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Are there general principles of signal design?

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SUMMARY

Explanations of signal design must meet three requirements: they must be logically coherent, they must explain the diversity in size of animal signals and they must explain the diversity in form of signals. Three selection pressures operating on animal signals are discussed: the degree of conflict or cooperation, the 'efficacy' of signals and how signalling costs are paid. A distinction is made between cases where costs of signalling are paid in the production of the signal and cases where costs are paid as a consequence of giving a signal on the grounds that differences in signal design result. This is illustrated by reference to the example of warning coloration. It is concluded that general principles still elude us because of the numbers of different selection pressures that operate on the design of animal signals.

1. INTRODUCTION

Do we now have a general theory of signal design? In other words, are there general principles in the form and nature of animal signals? I shall attempt to answer this question by, first, considering what a general theory of signalling would have to do and what phenomena it would have to explain. Next I shall consider the selective forces that are known to contribute to signal design, many of which are touched on by other contributors. I shall argue that, although we have some understanding of some of the selective forces at work on animal signals, we are not yet in a position to elucidate general theories of signalling because of the complexity of the ways in which these forces interact.

2. REQUIREMENTS OF A GENERAL THEORY OF SIGNALLING

A general theory of signalling has at least three requirements:

1. It has to lead to evolutionary stability. This almost goes without saying and, as emphasized by Grafen & Johnstone (this symposium), any theory to be really useful should be formalized into a mathematical model. However, it is important to remember that stability and mathematical precision are necessary rather than sufficient conditions. It is possible to produce models of animal signalling that fulfil both of these conditions but have little applicability to real animals. The real test of a theory is how it fulfils the next two requirements.

2. It has to explain the observed diversity in the size of animal signals. Some signals – such as the sexual displays of peacocks or lyrebirds, the claw-waving displays of fiddler crabs and stotting in gazelles (Fitzgibbon & Fanshawe 1988) – are conspicuous, energy-consuming or seem to involve considerable cost or risk to the animals giving them. These are the signals that have been most studied because they are the very signals that attract the attention of biologists just as they do that of other animals. But we should not ignore the fact that much animal communication takes place via signals that are so small as to be hardly noticeable to us. The soft grunts given by vervet monkeys are indistinguishable to the unaided human ear but carry considerable significance to any vervet that hears them (Cheney & Seyfarth 1982) and communication within flocks or herds of animals often takes place through signals that are the very opposite of large and costly. If we are to claim to be in possession of general principles covering all signals, therefore, we have to explain why and under what circumstances small, inconspicuous and apparently uncostly signals occur and why, under other circumstances signals evolve to become large and more noticeable. Diversity in size of signals demands an explanation.

3. It has to explain the observed diversity of form of animal signals. I do not mean why some animals use visual signals and others olfactory or electrical ones. Interesting though this question is, it is usually possible to answer it in terms of the sense organs an animal has evolved for non-communicatory purposes or the gross demands of its environment such as absence of light. What I mean by it in this context is why the signals of even closely related species all using the same modality may show major differences. For example, among the sea bass of the single genus *Hypoplectrus* (Hamlets), the colouring ranges from black in one species to blue with white stripes in another to yellow with iridescent face stripes in a third. Unless a theory can explain this diversity, it has no claim to be an adequate general theory of signal-

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ling. It is not enough to predict that a signal should be 'conspicuous' or 'costly'. To have real explanatory power, it also has to explain why it takes the particular form of conspicuousness or costliness that it does.

3. THREE SELECTIVE FORCES AFFECTING DIVERSITY OF SIGNAL SIZE AND FORM

(*a*) *Degree of conflict or cooperation*

Krebs & Dawkins (1978, 1984), argued that the degree of conflict between signaller and receiver is a major factor determining the size of signal that evolves. Where response by the receiver benefits both receiver and sender, they argued that inconspicuous signals ('conspiratorial whispers') will evolve. For example, if it is in the interests of all birds in a flock to remain motionless in the presence of a predator, then it will be in the interests of the giver of the signal to keep its voice as low as possible so as not to attract the attention of the predator and also in the interests of the birds receiving the signal to be as sensitive to the low-level alarm call as possible. Krebs & Dawkins argued that under such circumstances a coevolutionary arms race – of de-escalation – would be set up, with smaller signals and more sensitive responses on the part of the receivers leading in turn to even smaller signals until the lower end of the 'whispers' was halted only by the need to give a signal that would carry reliably over the distance between one animal and another.

But where the interests of two animals conflict, for example, in disputes over territory, they argued that there will be a different sort of coevolution, this time for larger or louder signals by the sender to manipulate the receiver and resistance to such manipulation by the receiver. Zahavi's (1977) idea that, in conditions of conflict, signals will evolve to be large and costly and that the 'honesty' of the signal is ensured by its cost has now become widely accepted. Grafen & Johnstone (this symposium) have shown how costly 'honest' signalling is stable and have argued that the handicap principle (Zahavi, this symposium) is capable of giving at least one explanation of extravagant signals. But are we entitled to say from this that the handicap principle is a general principle of animal signalling or even that it is a general principle that conflict between signaller and receiver leads to large costly signals and cooperation to small and uncostly ones? Neither of these claims stands up to scrutiny. Let me take the second point first. Although the degree of conflict or mutual interest that exists between two participants is one selective force underlying signal diversity, it cannot be the only one. 'Conspiratorial whispers' or very small signals can occur in situations of conflict, for example, between dominant and subordinate hens in a flock of birds that are familiar with each other. Conversely, large signals can evolve even in the conditions of clear mutual interest found in a colony of honeybees. Foragers dance vigorously to signal rich or nearby food sources (von Frish 1967), the dance becoming more energetic the greater the mutual benefit of the second forager responding. Also, as Krebs and Dawkins recognized, when the physical environment imposes barriers that necessitate a considerable expenditure of effort and energy to reach another animal, this in itself will lead to large signals even with the most 'cooperative' signals. A 'conspiratorial whisper' will be ineffective if there is so much background noise, or so many leaves forming sound baffles or just so much physical distance between signaller and receiver that even the most sensitive ears are unable to detect it.

In other words, it is already apparent that at least two selective forces can independently affect the size of signals and so contribute to signal diversity. A signal may evolve to be large, loud or otherwise conspicuous either because it has evolved in conditions of conflict in which it can be seen as a 'handicap' with the signaller demonstrating the cost it has paid. Or it may evolve that way because of the selective pressures of getting a signal's message across to a receiver: its 'efficacy' (Guilford & Dawkins 1991), as Romer, Ryan & Rand (this symposium) and Arak & Enquist (this symposium) have all pointed out.

(*b*) *Signal efficacy*

There are three ways in which the demands of signal efficacy can affect signal design.

(i) *Transmission through the environment*

Romer (this symposium) stresses that among insects much signal diversity comes from selection pressures imposed by the environment through which the signals have to travel. Similar diversity is found among birds living in different environments (e.g. Morton 1975; Hunter & Krebs 1979; Wiley & Richards 1983). The colour patterns of fish are affected by the light conditions and absorption properties of water in which they live (Lythgoe 1979). The spot colours of male guppies are designed to be more conspicuous to female guppies than to a predator *Crenicichla alta* in the particular light conditions in which these two potential receivers occur (Endler, this symposium). Properties of signals such as their intensity, spectral characteristics and repetition rate may be explicable largely as adaptations to the physical characteristics of the environment, especially where there are obstacles or where the medium of travel degrades some signals more than others. Larger and more intense signals will be detectable from greater distances and longer or repeated signals will have a greater chance of rising above background noise (Wiley 1993).

(ii) *Stimulation of the receiver's sense organs*

Success by a signaller in eliciting a response from a target receiver will be increased if the signal stimulates the sense organs of the receiver in a particularly effective way, as has been demonstrated by Ryan & Rand (this symposium). By exploiting sensory biases in the intended receivers of their signals, signallers may evolve powerful means of altering the behaviour of other animals, for example through making themselves particularly conspicuous or easy to discriminate against a background of other stimuli. Male jumping spiders (*Maevia inclemens*), for instance, may exploit pre-existing sensory mechanisms in females in their courtship. Jumping spiders always orient to movement in their peripheral field of vision as part of their adaptation for catching live prey. Clark & Uetz (1992) showed that female choice of males was based not on male morphology but on the ability of males to stimulate this turning movement in a female by waving their legs. The female responds because the male 'taps in' to a pre-existing tendency.

(iii) *Use of 'receiver psychology'*

Eliciting a behavioural response from a receiver takes more than just a signal arriving at its sense organs and processing going on with its sensory system. The brain of the receiver has to interpret what it has received and decide whether action should be taken or not. Many aspects of signal design may be understandable as adaptations to make use of the 'receiver's psychology' in quite subtle ways (Guilford & Dawkins 1991). Arak & Enquist (this symposium) have argued that pattern recognition systems may be inherently tuned to pick up certain kinds of stimuli and that if signallers evolve to provide such stimuli in their signals, those signals will have a particularly powerful effect on receivers. Supernormal stimuli derive their effect from relatively simple recognition rules such as 'respond to reddest (or roundest or largest) object around' being generalized to new objects with some of the same properties exaggerated. Fisherian sexual displays may also fall into this category. Other ways in which receiver psychology could work might be through producing visual illusions in receivers, for example, or through making it easier for them to learn associations between events (Guilford & Dawkins 1991). Signal efficacy in all its forms can, then, potentially affect both the size and the form of signals and it offers explanations for signal diversity that are quite independent of those offered by the Handicap Theory. As will be explained more fully later, this has important implications for general theories of signalling.

(*c*) *How costs of signalling are paid*

Maynard Smith & Harper (1988) argued that diversity in animal signals can be achieved through variation in the means by which evolutionary stability is maintained and, specifically, in the way in which signal costs are paid. They distinguished between 'assessment signals' that are reliably correlated with underlying quality (such as fighting ability) and cannot be faked and 'conventional signals' that may or may not be correlated with quality and are open to faking. They showed that conventional signalling could result in an evolutionarily stable mix of fakes and honest signallers if: (i) the value of the contested resource is small; and (ii) if individuals giving fake signals do not pay costs commensurate with what they gain.

At first sight, this would appear to put handicaps into the assessment signal category with other, potentially cheatable signals such as status badges into the conventional signal category. This would, however, be a misinterpretation. All cases where signaller quality and signal strength are not necessarily correlated but where the honesty of a signal is maintained by the cost of giving it can be described as 'conventional' in the sense that they include an element of information being taken 'on trust' or 'by convention'. Both strategic choice handicaps (Grafen 1990) and 'badges of status' (Rowher 1975) are therefore conventional signals in the sense that cheats could occur but would be unsuccessful if they did unless the conditions outlined by Maynard Smith & Harper are fulfilled. By far the majority of what are referred to as animal 'signals' are thus conventional. I suggest, however, that an important source of variation among conventional signals comes from considering the different ways in which costs of signalling can be paid.

In some cases, costs are paid in signal production, for example, in the physical or physiological costs of growing an ornament. Here the element of 'strategic choice' lies in the decision of how much of the body's resources should be put into producing a large ornament in the first place. In other cases, however, the signal may not be costly to produce (as in a badge of status) but the signaller pays costs as a consequence of giving it, for example in being challenged by a social dominant (Rowher 1975). Here there is also an element of strategic choice but this time it is in whether to risk what might happen in the future. The reason why this distinction between costs of signal production and signal consequence is important is that it opens the way to a divergence of selection pressures operating on signals and hence to a diversity of effects on the design of the signals involved. Where costs are paid in producing a signal, that signal will be designed to show that a signaller possesses a particular quality, such as fighting ability (Zahavi 1975, 1991) and the design of the signal is predicted to be related to the quality being signalled in a very specific way through the particular cost paid by the signaller. 'Honesty' through cost is not paid in a general fitness decrease but in a reduction of that quality of most interest to the receiver. In a discussion of sexual signals, Zahavi (1977) wrote: 'The adaptive significance of the attracting character should lower the fitness of the selected sex in relation to the main ecological problems of the species'. Grafen (1990) also stresses that 'the cost of a signal is a key to its meaning. A signal wasting energy shows possession of energy, a signal inviting predation demonstrates a low predation rate'.

If the nature of the cost paid reflects meaning, then the design of a signal should be predictable from an understanding of what those costs are. If a male is signalling his condition-dependent resistance to parasites that are particularly dangerous to young animals (for instance, by using a signal that is costly in terms of his ability to resist them), then it should be possible to understand the design of the signal he uses in terms of the optimum way of signalling long term disease resistance. His signal should reflect evidence of good body condition over a long timescale. But if the signal is 'designed' to be a good predictor of fighting ability, a quality that may vary considerably from week to week, then the signal should reflect current, but not necessarily past body condition (Moller & Pomiankowski 1993).

Where costs of signalling are paid as a consequence of giving a signal, however, this design for direct quality advertisement may be replaced by other pressures deriving from the costs paid by receivers of those signals. If the costly consequences of giving signals depend on the behaviour of receivers, these will in turn have a strategic choice as to whether or not to impose those costs. For example, if it is costly for an animal to 'probe' another's fighting ability or for a predator to 'taste' a brightly coloured prey, then the receivers may sometimes choose not to probe or taste and so the signaller will get away with not paying the full consequences of its signal. Under such circumstances, cheats will occur at least at a low level and the signalling system will become open to mimicry (Dawkins & Guilford 1991). This will then set up selection pressures on the signallers to demonstrate, for example, that they are a member of a class of individuals already encountered and tested by the receiver and for their signals to be designed primarily by selection pressures to be easily detectable, discriminable or memorable, and in general, to prove the optimum way to stimulate receivers (Guilford & Dawkins 1991; Ryan & Rand, this symposium; Arak & Enquest, this symposium). In other words, such signals will be designed primarily by efficacy considerations: because they are supernormal stimuli, for instance, or have some particularly attention-grabbing characteristic for the receiver or have some other salient feature that taps into the 'receiver psychology'. Signals that are costly to produce in the first place will also, of course, be affected by efficacy considerations (in addition, see Hassan (1989)) but their primary selective pressure will be in demonstrating that a particular cost has been paid. With signals that do not advertise quality directly, the primary selection pressure will come from the vast range of extra factors that can be grouped under the heading of signal efficacy.

We can see the importance of making this distinction by considering the design of one particular class of signals, namely warning signals (Guilford & Dawkins 1993). If warning signals evolved because they were costly to produce, we would expect their design to be explained as direct quality advertisement, such as the bright colours making the signallers less unpalatable through 'using up' some of their distastefulness. But if warning signals derive their meaning from the costly consequences that signallers incur from being brightly coloured, such as being more likely to attraction of naive predators, then their key design features should be shaped by selection pressure from efficacy considerations such as to enhance their effectiveness in predator learning: in making it easier for the predator to learn, or to discriminate them from other sorts of prey, for instance. Conspicuous colours do indeed appear inherently easier for a predator to learn (Turner 1975; Roper & Redston 1987), although it is not yet clear whether this is because predators more readily learn specific colours or patterns and these just happen to be conspicuous (Harvey 1981; Turner 1984; Rothschild 1985; Sillen-Tullberg 1985) or whether predators more readily associate unpalatability with coloration that contrasts with that of prey which they normally hunt (Shettleworth 1972; Edmunds 1974; Turner 1975).

The high degree of pattern convergence that exists within species (monomorphism) and between species (Mullerian mimicry) strongly suggests that warning signals have been designed to enhance predator learning rather than to advertise distastefulness directly. Black and yellow stripes or red, black and yellow colouring are widespread in many groups of animals. Because we know that the best way to be cryptic varies enormously depending on background (Endler 1978), it is difficult to believe that there is only a limited way of advertising conspicuously. Much more plausibly, warning colours are designed to persuade predators not to repeat unpleasant experiences they have had with similarly coloured prey in the past. The more similar they are to such prey, the better, hence the convergence within and between species and the detailed congruence that often evolves between model and mimic pattern (Turner 1971) involving form, posture, movement, and even body shape (Fisher 1930; Cott 1940).

The existence of Batesian mimics, too, suggests design for efficacy and costs paid as a consequence of giving a signal rather than direct advertisement of quality through costs paid in its production. Both genuinely distasteful prey and their Batesian mimics are able to produce warning signals but pay differential consequential costs if attacked by predators. The mimics suffer more heavily if attacked since they are likely to be eaten whereas the genuinely distasteful ones may escape. Cheats or mimics exist at a low frequency because the potential receiver costs paid by predators (in this case sampling a genuinely distasteful prey) make them cautious and allow some individual mimics not to pay the full costs of their signals.

Distinguishing between the different ways in which signal costs can be paid is thus important for understanding signal design and, moreover, leads to testable predictions as is illustrated by the example of warning signals. Where costs are paid as a consequence of giving a signal as opposed to in signal production, a whole new range of selective pressures on signal design opens up. As yet, we have only scant information about them but they are worth considering alongside the more obvious ones of quality advertisement. For example, we might ask: are the bright colours of reef fishes really quality advertisement or are they better explained aspects of signal efficacy, facilitating species identification in situations where confusion between species is particularly likely? (Erhlich et al 1977). Might not their diversity therefore arise out of the need to discriminate on sight many different categories (own species, feeding rivals, harmless non-competitors, females etc.) and have nothing at all to do with any 'cost' of producing them? Or we could ask whether some large signals were originally evolved to allow females to recognize unambiguously the males of their own species or to see them over large distances as Howard (this volume) suggests. Is it possible that the design of some of the signals used in sexual displays is less related to quality advertisement and more related to the demands of signal efficacy than we have so far considered?

4. CONCLUSIONS

In attempting to explain the diversity of animal signals, I have to conclude that there are no simple general principles. The diversity that we see is the result of many different selection pressures – to display quality, to attract attention, to tap into the 'psychology' of the receiver or, conversely, to avoid being responded to by unwanted receivers such as predators. Stability of signalling systems can be achieved in more than one way so that although some signals may more or less reliably indicate the quality of the signallers through the cost that they have already paid in producing the signal, others are better regarded as only loosely correlated with quality, and designed primarily by efficacy considerations of receiver receptivity, memory limitations or innate predispositions that we have only just begun to understand. To this extent there are more things in signal design than have yet been dreamt of in our current philosophy of animal communication. We have to understand far more about the mechanisms in receivers that constrain, limit and provide opportunities for the evolution of effective signals. We have to understand much more than we yet do of the conditions of stability for reliable and unreliable signals and we have to explore the effects of receiver costs. We have to be ready to ask questions and expect the answers to be multi-faceted results of many conflicting selection pressures, not the result of simple general principles.

REFERENCES

Cott, H.B. 1940 *Adaptive Coloration in Animals*. Methuen, London.

Cheney, D.L. 1982 How vervet monkeys perceive their grunts: field playback experiments. *Anim. Behav.* **30**, 739–751.

Clark, D.L. & Uetz, G.W. 1992 Morph-independent mate selection in a dimorphic jumping spider: demonstration of movement bias in female choice using video-controlled courtship behaviour. *Anim. Behav.* **43**, 247–254.

Dawkins, M.S. & Guilford, T. 1991 The corruption of honest signalling. *Anim. Behav.* **41**, 865–873.

Edmunds, M. 1974 *Defence in animals: a survey of anti-predator defences*. Longman, Harlow.

Endler, J.A. 1978 A predator's view of animal colour patterns. *Evol. Biol.* **11**, 319–364.

Ehrlich, P.R., Talbot, F.H., Russell, P.C. & Anderson, G.R. 1977 The behaviour of chaetodaitid fishes with special reference to Lorenz's 'poster coloration' hypothesis. *J. Zool., Lond.* **183**, 213–228.

Fitzgibbon, C.D. & Fanshawe, J.H. 1988 Stotting in Thomson's Gazelles: an honest signal of condition. *Behav. Ecol. Sociobiol.* **23**, 69–74.

Fisher, R.A. 1930 *The genetical theory of natural selection*, 2nd edn. New York: Doves Publications.

Fisch, K. von 1967 *The dance language and orientation of bees*. Cambridge, Massachusetts: The Belknap Press of Harvard University.

Gittleman, J.L. & Harvey, P.H. 1981 Why are distasteful prey not cryptic? *Nature, Lond.* **286**, 149–150.

Grafen, A. 1990 Biological signals as handicaps. *J. theor. Biol.* **144**, 517–546.

Guilford, T. 1986 How do warning colours work? Conspicuousness may reduce recognition errors in experienced predators. *Anim. Behav.* **34**, 286–288.

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

Guilford, T. & Dawkins, M.S. 1993 Are warning colours handicaps? *Evolution.* (In the press.)

Hasson, O. 1989 Amplifiers and the handicap principle in sexual selection: a different emphasis. *Proc. R. Soc. Lond.* B **235**, 383–486.

Hunter, M. & Krebs, J.R. 1979 Geographical variation in the song of the great tit (*Parus major*) in relation to ecological factors. *J. Anim. Ecol.* **48**, 759–785.

Lythgoe, J.N. 1979 *The ecology of vision*. Oxford University Press.

Maynard Smith, J. & Harper, D.G.C. 1988 The evolution of aggression: can selection generate variability? *Phil. Trans. R. Soc. Lond.* B **319**, 557–570.

Moller, A. & Pomiankowski, A. 1993 Why have birds got multiple sexual ornaments? *Behav. Ecol.* (In the press.)

Morton, E.S. 1975 Ecological sources of selection on avian sounds. *Am. Nat.* **109**, 17–34.

Roper, T.J. & Redston, S. 1987 Conspicuousness if distasteful prey affects the strength and durability of one-trial avoidance learning. *Anim. Behav.* **35**, 739–747.

Rothschild, M. 1985 *British aposematic lepidoptera*. In *The moths and butterflies of Great Britain and Ireland*, vol. 2 (ed. J. Heath & A. M. Emmet). Colchester: Harley.

Rowher, S. 1975 The social significance of avian winter plumage variability. *Evolution* **29**, 593–610.

Sillen-Tullberg, B. 1985 The significance of coloration per se, independent of background, for predator avoidance of aposematic prey. *Anim. Behav.* **33**, 1382–1384.

Shettleworth, S. 1972 The role of novelty in learned avoidance of unpalatable prey by domestic chicks. *Anim. Behav.* **20**, 29–35.

Turner, J.R.G. 1975 A tale of two butterflies. *Nat. Hist.* **84**, 28–37.

Turner, J.R.G. 1984 Mimicry: the palatability spectrum and its consequences. In *The biology of butterflies* (ed. R. I. Vane-Wright & P. R. Ackery), pp. 141–161. Academic Press, London.

Wiley, R.H. 1993 Errors, exaggeration and deception in animal communication. In *Behavioral mechanisms in ecology* (ed. L. Real) University of Chicago Press. (In the press.)

Wiley, R.H. & Richards, D.G. 1978 Physical constraints on acoustic communication in the atomsphere: implications for the evolution of animal vocalisations. *Behav. Ecol. Sociobiol.* **3**, 69–94.

Zahavi, A. 1975 Mate selection: selection for a handicap. *J. theor. Biol.* **53**, 205–214.

Zahavi, A. 1991 On the definition of sexual selection, Fisher's model and the evolution of waste and of signals in general. *Anim. Behav.* **42**, 501–503.