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The corruption of honest signalling

MARIAN STAMP DAWKINS & TIM GUILFORD
Animal Behaviour Research Group, Department of Zoology, South Parks Road, Oxford OX1 3PS, U.K.

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Abstract. It is argued that recent analyses of the evolution of animal signals, which claim that signalling systems must be honest indicators of underlying quality, have neglected a vital consideration: the costs receivers pay in assessment. Where the costs of fully assessing a signaller are high, in terms of energy, time, or risk, and the value of the extra information gained is low, then it will pay receivers to settle for cheaper, but less reliable, indicators of quality instead. Thus, it is argued, honest assessment will be replaced by conventional signalling. Conventional signals are open to cheating, but cheating will be kept at low frequencies by the frequency-dependent benefits of occasional assessment (or 'probing'), so dishonest signalling remains stable. The concept of 'honesty' is discussed.

Zahavi (1975, 1987) argued that animal signalling systems are 'honest' in the sense that the level of a signal reliably reflects the underlying quality of the signaller, and this view is now becoming widely accepted (e.g. Kodric-Brown & Brown 1984; Petrie 1988; Dawkins 1989). Zahavi's argument rests on the assumption that signals such as loud calls or displays that consume energy are costly (fitness-reducing) to produce and so the signaller can demonstrate its quality by its ability to survive despite the 'handicap' of the signal. Grafen (1990a, b) has recently produced an evolutionarily stable strategy (ESS) model in which, at equilibrium, costly signals are reliable indicators of signaller quality. Grafen agrees with Zahavi that the honesty of a signal's message is guaranteed by cost. High quality animals suffer lower cost for a given level of signal than lower quality ones and so at the ESS, the signal level adopted will correlate with underlying quality.

We argue here, in contrast, that dishonest signals are likely to be a widespread component of signalling systems concerned with quality advertisement, and that previous discussions have neglected a vital evolutionary consideration, the cost to the receiver of eliciting and evaluating honest signals. If both signaller and receiver pay costs, it will be to their mutual (but not necessarily equal) advantage to reduce them wherever the value of the extra information contained in a costly (rather than a less costly) signal is outweighed by the costs of giving and receiving the costly signal. We first argue that receiver costs are widespread and then show how this results in the favouring of conventional rather than full assessment signals. Conventional signals (Maynard Smith & Harper 1988) are those that indicate membership of a particular category of signaller, and are not necessarily reliable indicators of signaller quality. We suggest that because conventional signalling systems are open to low level cheating, many, if not most, signalling systems will consequently contain a considerable degree of dishonest signalling.

RECEIVER COSTS IN SIGNALLING

Most accounts of animal communication assume that the costs of signalling are borne entirely by the sender of a signal. Thus, roaring, calling, singing and other sorts of display are seen as costly to the performer (e.g. Burk 1988; Ryan 1988) but not to the recipient. This one-sided view is, however, quite erroneous. In the classic case of roaring in red deer stags, *Cervus elaphus* (Clutton-Brock & Albon 1979; Clutton-Brock et al. 1979), for example, the only way in which a challenger can elicit an 'honest' signal from a harem-holder is by paying the cost of roaring at his own honest rate. At the beginning of an encounter, the roaring rate of a stag defending his group of females will be low and will not be a reliable indicator of his true fighting ability. Only if the roaring contest escalates with the challenger and the defender both being prepared to pay the costs of roaring at a high rate will the roaring rate of

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a stag accurately reflect quality. Both stags may end up exhausted. The cost of having an honest signal to assess its rival with is giving a costly signal itself.

In other areas of signalling, too, receivers pay costs. Females often use the duration, variety or persistence of a male's display to choose a mate (e.g. red deer: McComb 1987; crickets: Hedrick 1986; frogs: Ryan 1988). This involves inevitable costs to the female, if only in time that could otherwise be spent on other activities. Assessment of the size of a male's song and syllable repertoire (Catchpole 1980, 1987; Baker et al. 1986; Searcy & Andersson 1986) implies that females spend enough time listening to a male to evaluate how many songs he has. Female sage grouse, *Centrocercus urophasianus*, prefer males with regular attendance on a lek over a period of days (Gibson & Bradbury 1985). This means that the females must themselves attend the lek for long enough or often enough to evaluate male attendance (see also Pomiankowski 1987). In fact so many displays used for quality advertisement involve duration (Burk 1988) that it may be that receivers almost always have to pay time costs if they want an honest assessment. In addition, male courtship displays often involve increased predation risks to calling males (e.g. in frogs, Ryan 1985, and crickets, Cade 1975). Females that approach and stay close to such males for any length of time will be putting themselves at risk and pay a consequent cost for being the receivers of signals. If assessment requires very close contact then there may be additional risks from disease transmission as well as from predation (Pomiankowski 1987). For these reasons, then, it would seem that the receiver's ideal signal (one that is costly to give, and so gives an honest indication of quality, but costs nothing to receive) will be a rare commodity. In many cases, the very feature of the signal (e.g. duration or variety) that makes it costly to give also makes it costly to measure.

The costs that choosy females incur in travelling, or waiting, during the 'search' for preferred males (e.g. Pomiankowski 1987; Alatalo et al. 1988; Engelhard et al. 1989) are part of the costs of choice but are not the same as the receiver costs we are referring to here. Search costs are paid regardless of the cost a female subsequently pays in being the receiver of a male's signal; receiver costs, on the other hand, vary with whether the receiver chooses to pay full assessment costs or, as we shall argue is the more frequent occurrence, settles for a less informative signal that is less costly to receive.

It is clear, then, that receivers as well as senders of signals pay costs of various sorts. With signals where levels may be easy to assess, such as the size of antlers, receivers pay little cost while signallers incur very large costs. Wherever a signaller pays costs in time, for example in the duration of a display, on the other hand, the costs paid by signaller and receiver become much more symmetrical. Receiver costs will in general be less than those paid by senders even under these circumstances but nevertheless the very existence of costs to receivers will have important evolutionary effects on communication systems. What might these effects be?

EVOLUTIONARY CONSEQUENCES OF RECEIVER COSTS

If both senders and receivers of signals pay costs, albeit unequal ones, then there may be circumstances in which it is to their mutual advantage to avoid paying these costs in full. We now argue that these circumstances are so widespread that truly honest (full cost) signalling systems are likely to be comparatively rare, because conventional signalling systems will be favoured in their place. Let us begin by looking at the signals given when two animals are in conflict over a resource.

Maynard Smith & Harper (1988) listed three ways in which contests between animals may be settled: by all out fighting, by limited fighting and by signals. To conserve energy and to avoid the risk of injury, animals tend to avoid dangerous fights (Maynard Smith 1982) and to limit their fights or to rely on signals. Signals in turn can be of two types (Maynard Smith & Harper 1988).

(1) Assessment signals are necessarily correlated with fighting ability or resource-holding potential and are therefore 'honest'. An example would be the roaring of red deer stags where it appears that stags with a low fighting ability simply cannot roar at a high rate (Clutton-Brock et al. 1979).

(2) Conventional signals may or may not be correlated with fighting ability and therefore need not be honest. Examples of conventional signals are the plumage 'badges of status' found in many birds (Roper 1986; Whitfield 1987). Maynard Smith & Harper (1988) argued that conventional signals will be honest only where a dishonest signaller is punished for cheating and pays the full cost of the signal level it is giving. The fact that in a number of bird species, individuals with high status plumage

badges are attacked more by dominants than are birds with subordinate plumage (Rohwer & Rohwer 1978; Balph et al. 1979; Møller 1987) is evidence that dishonest signallers might indeed suffer extra costs. However, if a dishonest signaller can avoid paying these costs a cheating mutant could spread through the population because it would win some of the contests that an honest signaller would lose and pay no costs not also paid by honest signallers. In other words, dishonest conventional signals can be stable provided that dishonest signallers do not pay the full costs appropriate to their level of signalling. Since many of the costs paid by dishonest signallers will come from 'probing' by receivers (Maynard Smith & Price 1973) and probing will itself be costly to those receivers, it will often not pay the receivers to bear these costs. Hence the door is open to dishonest signallers, although their advantage will be frequency-dependent since probing will bring more benefits when cheats are common than when they are rare (Maynard Smith & Price 1973; Barnard & Burk 1979).

If we want to assess the roles of honesty and dishonesty within signalling systems we must, then, consider how likely signalling systems are to fall into the category of necessarily honest assessment, rather than conventional systems open to cheating. We argue that relatively few signalling systems fall into the first category because both senders and receivers will be under constant selection pressure to reduce the cost of signals. Animal communication gives the appearance of consisting mainly of large conspicuous signals because these are the most obvious to human observers, but a great deal of animal communication is carried out through smaller, more subtle signals (Dawkins 1986). With conventional signals, the conditions for honesty are frequently not met because of costs paid by receivers in probing. This leaves a very large number of signalling systems as conventional, and open to cheating.

HOW WIDESPREAD ARE HONEST ASSESSMENT SIGNALS?

The fact that it is possible to point to signals that are costly (Zahavi 1975; Burk 1988; Vehrencamp et al. 1989) does not mean that the signals are costly enough to be considered as necessary correlates of some underlying quality such as fighting ability. Also, as Andersson (1980) argued, there may be a limit on the number of signals that can be considered as 'raw material' in this respect and proliferation in the number of threat signals may be the result of a never-ending evolutionary search for an honest signal. Even more importantly, it is clear that many signals are not the costly, fitness-reducing displays that the handicap principle would predict. Plumage badges, crests that can be raised or lowered and the contact calls given by members of flocks or herds are examples of low level signals and certainly not obviously costly at all. Even when costly signals are available, they are not always used. As previously mentioned, red deer stags do not roar at their 'honest' rate at the beginning of an encounter. Rather, they escalate, giving low level signals at first and only roaring at a high costly rate when it becomes clear that their rival is not giving up (Clutton-Brock & Albon 1979).

The reason why animals adopt less costly conventional rather than very costly assessment signals is similar to the reason why it does not always pay animals to fight even when their interests conflict (Maynard Smith 1982; Parker 1984; Huntingford & Turner 1987). Where the costs of fighting (energy expended, risk of injury, etc.) are high, overt fights are often replaced with signals that are used to assess asymmetries between individuals to the mutual (although not necessarily equal) advantage of both participants which both avoid a damaging fight. Use of signals for assessment will be favoured when (1) the cost of assessment is low and (2) the costs of escalated fighting are relatively high (Maynard Smith 1982). In an exactly parallel way, where the costs of honest signalling are high (which they have to be to achieve the required degree of 'honesty'), we might expect that fully honest signalling systems will be replaced by less costly and therefore less honest ones to the mutual advantage of both signallers and receivers. This will occur when (1) the costs both of giving and of receiving conventional signals are low, and (2) the costs both of giving and of receiving assessment signals are high (e.g. involve expenditure of time and energy in exchange for knowledge about the opponent that is either not new or not valuable). Signallers gain through not having to pay the costs of the signal and receivers gain through avoiding the costs of receiving the signal. The very costs that make a signal honest may set up selection pressures for animals to adopt conventional and less costly ways of communicating.

The key point here concerns the value to the recipient of the information contained in the sender's display and this in turn requires a clarification of what 'information' means. It is easy to assume that if the 'message' (Smith 1977) an animal is emitting is that it is, say, a strong male capable of fighting hard, then there is information to this effect in its display. This would, indeed, be the colloquial use of the term 'information' (Slater 1983; Krebs & Dawkins 1984; Dawkins 1986). It would not, however, be the technical meaning of information (Shannon & Weaver 1949) which is the critical one in this context. Information in this technical sense refers to a reduction in uncertainty: learning something that was not known before. If a receiver was already aware that a given male was the best fighter on the block, then seeing that male's display containing the message to this effect would not give any extra information about that male's quality. We would not expect a receiver to pay costs to learn something it already knew.

In deciding whether animals would be expected to pay the costs of receiving signals, therefore, one of the critical things we need to know is whether their uncertainty (e.g. about the resource-holding potential of a signaller) is likely to be much reduced if they pay these costs (Enquist & Leimar 1983). If it is not, we would expect animals to adopt conventional signals, less reliable but less costly to both sender and receiver.

THE CASE FOR CONVENTIONAL SIGNALS

Conventional signals allow both senders and receivers of signals to avoid the full costs of honest signalling and at the same time provide receivers with as much information about the signaller as they are prepared to pay for. There are two common situations in which it is clear that the full costs of honest signalling are avoided: where animals recognize each other as individuals and where they recognize a member of a familiar set of individuals. While these categories may overlap (Barnard & Burk 1979), it is useful to begin by considering them separately.

Individual Recognition with Remembered Assessment

Provided that the quality (e.g. resource-holding potential) of the individuals concerned is fairly stable, animals can avoid the costs both of frequent fights and of constantly receiving costly honest signals by remembering how each individual performed in the past. The stable peck-orders of chickens, *Gallus gallus domesticus*, for example, are not maintained by costly displays. Rather the birds use fights and assessment displays when they are first introduced to one another and then learn their place in the hierarchy (Guhl 1968), probably through individual recognition (Bradshaw 1990). Given that the results of a fight or assessment display in the past accurately reflect the likely outcome of a potential fight in the present, a given bird does better to accept even a lowly place in the hierarchy than constantly to challenge birds that have already defeated it (Rohwer 1975). A similar 'giving way' to individuals that have beaten them in the past is reported for red deer females (Thouless & Guinness 1986).

Such a peaceful option is not, however, open to the roaring red deer stags. Unlike the females, body condition of the males is changing so rapidly that previous experience (either of fighting or roaring) of another individual may be a very poor guide to future performance. Harem-holding stags are often so busy defending their group of hinds that they have little time to eat and may lose weight throughout the rut (Clutton-Brock et al. 1982). Under such circumstances, the information gained by both sides in entering a costly roaring match may well be sufficient to justify the costs of frequent assessment.

The situations in which individual recognition (together with a memory of that individual's resource-holding potential) can be used to avoid the costs of honest assessment are, however, limited. Not only must there be a degree of stability in the qualities of the individuals concerned, there is also a limit on the number of individuals that can be assessed and remembered imposed by memory constraints (e.g. Pearce 1987). Constant contact with strange individuals makes this option impossible. Nevertheless, even where animals interact frequently with other animals they have not encountered before, they can still avoid paying the full costs of honest signalling to mutual advantage by recognizing and being recognized as belonging to particular categories of signallers that have been experienced before.

Category Recognition

The most obvious example of category recognition is warning coloration (e.g. Edmunds 1974).

Here, a prey is treated as distasteful not because it, as an individual, has been tasted before and found to be nasty, but because of its resemblance to other individuals that the predator has encountered in the past. The predator learns that prey in that category (e.g. bright yellow with black stripes) are distasteful and does not assess each prey it comes across (e.g. Guilford 1988, 1990). The warning coloration is therefore not an assessment signal as Grafen (1990a) implicitly claims, but a conventional signal, the conventional signal deriving its power from associations made in a predator's mind between the signal and previously costly experiences (attempting to eat a distasteful prey; Guilford & Dawkins, in press). Because probing (making another attempt to eat a bright yellow prey) is costly, cheats in the form of Batesian mimics can and do exist at low frequencies.

Similar learned associations are likely to be widespread in animal signalling systems. The costs of assessment (by receivers) have led to the evolution of conventional rather than honest assessment signals and many conventional signals arise because of learned associations in a receiver's mind between costly past experience (such as a fight or a bout of honest assessment) and some feature of a present signaller. For example, if a bird has been repeatedly defeated by other birds all of which have the same distinctive plumage pattern, it may learn to avoid not just those particular individuals but all individuals in the category of birds having the same patterns on their plumage. Learning of some form is involved in the development of social status hierarchies in a wide variety of animals (Ratner 1961; Beacham & Newman 1987; Nilsson 1989) and does not necessarily involve the recognition of individuals (Barnard & Burk 1979). Shawcross & Slater (1984) showed that in groups of male *Quelea*, individual recognition did not seem to be important; rather, the birds recognized the rank even of unfamiliar individuals, apparently on the basis of beak colour. Learning to recognize categories of individuals could explain the evolution of conventional 'badges of status' in birds (Roper 1986; Whitfield 1987). It would also explain some of the more puzzling aspects of status badge signals, for example, that they do not seem to be particularly reliable guides to actual dominance (see Maynard Smith & Harper 1988 for a review) and are used more in some contexts than others (Wilson 1990). Rohwer (1975) found that badges of status were more likely to be respected in less intense contests (for example, where food was scattered rather than clumped). This would suggest that where the value of the resource being contested is low, a conventional signal is obeyed even though it is open to cheating because the cost of true assessment is not justified by what could be gained from uncovering a cheat. When the value of the resource is higher, the value of the information is consequently higher.

If males use badges of status even partially to decide the outcome of interactions, then females may also use them in choosing a mate (e.g. Brodsky et al. 1988; Komers & Dhindsa 1989). Females may even use their own experience to learn that particular categories of males are desirable (e.g. because a similar male has, in the past, completed copulation, brought food, been the owner of a desirable territory, etc.). Furthermore, Losey et al. (1986) considered the role of learning in female choice and concluded that it could benefit females to copy other females in their choice of mate. If true honest signals are costly for females, as receivers, to assess (perhaps because they demand a great deal of time standing watching), it may be to their advantage to cut corners and use category resemblance of a present male to males from previous encounters where they have paid the full costs of assessment. Extra-pair copulations are a possible instance where a female may have to decide quickly whether to accept a male or to eject his sperm without the benefit of a lengthy, honest display. If costs of assessment are paid in time, then she may be especially unwilling to pay these costs in such circumstances.

ARE DISHONEST SIGNALS STABLE?

Within-category signal mimicry is common between species. Palatable Batesian mimics cheat on their unpalatable models (Edmunds 1974), and interspecific brood parasites, such as the European cuckoo, *Cuculus canorus*, mimic the size and coloration of their host eggs (Davies & Brooke 1988, 1989). The existence of dishonest signalling where the cheats are from the same species, however, is perhaps more controversial. If a signal is not reliable, one possible evolutionary consequence is that the signal becomes no longer used (Andersson 1980). However, unreliable signals can be stable and persist indefinitely if cheats have a frequency-dependent advantage (Barnard & Burk 1979; Maynard Smith & Harper 1988). Probing provides a frequency-dependent mechanism for the persistence of cheats in a population because the rewards of probing are greatest (a cheat is most likely to be uncovered) when cheats are common and fall when cheats are rare, since probing is then more likely to result in an individual finding itself in a conflict with a genuinely good fighter. It is important to emphasize that cheats can persist only if there are also honest signallers around to me mimicked. If cheats have such an advantage that they spread through the population completely, receivers will no longer use the signal at all. But if cheats suffer costs through signalling at a level that is not a true indicator of their quality, they will persist side by side with honest signallers (Maynard Smith & Harper 1988), deriving their benefit from the rule previously set up in the minds of receivers of the relationship between signal level and quality. Just as there have to be some genuinely distasteful (honestly signalling) models for Batesian mimicry to persist, so there have to be some genuinely high quality (honestly signalling) individuals for other sorts of less-than-honest signalling to persist. The less-than-honest signal can exist only because honest signallers set up a cost to probing by receivers. Dishonest signalling is therefore only 'permitted' because of receiver probing and is parasitic on honest signals.

Barnard & Burk (1979) argued that dishonest signals may often arise in social hierarchies. Certainly, the reported cases of within-species mimicry lead us to conclude that honesty is not the rule. Gender mimicry has been reported in many groups of animals, particularly where males mimic females to gain copulations (e.g. van den Berghe et al. 1989), but also where females mimic males apparently to avoid sexual harassment (e.g. Robertson 1985). In the threat displays of stomatopods, too, individuals made temporarily vulnerable by moulting use bluff to deter intruders effectively (Adams & Caldwell 1990). Here the stability of dishonesty is maintained because its frequency is constrained by the duration of moulting itself rather than by simple frequency-dependent selection, and because moults and inter-moults are presumably indistinguishable to intruders. Intraspecific brood parasitism involves such effective cheating that only recently has it become clear just how common it is (Davies 1988; Brown & Brown 1989). Dishonest signals are therefore not just stable in theory; they are probably much more widespread in practice than we have yet realized.

THE CORRUPTION OF HONEST SIGNALLING

'Honesty', 'reliability' and 'assessment' are often used interchangeably, resulting in considerable confusion. In this final section of the paper we point out the various ways in which these concepts can be used, allowing us to summarize our arguments more formally.

(1) No signal can be a perfect predictor of the outcome of a fight since even between unequally matched opponents chance factors can affect the result. The same is true of the outcome of mating decisions or any other circumstance in which prediction might be useful. Animals will therefore be forced to rely on assessments or estimates of some quality that may be a useful, but not perfect, predictor of fight outcomes (or whatever is of ultimate interest). If 'honesty' is used to mean a necessary relationship between signal level and perfect information about what the receiver wants to know, then in this sense, no signal is likely ever to be honest.

(2) Some signals, however, could in theory show a necessary and perfect relationship with some quality (e.g. strength, or parasite load) that receivers would settle for assessing. These signals could be described as 'honest' in the sense that they are necessarily and reliably related to something that it is worth predicting.

(3) Yet other signals could be necessarily related to such a quality, but not reliably so. In other words, the correlation between the quality and the signal could be positive but not perfect, because of variation that cannot be controlled. Perhaps no signal is available with the requisite property of perfect correlation with quality (Andersson 1980), but if there is a signal that gives a significantly better than chance correlation, this may be used for assessment. Even if the signal is described as 'honest' to mean that it is uncheatable through being maintained by cost, it may not be entirely reliable. The necessary connection between assessment signals and quality (Maynard Smith & Harper 1988) does not therefore guarantee reliability. Thus, even allowing that no signal is 'honest' in the sense of being a perfect predictor of outcome, it could still be described as 'honest' in at least two senses. 'Honest' could mean a necessary and perfectly reliable indication of a quality that gives the best estimate of outcome (e.g. resource-holding potential), or it could mean a necessary but not entirely reliable indication of such a quality.

(4) We have argued, however, that whether honest signals are thought of as perfectly or only partially reliable, they are likely to be replaced by conventional signals. A conventional signal is one where the relation between quality and signal level is not guaranteed and where its effect is derived at least partly through the receivers generalizing from full assessment of similar signals in the past. The receiver learns from past experience and does not pay the full costs of assessment at every encounter. Once the receiver stops paying the full costs of assessment, then cheats (signallers that give a signal at a level not necessarily commensurate with their quality) can arise. The system will become a conventional signalling system, because the necessary connection between signal and quality has been lost. Receivers can, however, retaliate in evolutionary terms by probing and imposing at least some costs on cheats when they are discovered. The system is unlikely to become cheat-proof (i.e. revert to honest assessment) as long as conventional signalling and probing gives receivers, on average, more benefits than paying the full costs of assessment. As probing is also costly to receivers and will therefore place a limit on the 'punishment' cheats have to face, it is likely that cheats will persist through not paying the full cost of their level of signalling (Maynard Smith & Harper 1988). As we have already pointed out, a signalling system with cheating will persist only as long as there are enough honest signallers around to set up a cost to probing by receivers. It might therefore be conceivable to call a conventional system 'honest' since on average signals within the system are worth paying attention to. But this would trivialize the concept of 'honesty' since it could then be used to describe a system in which cheating and mimicry were rife.

(5) Conventional signals will be stable even in the face of cheating as long as the costs of cheating rise if cheating gets too common. This may occur if (1), the cost of being probed (that is, fully assessed by the occasional receiver who does not always or does not yet trust the convention) is much greater for cheats than for those who signal at the level appropriate to their quality, and (2), the benefits of probing increase as the frequency of cheats increases. The exact level of cheating tolerated by a signalling system, that is how far its honesty is corrupted, will therefore depend on (1), the costs of full assessment relative to the costs of reading the convention and (2), the benefits of full assessment relative to trusting the convention. Whether full assessment or conventional signalling is favoured will in turn depend on two factors: (1) the value of any extra information that can be obtained by assessment but not by receiving the conventional signal; this value will incorporate the probability that extra new information will be obtained by assessment and also the cost of being duped by a cheat; and (2) the frequency of cheats, which will in turn be related to the probing costs that receivers are prepared to pay.

CONCLUSIONS

Whichever sense of 'honesty' we use (except the trivial sense 4 above), the costs that receivers have to pay in accurately interpreting 'honest' signals constitute a selective pressure towards the use of conventional rather than assessment signals as defined by Maynard Smith & Harper (1988). These costs, together with the possible scarcity of necessary signal correlates of quality (Andersson 1980) mean that truly honest, costly signals (i.e. handicaps) will not be widespread. Just as overt fighting is comparatively rare (though it does occur), costly signalling should also be rare.

We conclude that honest signalling systems, wherever they occur, are always prone to corruption by the insidious effects of receiver costs, and will be replaced by conventional signalling systems which are susceptible to cheating. Contrary to the expectations of recent theorists, dishonest signals will be widespread.

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REFERENCES

Adams, E. S. & Caldwell, R. L. 1990. Deceptive communication in asymmetric fights of the stomatopod crustacean *Gonadodactylus bredini*. *Anim. Behav.*, **39**, 706–717.

Alatalo, R. V., Carlson, A. & Lundberg A. 1988. The search cost in mate choice of the pied flycatcher. *Anim. Behav.*, **36**, 289–291.

Andersson, M. 1980. Why are there so many threat displays? *J. theor. Biol.*, **86**, 773–781.

Baker, M. C., Bjerke, T. K., Lampe, H. & Epsmark, Y. 1986. Sexual response of female great tits to variation in size of males' song repertoires. *Am. Nat.*, **128**, 491–498.

Balph, M. H., Balph, D. F. & Romesburg, H. C. 1979. Social status signalling in winter-flocking birds: an examination of a current hypothesis. *Auk*, **96**, 78–93.

Barnard, C. J. & Burk, T. 1979. Dominance hierarchies and the evolution of 'individual recognition'. *J. theor. Biol.*, **81**, 65–73.

Beacham, J. L. & Newman, J. A. 1987. Social experience and the formation of dominance relationships in the pumpkinseed sunfish, *Lepomis gibbosus*. *Anim. Behav.*, **35**, 1560–1562.

van den Berghe, E. P., Wernerus, F. & Warner, R. R. 1989. Female choice and the mating cost of peripheral males. *Anim. Behav.*, **38**, 875–884.

Bradshaw, R. H. 1990. Investigations into the formation and maintenance of dominance hierarchies and the role of individual recognition in the laying hen. D.Phil. thesis, University of Oxford.

Brodsky, L. M., Ankey, C. D. & Dennis, D. G. 1988. The influence of male dominance on social interactions in black ducks and mallards. *Anim. Behav.*, **36**, 1371–1378.

Brown, C. R. & Brown, M. B. 1989. Behavioural dynamics of intraspecific brood parasitism in colonial cliff swallows. *Anim. Behav.*, **37**, 777–796.

Burk, T. 1988. Acoustic signals, arms races and the costs of honest signalling. *Fla Entomol.*, **71**, 400–409.

Cade, W. H. 1975. Acoustically orienting parasitoids: fly phonotaxis to cricket song. *Science*, **190**, 1312–1313.

Catchpole, C. K. 1980. Sexual selection and the evolution of complex songs among European warblers of the genus *Acrocephalus*. *Behaviour*, **74**, 149–166.

Catchpole, C. K. 1987. Bird song, sexual selection, and female choice. *Trends Ecol. Evol.*, **2**, 94–97.

Clutton-Brock, T. H. & S. D. Albon. 1979. The roaring of red deer and the evolution of honest advertisement. *Behaviour*, **69**, 145–170.

Clutton-Brock, T. H., Albon, S. D., Gibson, R. M. & Guinness, F. E. 1979. The logical stag: adaptive aspects of fighting in red deer (*Cervus elaphus* L.). *Anim. Behav.*, **27**, 211–225.

Clutton-Brock, T. H., Guinness, F. E. & Albon, S. D. 1982. *Red Deer: Behavior and Ecology of Two Sexes*. Chicago: University of Chicago Press.

Davies, N. B. 1988. Dumping eggs on conspecifics. *Nature, Lond.*, **331**, 19.

Davies, N. B. & Brooke, M. de L. 1988. Cuckoos versus reed warblers: adaptations and counteradaptations. *Anim. Behav.*, **36**, 262–284.

Davies, N. B. & Brooke, M. de L. 1989. An experimental study of co-evolution between the cuckoo, *Cuculus canorus*, and its hosts. I. Host egg discrimination. *J. Anim. Ecol.*, **58**, 207–224.

Dawkins, M. S. 1986. *Unravelling Animal Behaviour*. Harlow: Longman.

Dawkins, R. 1989. *The Selfish Gene*. 2nd edn. Oxford: Oxford University Press.

Edmunds, M. E. 1974. *Defence in Animals: a Survey of Anti-predator Defences*. Burnt Mill: Longman.

Engelhard, G., Foster, S. P. & Day, T. H. 1989. Genetic differences in mating success and female choice in seaweed flies (*Coelopa frigida*). *Heredity*, **62**, 123–131.

Enquist, M. & Leimar, O. 1983. Evolution of fighting behaviour: decision rules and assessment of relative strength. *J. theor. Biol.*, **102**, 387–410.

Gibson, R. M. & Bradbury, J. W. 1985. Sexual selection in lekking sage grouse: phenotypic correlates of male mating success. *Behav. Ecol. Sociobiol.*, **18**, 117–123.

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

Grafen, A. 1990b. Sexual selection unhandicapped by the Fisher process. *J. theor. Biol.* **144**, 475–516.

Guilford, T. C. 1988. The evolution of conspicuous coloration. *Am. Nat.*, **131**, S7–S21.

Guilford, T. C. 1990. The evolution of aposematism. In: *Insect Defenses: Adaptive Mechanisms and Strategies of Prey and Predators* (Ed. by J. O. Schmidt & D. L. Evans), pp. 23–61. New York: State University of New York Press.

Guilford, T. C. & Dawkins, M. S. In press. Receiver psychology and the evolution of animal signals. *Anim. Behav.*

Guhl, A. M. 1968. Socialisation and social stability in chickens. *Anim. Behav.*, **16**, 219–232.

Hedrich, A. V. 1986. Female preference for male calling bout duration in a field cricket. *Behav. Ecol. Sociobiol.*, **19**, 73–77.

Huntingford, F. & Turner, A. 1987. *Animal Conflict*. London: Chapman & Hall.

Kodric-Brown, A. & Brown, J. H. 1984. Truth in advertising: the kinds of traits favoured by sexual selection. *Am. Nat.*, **124**, 309–323.

Komers, P. E. & Dhindsa, M. S. 1989. Influence of dominance and age on mate choice in black-billed magpies: an experimental study. *Anim. Behav.*, **37**, 645–655.

Krebs, J. R. & Dawkins, R. 1984. Animal signals: mind-reading and manipulation. In: *Behavioural Ecology. An Evolutionary Approach* (Ed. by J. R. Krebs & N. B. Davies), pp. 380–402. Oxford: Blackwell Scientific Publications.

Losey, G. S., Jr, Stanton, F. G., Telecky, T. M. & Tyler, W. A. 1986. Copying others, an evolutionarily stable strategy for mate choice: a model. *Am. Nat.*, **128**, 653–664.

McComb, K. 1987. Roaring by red deer stags advances the date of oestrous in hinds. *Nature, Lond.*, **330**, 648–649.

Maynard Smith, J. 1982. *Evolution and the Theory of Games*. Oxford: Oxford University Press.

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

Maynard Smith, J. & Price, G. R. 1973. The logic of animal conflict. *Nature, Lond.*, **246**, 15–18.

Møller, A. P. 1987. Social control of deception among status signalling house sparrows *Passer domesticus*. *Behav. Ecol. Sociobiol.*, **20**, 307–311.

Nilsson, J. A. 1989. Establishment of juvenile marsh tits in winter flocks: an experimental study. *Anim. Behav.*, **38,** 586–595.

Parker, G. 1984. Evolutionarily stable strategies. In: *Behavioural Ecology. An Evolutionary Approach* (Ed. by J. R. Krebs & N. B. Davies), pp. 30–61. Oxford: Blackwell Scientific Publications.

Pearce, J. M. 1987. *An Introduction to Animal Cognition.* Hove: Lawrence Erlbaum.

Petrie, M. 1988. Intraspecific variation in structures that display competitive ability: large animals invest relatively more. *Anim. Behav.*, **36,** 1174–1179.

Pomiankowski, A. N. 1987. The costs of choice in sexual selection. *J. theor. Biol.*, **128,** 195–218.

Ratner, S. C. 1961. Effects of learning to be submissive on status in the peck order of domestic fowl. *Anim. Behav.*, **9,** 34–37.

Robertson, H. M. 1985. Female dimorphism and mating behaviour in a damselfly, *Ischnura ramburi:* females mimicking males. *Anim. Behav.*, **33,** 805–809.

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

Rohwer, S. & Rohwer, F. C. 1978. Status signalling in Harris' sparrows: experimental deceptions achieved. *Anim. Behav.*, **26,** 1012–1022.

Roper, T. J. 1986. Badges of status in avian societies. *New Scient.*, **109,** 38–41.

Ryan, M. J. 1985. *The Tungara Frog: a Study in Sexual Selection and Communication.* Chicago: University of Chicago Press.

Ryan, M. J. 1988. Energy, calling, and selection. *Am. Zool.*, **28,** 885–898.

Searcy, W. A. & Andersson, M. 1986. Sexual selection and the evolution of song. *A. Rev. Ecol. Syst.*, **17,** 507–533.

Shannon, C. E. & Weaver, W. 1949. *The Mathematical Theory of Communication.* Urbana: University of Illinois Press.

Shawcross, J. E. & Slater, P. J. B. 1984. Agonistic experience and individual recognition in male *Quelea quelea. Behav. Proc.*, **9,** 49–60.

Slater, P. J. B. 1983. The study of communication. In: *Animal Behaviour. Vol. 2. Communication* (Ed. by T. R. Halliday & P. J. B. Slater), pp. 9–42. Oxford: Blackwell Scientific Publications.

Smith, W. J. 1977. *The Behaviour of Communicating: an Ethological Approach.* Cambridge, Massachusetts: Harvard University Press.

Thouless, C. R. & Guinness, F. E. 1986. Conflict between red deer hinds: the winner always wins. *Anim. Behav.*, **34,** 1166–1171.

Vehrencamp, S. L., Bradbury, J. W. & Gibson, R. M. 1989. The energetic cost of display in the male sage grouse. *Anim. Behav.*, **38,** 885–896.

Whitfield, D. P. 1987. Plumage, variability, status signalling and individual recognition in avian flocks. *Trends Ecol. Evol.*, **2,** 13–18.

Wilson, J. 1989. The functions of agonistic interactions, social dominance and display in a winter population of the great tit, *Parus major* L. Ph.D. thesis, University of Edinburgh.

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

Zahavi, A. 1987. The theory of signal selection and some of its implications. In: *International Symposium of Biological Evolution* (Ed. by V. P. Delfino), pp. 305–327. Bari: Adriatic Editrice.