Conflict, Receiver Bias and the Evolution of Signal Form

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Conflict, receiver bias and the evolution of signal form

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SUMMARY

In a model, conflicts of interest between communicating individuals are shown to have an important influence on the cost and form of signals that evolve. Two types of conflict are considered: competition between senders to obtain a response from the receiver, and conflict between the sender and the receiver. The receiver system is modelled as an artificial neural network whose 'resistance' to signals is represented as a motivational factor that varies independently of the signal. Biases in the receiver system act as the selective force on signals, causing them to become more costly and conspicuous as the intensity of conflict increases. There is some evidence that competition between senders and sender–receiver conflict may have qualitatively different outcomes. We give examples of some situations to which the model might be applied and point out some predictions that could be tested empirically.

1. INTRODUCTION

Traditionally, biologists have investigated the function of animal signals by experimenting with artificial stimuli. Numerous studies have shown that certain artificial stimuli can provoke much stronger responses from a receiver than natural stimuli do; such stimuli are said to be 'supernormal' (Tinbergen 1948). Similarly, in experimental studies of learning psychology, when subjects are trained to perform a particular discrimination, they may subsequently respond maximally to a novel variation of the stimulus, one that was not included in the training set. This phenomenon has been referred to as 'peak shift' (Hanson 1959). These findings suggest that the receiver mechanism is not a precisely tuned filter, responding only to those familiar stimuli that are relevant to the organism, but instead appears to involve intrinsic biases.

Such biases are important in an evolutionary context because they provide the opportunity for signal forms to evolve in new directions (see, for example: Staddon 1975; West-Eberhard 1979; Krebs & Dawkins 1984; Burley 1985; Leimar *et al.* 1986; Basolo 1990; Guilford & Dawkins 1991; Ryan 1991; Endler 1992; Arak & Enquist 1993; Enquist & Arak 1993). Biases in the receiver may be found either in the sense organs (Ryan *et al.* 1990; Endler 1992) or in neural processes responsible for recognition and decision-making (Staddon 1975; Leimar *et al.* 1986; Guilford & Dawkins 1991; Arak & Enquist 1993). Although many studies do not specify at what physiological level such biases occur, the distinction between peripheral and central biases is sometimes important. A sensory bias may eventually disappear as sense organs and signals tune to each other, whereas biases at higher levels of neural processing can never be exhausted because any adaptation in the receiver invariably generates new biases (Arak & Enquist 1993).

Only a few attempts have been made to incorporate bias into evolutionary models and all these have been concerned with biases in central processes. Leimar *et al.* (1986), building on an earlier model of intradimensional discrimination learning (Spence 1937), showed how aposematic coloration could evolve as a consequence of receiver bias. More recently, the use of artificial neural networks has provided a useful framework for studying the theoretical consequences of receiver bias on the evolution of signal form (Arak & Enquist 1993; Enquist & Arak 1993, 1994; Johnstone 1994; Hurd *et al.* 1995). Such models share several primary computational principles with real nervous systems (Durbin 1989; Churchland & Sejnowski 1994) and exhibit similar emergent behaviour, such as the ability to form complex associations, recognize degraded stimuli and perform generalizations. They also show the same kind of biases that animals do when responding to signals, sometimes displaying a preference for novel over familiar stimuli.

In this paper we investigate possible causes for the variation observed in signal form. Although most attention has been directed towards conspicuous, presumably costly, signals, it is clear that many signals used by animals are extremely subtle, sometimes almost imperceptible to human observers, and such signals are unlikely to involve appreciable costs. A worthy challenge for a general model is to account for this enormous diversity of signal form, from the sublime to the ridiculous.

An intriguing idea is that the kind of signals that evolve depends on the degree of common interest between the sender and the receiver in an interaction (Krebs & Dawkins 1984). Two coevolutionary pathways are envisaged. If there is a high degree of common interest between sender and receiver, selection acts on receivers to become more sensitive to signals and on signals to become simple and inconspicuous (i.e. cryptic). But if sender and receiver interests differ,

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selection favours 'resistance' in receivers and acts on senders to overcome receiver resistance, promoting the evolution of complex, conspicuous signals (see also Williams 1966).

In species that display in groups, senders are also in conflict with one another whenever the resources or services that receivers offer are in limited supply. Short of physical combat, senders may compete for the attention of receivers by using signals. In the context of courtship, such contests have been referred to as 'sexual advertisement scrambles' (Parker 1982). A model by Grafen (1990) predicts that, in situations where females assess the quality of potential mates, more costly displays evolve as the number of displaying males increases. These models bear analogy to games played between traders on human commercial markets. In a market with many competitors, a brand must advertise more heavily and advertising must be more persuasive in order to build up selective demand (Kotler & Armstrong 1994). Although it is now widely accepted that physical competition has promoted the evolution of diverse forms of weaponry (since Darwin 1871), the possibility that elaborate forms of signalling have evolved through the operation of biological market mechanisms (see Noë & Hammerstein 1994) has rarely been addressed.

We here explore the role of conflict on the evolution of signals with use of an artificial neural network as a model of a visual recognition system. To study the effects of conflict between sender and receiver we include a motivational variable in the model that depends on the level of receiver 'resistance' to signals. We also vary the probability that a given sender is alone with the receiver or competing for the receiver's attention together with another sender. Changes in the signal, arising by random mutation, spread in the population of senders only when they correspond to biases in the receiver system. The results of coevolutionary simulations are then compared with empirical observations suggesting a link between the intensity of conflict in interactions and the degree of signal conspicuousness.

2. THE MODEL

(*a*) *Definition of conflict*

The model could represent a situation in which males are competing to attract females, or flowers are competing for the attention of insect pollinators. We assume that senders compete for the resources or services of receivers by using signals only; the possibility of direct physical contests is excluded from the model. The degree of conflict between signallers, α, is defined as the probability of competing with one other signaller for the receiver's attention. In this situation, we assume that it always pays the receiver to react to the signal.

To model conflict between a sender and a receiver we assume that it is in the sender's interest that the receiver always reacts to the signal; however, the receiver does not always benefit by responding because additional factors, such as the receiver's internal state, influence the fitness of the receiver. We model these additional factors with a variable m that varies independently of the signal according to a normal distribution. For simplicity, m is scaled to equal the receiver's change in fitness caused by reacting to the signal. The degree of conflict between sender and receiver (the receiver's 'resistance' to signals) is controlled by varying the mean of the distribution of m; a decrease in the mean of m represents increasing conflict and vice versa. The standard deviation of the distribution is held constant at 0.05.

(*b*) *The signal and recognition mechanism*

The signal is represented by an array of 5×4 boxes, each box filled with shades of grey between white and black (scaled 0–1). The recognition mechanism is an artificial neural network consisting of three interconnected layers of cells: a layer of input cells arranged as an 9×9 sensory array (i.e. an artificial retina), a 'hidden' layer of ten cells and an output layer consisting of one cell. Each cell in a given layer connects to all cells in the next layer and each connection has its associated 'weight' that regulates the strength of the signal passing between cells. There are no connections between cells within a given layer.

Signals are presented to the network by 'pasting' them onto the artificial retina in various positions. Each signal is presented in 30 different positions on the retina, by different translations; rotations and reflections are disallowed.

When the network is stimulated by a signal, each of the input cells receives input between zero and one (represented by different shades of grey in the signals). The output from these cells equals the input. The input to all other cells (i.e. hidden cells and output cell) is a weighted sum of the output from all cells in the previous layer:

$$\text{net input}_j = x_j = \sum w_{ji} y_i,$$

where j is the index of the cell, y_i the output of cell i in the previous layer and w_{ji} the connection weight between cell i in the previous layer and cell j.

The output from a hidden cell or the output cell is a sigmoid function of its net input:

$$\text{output}_j = y_j = \begin{cases} 1 - 1/2[1/(1+x_j)] & x_j \geqslant 0 \\ 1/2[1/(1-x_j)] & x_j < 0. \end{cases}$$

Whether the receiver responds to the signal depends not only on the activity, y_o, in the output cell caused by the stimulus, but also on the internal factor, m. The receiver reacts to a signal when the sum of these factors exceeds an arbitrary threshold value of 0.5, that is, when

$$z = y_o + m > 0.5.$$

(*c*) *Training the network*

We start with a signal that is optimal for survival and a receiver that is trained to discriminate this signal almost perfectly from two 'incorrect' stimuli. The optimal signal is assumed to be a uniformly medium grey patten (grey value 0.5; see figure 1) and the two incorrect stimuli are uniformly dark grey (0.8) and light grey (0.2).

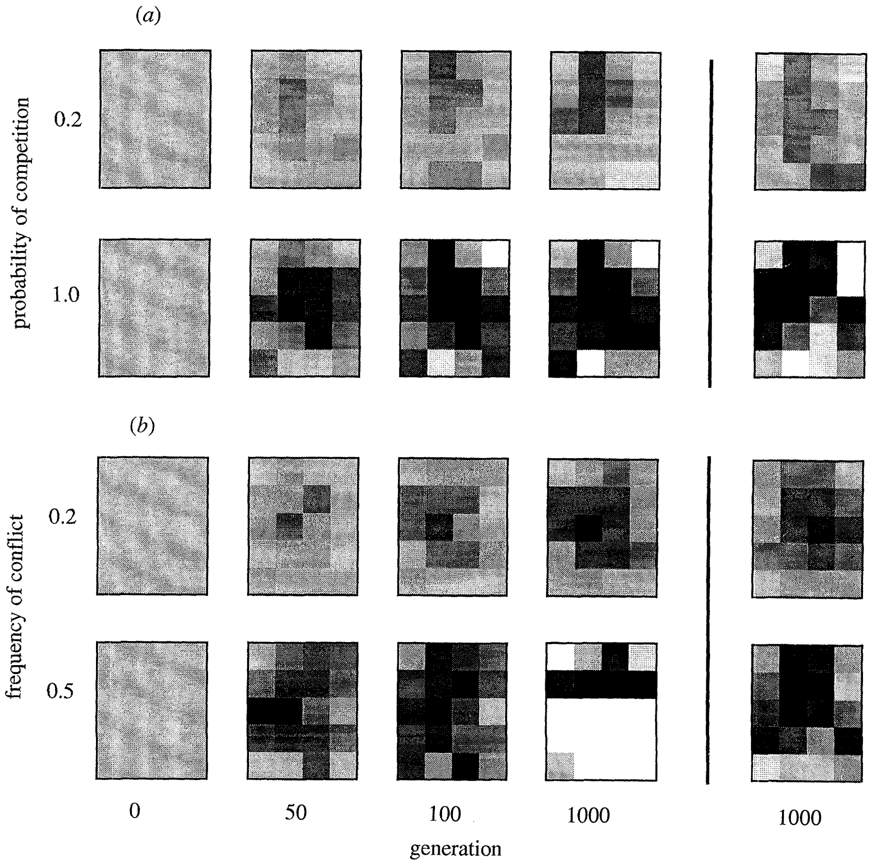

Figure 1. Examples of signals evolving during coevolutionary simulations. (*a*) Sender–sender conflict; (*b*) sender–receiver conflict. The starting signal (first column) is the same in each case and is assumed to be the optimal signal with respect to survival. The column on the far right (separated from the others by a line) shows the resulting signals after 1000 generations in a second example run of each simulation, with use of the same parameter values as in the first example.

Training is achieved by adjusting the connection weights between cells until the optimal signals gives rise to an above threshold output in the network, whereas incorrect stimuli give rise to a subthreshold output. In conventional network studies connection weights are usually adjusted during the training phase by using a mathematical algorithm that tends to maximize the rate of learning, such as the back-propagation learning rule (Rumelhart *et al.* 1986). Our procedure differs in that we adopt an evolutionary approach. We start with some random vector of connection weights. A new vector is then created by random mutations of some of the weights. The probability of mutation for a particular weight was set at 0.01 and when a mutation occurred an increment drawn from a normal distribution (-0.2 to 0.2) was added to the weight. The performance of the mutated network in the recognition task was then compared with that of the original network and the best retained. This iteration continued until a certain criterion of success (probability of incorrect decision by the network $< 10^{-5}$) was achieved. Such a discriminating network formed our starting point for simulations of coevolution between signals and receiver mechanisms.

(*d*) *Coevolutionary simulations*

The coevolution consisted of a sequence of generations. In each generation 200 different signal mutations were presented to the network and the best retained. The same procedure was then done for 200 mutations of the receiver (network).

Mutations of the signal were produced by changing the shade of grey in each cell of the signal with probability 0.01, then adding (where possible) a normally distributed increment (zero mean, s.d. 0.02) to the value of each mutated cell. The fitness, F, of a new signal, s, arising by mutation in a population having initially s_0 and r_0 was calculated as

$$F(s, s_0, r_0) = t(s)\, g(s_0, r_0)\, p(s, s_0, r_0),$$

where t is the lifetime for the signal, g the rate at which receivers are encountered and p the probability that the receiver reacts to the signal.

The original signal was considered the optimal signal with respect to survival and deviations from this entail a survival cost that reduces the lifetime of the signal. Hence,

$$t = t_{\text{opt}} \exp -kd^2,$$

where d is the sum of differences between the stimulus in each cell of a particular signal s and the equivalent cells in the signal that is optimal for survival. For the constant k the values 5 or 10 were used.

The probability that the receiver reacts to a signal depends not only on the form of the signal itself but also on the presence or absence of other signallers. Thus,

$$p = (1-\alpha)\,\Pr[z(s,r_0) > 0.5] + \alpha\,\Pr[z(s,r_0) > 0.5,\, z(s,r_0) > z(s_0,r_0)],$$

where α is the degree of conflict between senders defined as the probability of competing with one other sender for the receiver's attention.

Fitness of the receiver strategy was calculated as follows: reaction to an incorrect stimulus gives -1, no reaction gives 0 and reaction to the correct signal gives 1 (for sender–sender conflict) or m (for sender–receiver conflict). Fitnesses are summed over all projections of the signal onto the retina, and for sender–receiver conflict they are also summed over the distribution of internal states. Artificial selection of mutant signal and receiver strategies was continued for 1000 generations per simulation.

3. RESULTS

Examples of the simulation results are shown in figures 1 and 2, for different degrees of conflict. Figure 1 shows the appearance of the evolving signals at different stages in the simulation. Sender–sender conflict and sender–receiver conflict both have similar effects in causing signals to deviate increasingly in appearance from the survival optimum as the degree of conflict increases. The tendency is for signals to develop more internal contrast as conflict increases. However, the exact form of signals that evolve from the same starting point varies between different runs of the simulation. This demonstrates that there is no tendency for patterns to converge towards a particular form during evolution. Occasionally a certain signal form may persist or change only slightly over many generations, which suggests that the recognition mechanism sometimes becomes temporarily 'stuck' on a particular pattern.

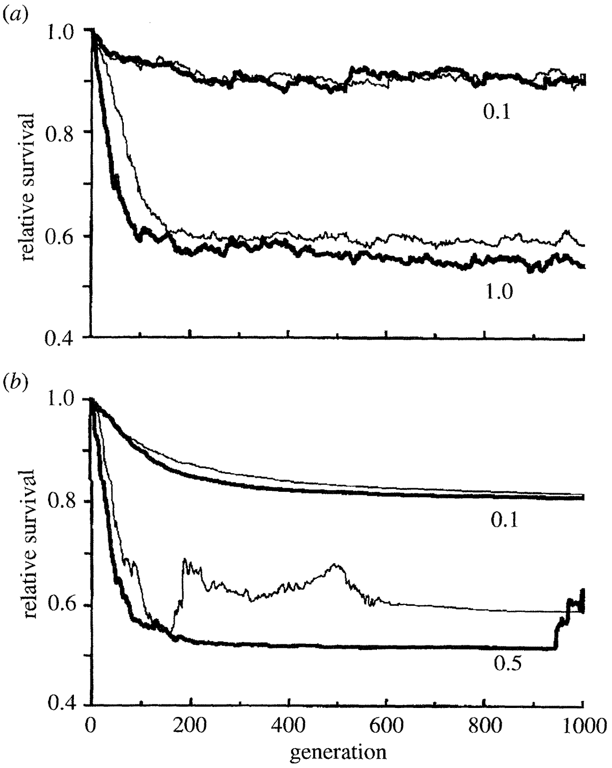

Figure 2. Evolutionary trajectories showing how signal cost (survival relative to optimum) changes during (*a*) four simulations of sender–sender conflict, when $\alpha = 0.1$ (two upper lines) and $\alpha = 1.0$ (two lower lines), and (*b*) during four simulations of sender–receiver conflict with the frequency of conflict at 0.1 (two upper lines) and 0.5 (two lower lines).

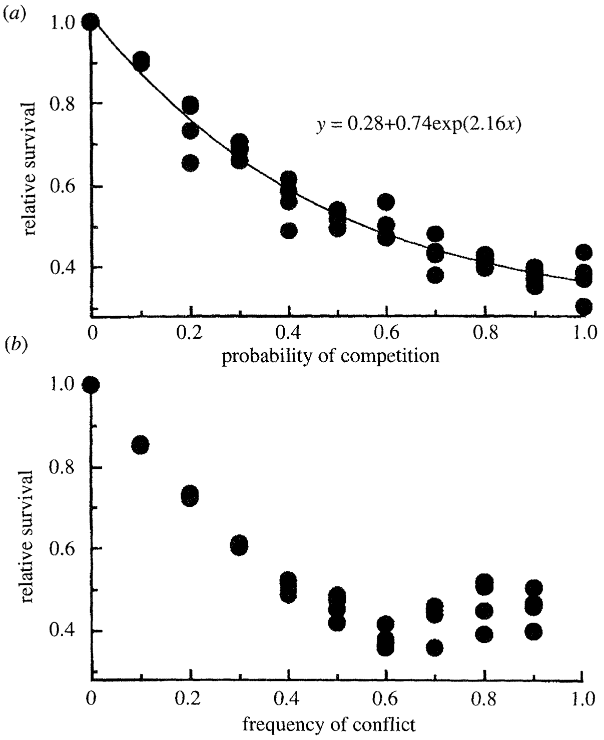

Figure 3. The relation between the cost of signals that evolve after 1000 generations and (*a*) the probability of competition in sender–sender conflict and (*b*) the frequency of sender–receiver conflict. For each level of conflict, results are shown for four different runs of the simulation; some points overlap.

Figure 2 shows examples of how signal cost (survival relative to starting signal) changes during the course of simulations. In all cases there is an initial rapid increase in signal cost followed by a levelling off such that signal cost eventually tends to fluctuate within a narrow range of cost values. The relation between the degree of conflict and signal costs is shown more directly in figure 3, which combines the results of several runs of the simulations. In sender–sender conflict, more costly signals evolve as the probability of competition increases. In sender–receiver conflict, the situation is slightly more complex: although signal cost increases up to moderate levels of conflict with the receiver, signal cost begins to decrease again when conflict becomes severe. This suggests that it does not pay the sender to use very costly signals in situations when the receiver's resistance to signals is so strong that it will almost never react to the signal. More formally, in terms of our model, the cost of signals that evolve is influenced by the shape of the distribution of m as well as by the mean.

A qualitative difference between sender–sender and sender–receiver conflict is also suggested by the smoother trajectories of signal cost in the latter (figure 2). The dynamics of the two types of conflict situation may differ because in sender–receiver conflict there is selection on the receiver to resist reacting to the signal. In some simulations of sender–receiver conflict, there are prolonged periods of relative stability in the appearance of the signal, occasionally interrupted by sudden changes that correspond with a marked decrease in signal cost. This suggests that random mutation may occasionally produce signals that are much more efficient at eliciting a response from the receiver. Such signals spread at the expense of more costly signals until the receiver builds up resistance to them.

4. DISCUSSION

(*a*) *General conclusions*

Our model suggests that the degree of conflict between interacting individuals has a strong influence on the extent to which signals become exaggerated during evolution. Subtle, non-costly signals are favoured in situations where there is little or no conflict of interest between individuals. By contrast, competition between senders, or 'resistance' in receivers, promotes the evolution of costly, conspicuous signals. Both types of conflict may act as a potent force on the evolution of signal form. In our model, a relatively modest degree of conflict led to a dramatic reduction in the survival of senders, which can be ascribed solely to the costs associated with signalling (figure 3).

Most previous models have focused on the evolution of costly signals used in courtship behaviour, such as bright colours, long plumes and loud song (reviewed by Andersson 1994). Most such models have emphasized factors that lead to equilibria between a trait used for signalling by males and a preference for the trait in females. In contrast, our model is more concerned with the mechanism and dynamics of the evolutionary process than with evolutionary end points. In our model, biases in the receiver mechanism act as the main selective pressure causing changes in signal form. Moreover, because these biases change continuously during evolution, equilibria between signal form and receiver preferences are never reached (see also Arak & Enquist 1993).

Our model provides a more parsimonious explanation for the evolution of exaggerated secondary sexual traits than many other models. Specifically, it demonstrates how receiver biases may increase the conspicuousness of signalling traits in the absence of genetic correlations between the trait and preference (cf. 'Fisherian' models); it does not assume heritable differences in viability among males (cf. 'good genes' models (see Andersson 1994)). Because of its simplicity, the model can be applied to a much wider range of circumstances in which conspicuous signals have evolved than models specifically relating to sexual selection. For example, it is likely to be relevant to the evolution of interspecific signals, such as aposematic coloration and conspicuous flowers in plants, as well as to many types of intraspecific signals.

We have identified two mechanisms that may contribute to the selection pressure for increased conspicuousness; competition between senders and resistance in receivers. However, there appears to be a qualitative difference between these two mechanisms in the way that evolution proceeds (see figure 2). When senders compete with each other to elicit a response from the receiver, they compete to exploit the same biases in the receiver mechanism. The success of a given sender depends only on the degree of development of its ornaments, in the direction of the bias, relative to that of other senders. With no conflict between the sender and receiver, selection on the receiver is weak, leading to improved recognition of signals. The expected outcome is that receiver responses constantly tend to 'track' changes in the senders' signals.

When the interests of senders and receivers diverge, however, selection on signals and receiver mechanism is in direct opposition. In these circumstances there is strong selection on the receiver to resist any increase in efficacy of the senders' signals, and on the sender to overcome receiver resistance. Evolution of the receiver mechanism may sometimes bring to a halt progressive changes that have been occurring in the signal along a certain dimension, until, by random mutation, a new signal form arises that can exploit another dimension of bias. This may result in long periods of stasis when signals change very little, occasionally interrupted by periods of rapid change (evident in figure 2, sender–receiver conflict).

Whether such qualitative differences in the nature of the two types of conflict promote the evolution of qualitatively different types of signals is not known, though it seems plausible (see: Dawkins & Krebs 1979; Dawkins 1986). For example, competition between senders may lead to progressive increases in signal size, brightness or loudness, whereas conflict between sender and receiver may promote the evolution of ever greater sophistication and complexity in signal form (e.g. intricate patterns, complex song repertoires, more modalities of signalling).

Although based on different assumptions, our model makes some predictions in common with the 'handicap principle' (Zahavi 1975) and more recent models inspired by it. For example, handicap models make the general prediction that greater conflict between sender and receiver will lead to greater signal cost, because of the stronger incentive for dishonesty. Johnstone & Grafen (1992) investigate how variation in the degree of conflict between sender and receiver influences signal evolution, focusing on the consequences of relatedness between sender and receiver. As in the present study, they found that signal cost increases up to moderate levels of conflict (i.e. relatedness) but begins to decrease again when conflict becomes severe, the reason being that in the latter case receivers respond only very rarely to signals and so the potential benefits of display are reduced. In common with handicap models, our model also suggests that lower quality individuals should use less costly displays than higher quality individuals. If a given signal is made more costly for a low quality individual than a high quality one (the constant k is set higher for the low quality individual), then low quality individuals develop less costly signals. However, whereas handicap models assume that a preference for more costly signals is maintained only because of the quality–cost correlation, our model suggests that such preferences can arise in the absence of any such correlation, as a random perceptual bias.

(*b*) *Empirical observations*

We predict that more conspicuous signals are favoured as the degree of competition between senders increases, owing to the operation of 'market mechanisms'. Some examples suggesting that market mechanisms have been influential on signal form are given below.

(1) In some chorusing insects and anurans, competition between males for females is entirely acoustically mediated. In anurans, males produce longer calls or call more often as chorus size increases or the distance between competitors decreases (Wells 1988). Such changes in calling behaviour involve increased energy expenditure (Taigen & Wells 1985; Wells & Taigen 1989). In natterjack toads, *Bufo calamita*, males that emit the loudest calls achieve the greatest mating success. Females do not appear to compare individual males, but simply move down a sound gradient towards calls of the highest perceived intensity, often the closest male (Arak 1988). These observations suggest that, even if females gain nothing by choosing between males, market mechanisms may have been important in the evolution of longer or louder calls in anurans.

(2) Elaborate male structures and behaviour used in courtship appear to be most striking in species that display in groups or 'leks'. The critical test is whether courtship displays are significantly more conspicuous in lekking species than in closely related polygynous species that display alone from dispersed sites. Few studies have specifically addressed this question (but see: Höglund 1989; Oakes 1992).

(3) Experiments by Bell (1985) on the attraction of insect pollinators to flowers have shown that the presence of neighbouring plants of the same species tends to reduce the number of insect visits per flower. Since larger flowers attract more pollinators than smaller ones, market mechanisms should promote the evolution of larger (and possibly brighter) flowers in plant species that grow in large stands compared with those in which individual plants are dispersed throughout the habitat.

(4) Market mechanisms may be important in promoting the evolution of conspicuous begging behaviour in nestling birds. This hypothesis could be tested by comparing the conspicuousness of nestling begging behaviour between species with different brood sizes. A recent study of American coots, *Fulica americana*, suggests that a special ornament exhibited by chicks has evolved in response to competition among siblings for parental food (Lyon *et al.* 1994). The youngest chicks sport bright orange plumes for the first few weeks of life and are fed by parents in preference to older chicks lacking such plumes. Controlled experiments confirm it is the ornament itself, and not other aspects of the chicks' behaviour, that elicits preferential feeding by parents. In another recent study (Briskie *et al.* 1994) chick begging was found to be more pronounced when the degree of relatedness among chicks was lower and conflict consequently more intense.

(5) Among aposematic organisms, species that are gregarious are predicted to be more conspicuous than solitary species. This relation, however, would also be expected if groups tend to consist of closely related individuals (Leimar *et al.* 1986).

Evidence that the intensity of conflict between sender and receiver influences signal conspicuousness is more compelling. Signals often appear to be relatively inconspicuous and inexpensive in cooperative interactions between close kin (e.g. social insects (Wilson 1971)) and, in some species, when used for communicating species identity (e.g. gulls (Griffith-Smith 1966)) or sex identity (e.g. budgerigars (Cinat-Thomson 1926)). In contrast, highly complex, 'ritualized' signals (Huxley 1966) are often observed in situations where there is a conflict of interest between sender and receiver, for example during disputes at territory boundaries, in aggressive interactions and in courtship behaviour.

In many polygynous species, the sexes are strongly dimorphic with males displaying elaborate structures and behaviour while females are dull and cryptic. The striking displays of males can be explained, at least in part, as a result of selection to overcome the female's resistance to mating. However, there is no corresponding selection on females to use conspicuous signals because males mate indiscriminately.

Monogamous species generally tend to be less sexually dimorphic than related polygamous species. It has sometimes been suggested that this is because sexual selection is weaker in monogamous species (see, for example: Payne 1984; Björklund 1984). It is important to note, however, that the sexes are often similar in monogamous species, not because of an absence of conspicuous display structures, but because similar signals have evolved in both sexes. Examples include the bright plumage of many monomorphic parrots, ornamental plumes in males and females of the crested auklet *Aethia cristatella* (Jones & Hunter 1993) and elaborate mutual display in pairs of great crested grebes *Podiceps cristatus* (Huxley 1914).

The highly exaggerated displays found in these species suggests that conflicts of interest between the sexes also exist in monogamous animals. Indeed, conflict is likely to be both more severe and more prolonged in monogamous than in polygamous species because of the high costs associated with raising offspring alone if one of the partners deserts and/or the poor chances of finding an alternative mate. Elaborate mutual display, involving an exchange of similar movements and signals by each sex, often occurs in situations of maximum uncertainty about the mate's behaviour, for example when one individual returns to the nest after a period of feeding alone (e.g. 'greeting ceremonies' in egrets (Huxley 1923)) and in environments where reduced visibility makes it difficult to track the partner's movements and behaviour (e.g. 'duetting' is more common among bird species inhabiting tropical forests (Farabaugh 1982)). These observations seem to fit better with the traditional view, that such displays serves to maintain and strengthen the pair bond (see, for example, Lorenz 1966), than with attempts to reconcile the facts within the framework of sexual selection theory.

In summary, empirical observations generally concur with the view that variation in signal conspicuousness between species, and between the sexes, is related to differences in the degree and nature of conflict between interacting individuals. However, much of the evidence supporting the predictions of our model is suggestive rather than conclusive. Other mechanisms, such as 'Fisherian' self-reinforcing selection, selection of indicator traits and selection for efficient transmission, may to a greater or lesser extent influence the evolution of signal form in different species. Detailed comparative studies are needed to test the relative importance of these different mechanisms in nature.

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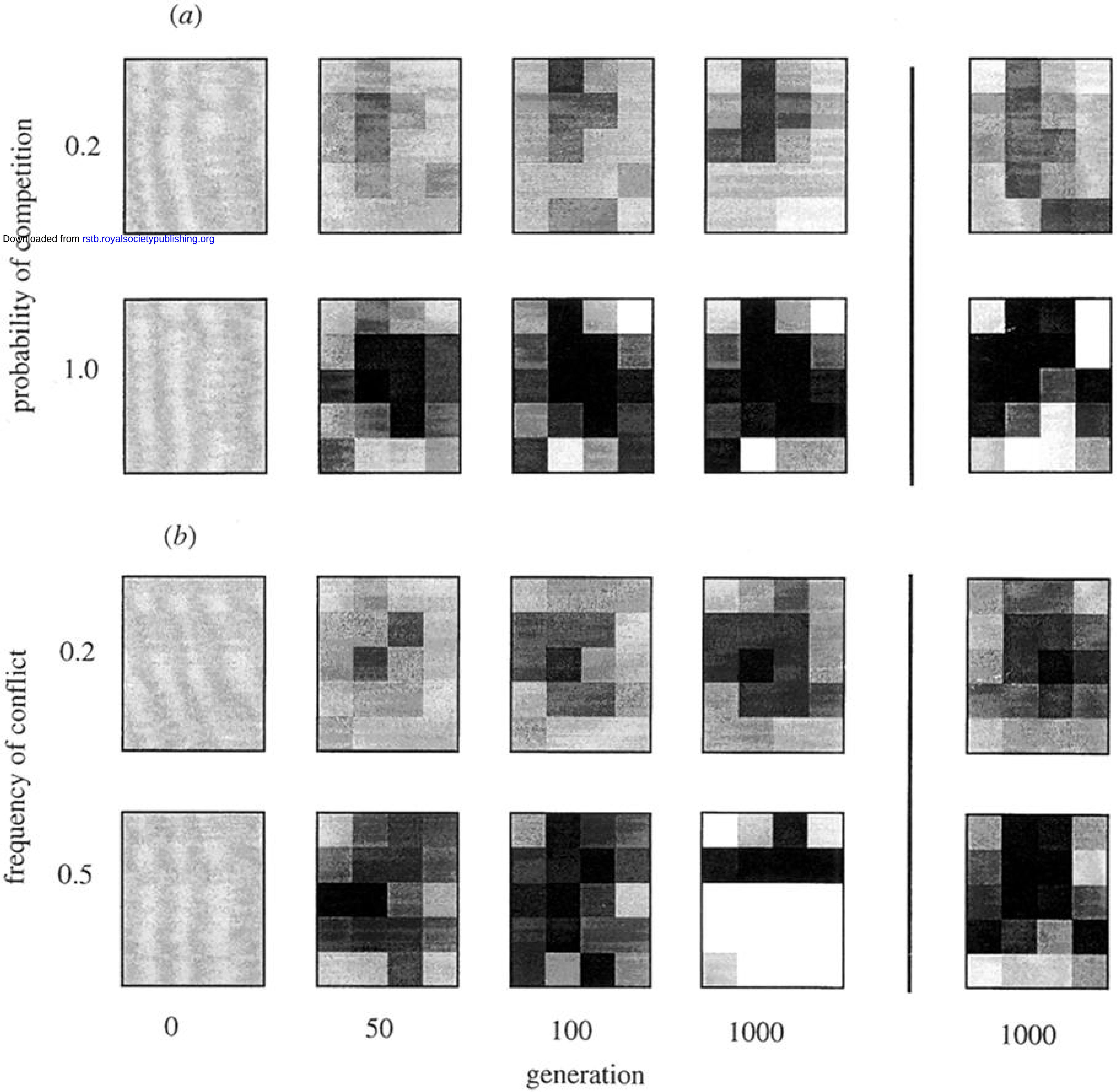

gure 1. Examples of signals evolving during coevolutionary simulations. (*a*) Sender–sender conflict; (*b*) nder–receiver conflict. The starting signal (first column) is the same in each case and is assumed to be the optimal gnal with respect to survival. The column on the far right (separated from the others by a line) shows the resulting gnals after 1000 generations in a second example run of each simulation, with use of the same parameter values as the first example.