspecific variation in the advertisement call of a cricket frog (*Acris crepitans*, Hylidae),** *Biol. J. Linn. Soc. London* 44, 249–271

23 Marchetti, K. (1993) **Dark habitats and bright birds illustrate the role of the environment in species divergence,** *Nature* 362, 149–152

24 Sherman, P.W. and Wolfenbarger, L.L. (1995) **Genetic correlations as tests for sensory exploitation,** *Trends Ecol. Evol.* 10, 246–247

25 Holland, B. and Rice, W.R. (1998) **Chase-away sexual selection: antagonistic seduction versus resistance,** *Evolution* 52, 1–7

26 Basolo, A.L. and Endler, J.A. (1995) **Sensory biases and the evolution of sensory systems,** *Trends Ecol. Evol.* 10, 489

27 Johnstone, R.A. (1994) **Female preference for symmetrical males as a by-product of selection for mate recognition,** *Nature* 372, 172–175

28 Lande, R. (1981) **Models of speciation by sexual selection on polygenic traits,** *Proc. Natl. Acad. Sci. U. S. A.* 78, 3721–3725

29 Ryan, M.J. and Rand, A.S. (1993) **Sexual selection and signal evolution: the ghost of biases past,** *Philos. Trans. R. Soc. London Ser. B* 340, 187–195

30 Ryan, M.J. and Rand, A.S. (1995) **Female responses to ancestral advertisement calls in Túngara frogs,** *Science* 269, 390–392

31 Shaw, K. (1995) **Phylogenetic tests of the sensory exploitation model of sexual selection,** *Trends Ecol. Evol.* 10, 117–120

32 Christy, J.H. (1988) **Pillar function in the fiddler crab *Uca beebei*. (II) Competitive courtship signalling,** *Ethology* 78, 113–128

33 Proctor, H.C. (1992) **Sensory exploitation and the evolution of male mating behaviour: a cladistic test using water mites (Acari: Parasitengona),** *Anim. Behav.* 44, 745–752

34 Endler, J.A. (1993) **Some general comments on the evolution and design of animal communication systems,** *Philos. Trans. R. Soc. London Ser. B* 340, 215–225

35 Endler, J.A. (1993) **The color of light in forests and its implications,** *Ecol. Monogr.* 63, 1–27

36 Dawkins, M.S. and Guilford, T. (1996) **Sensory bias and the adaptiveness of female choice,** *Am. Nat.* 148, 937–942

37 Lythgoe, J.N. (1979) *The Ecology of Vision*, Oxford University Press

38 Lythgoe, J.N. and Partridge, J.C. (1989) **Visual pigments and the acquisition of visual information,** *J. Exp. Biol.* 146, 1–20

39 Chittka, L. *et al.* (1992) **Opponent colour coding is a universal strategy to evaluate the photoreceptor inputs in Hymenoptera,** *J. Comp. Physiol. Ser. A* 170, 545–563

40 Chittka, L. and Menzel, R. (1992) **The evolutionary adaptation of flower colors and the insect pollinators' color vision systems,** *J. Comp. Physiol. Ser. A* 171, 171–181

41 Arak, A. and Enquist, M. (1993) **Hidden preferences and the evolution of signals,** *Philos. Trans. R. Soc. London Ser. B* 340, 207–213

42 Enquist, M. and Arak, A. (1994) **Symmetry, beauty and evolution,** *Nature* 372, 169–172

43 Dawkins, M.S. and Guilford, T. (1995) **An exaggerated preference for simple neural network models of signal evolution?** *Proc. R. Soc. London Ser. B* 261, 357–360

44 Alexander, R.A. (1962) **Evolutionary change in cricket acoustical communication,** *Evolution* 16, 443–467

45 Hinde, R.A. (1970) *Animal Behaviour, A Synthesis of Ethology and Comparative Psychology* (2nd edn), McGraw–Hill

46 Barlow, G.W. (1977) **Modal action patterns,** in *How Animals Communicate* (Sebeok, T.A., ed.), pp. 98–134, Indiana University Press

47 Weary, D.M., Guilford, T. and Weisman, R.G. (1993) **A product of discriminative learning may lead to female preferences for elaborate males,** *Evolution* 47, 333–336

48 Houde, A.E. (1993) **Evolution by sexual selection – what can population comparisons tell us?** *Am. Nat.* 141, 796–803

49 Ryan, M.J. and Keddy-Hector, A. (1992) **Directional patterns of female mate choice and the role of sensory biases,** *Am. Nat.* 139 (Suppl.), S4–S35

50 Bennet-Clark, H.C. (1970) **The mechanism and efficiency of sound production in mole crickets,** *J. Exp. Biol.* 51, 519–652

51 Dusenbery, D.B. (1992) *Sensory Ecology: How Organisms Acquire and Respond to Information*, W.H. Freeman

52 Fleishman, L.J. (1992) **The influence of the sensory system and the environment on motion patterns in the visual displays of Anoline lizards and other vertebrates,** *Am. Nat.* 139 (Suppl.), S36–S61

53 Hasson, O. (1994) **Cheating signals,** *J. Theor. Biol.* 167, 223–238