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Multiple Displays in Animal Communication:`Backup Signals' and `Multiple Messages'

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Phil. Trans. R. Soc. Lond. B 1996 **351**, 329-338
doi: 10.1098/rstb.1996.0026

Multiple displays in animal communication: 'backup signals' and 'multiple messages'

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SUMMARY

Why are animal displays so complex? In contexts ranging from courtship and mating to parent-offspring communication to predator deterrence, biological signals often involve a number of different visual, auditory and/or olfactory components. Previous models of communication have tended to ignore this complexity, assuming that only one kind of display is available. Here, a new game-theoretical model of signalling is described, in which signallers may use more than one display to advertise their qualities. Additional displays may serve to enhance the accuracy with which receivers assess a single quality (the 'backup signal' hypothesis), or to provide information about different qualities (the 'multiple message' hypothesis). Multiple signals are shown to be stable, even when multiple receiver preferences entail significant costs, provided that signalling costs are strongly accelerating. In such cases, signallers bias their investment towards more efficient forms of signal, but not to the exclusion of other display types. When costs are not strongly accelerating, by contrast, individual signallers employ only a single display at equilibrium. If different signals provide information about different qualities, however, then the equilibrium may feature alternative signalling strategies, with signallers who excel in one quality employing one kind of display, and those who excel in another quality employing another kind.

1. INTRODUCTION

Why are biological displays so complex? In contexts ranging from courtship and mating (Møller & Pomiankowski 1993; Johnstone 1995*a*) to parent-offspring communication (e.g. Redondo & Castro 1992) to predator deterrence (Edmunds 1974), animals often use displays that involve a number of different visual, auditory and/or olfactory components. Female red jungle fowl (*Gallus gallus*), for example, are influenced in their choice of mate by a suite of male traits, including comb size and colour, eye colour and tail feather length (Zuk *et al.* 1990, 1992). Magpie nestlings solicit food with a begging display that comprises both vocal and postural elements (Redondo & Castro 1992). As a final example, the arctiid moth *Rhodogastria leucoptera* exhibits a defensive display involving both visual and olfactory elements, in which it raises its wings to expose its red abdomen and simultaneously exudes a smelly yellow froth from glands on the thorax (Edmunds 1974).

Several competing hypotheses have been proposed to explain the evolution of complex displays, including the 'backup signal' hypothesis (multiple signals allow more accurate assessment of a single aspect of the signaller's condition), and the 'multiple message' hypothesis (different signals convey information about different aspects of the signaller's condition). However, despite the recent growth of interest in signal evolution, few attempts have been made to evaluate these hypotheses. Models of signalling, for example, have generally assumed that only a single kind of display is available to signallers (Grafen 1990; Godfray 1991; Maynard Smith 1991; Johnstone & Grafen 1992*a*; Hutchinson *et al.* 1993; Vega-Redondo & Hasson 1993), and have rarely addressed the issue of complex, multi-component displays (see Schluter & Price 1993; Iwasa & Pomiankowski 1995; Johnstone 1995*b*, for exceptions). The question of why animal displays involve multiple components thus remains unresolved.

Here, I describe a game-theoretical model of signalling (based on earlier analyses by Johnstone & Grafen 1992*b*; Grafen & Johnstone 1993; Johnstone 1994), in which signallers may employ multiple displays to advertise their quality. Receivers in the model are prone to errors of discrimination, so that additional displays may serve as 'backup signals' to enhance the accuracy of assessment. Furthermore, because signallers may vary in more than one quality, multiple displays can also function as 'multiple messages' by providing information about different qualities.

Iwasa & Pomiankowski (1995) have shown that the costs of female choice can have an important influence on the evolution of multiple sexual displays. Consequently, this model incorporates costly choice, with receivers sampling signallers sequentially (at some cost to themselves), and attempting to select a high quality individual from among those encountered. Although applicable to many instances of quality advertisement, the model will be described in terms of mate choice, with signallers referred to as passive mates, and receivers as active mates (Real 1990).

2. A MODEL OF MULTIDIMENSIONAL SIGNALLING DURING MATE CHOICE

1. Discrimination is restricted to one sex, members of which may mate only once and are referred to as active mates. Members of the opposite sex, who may mate any number of times, are referred to as passive mates.

2. Active mates search among potential passive mates, who vary in one or more qualities (for the sake of simplicity, I assume there are either one or two qualities, though the analysis could easily be extended to consider a larger range). These qualities are represented by an n-dimensional vector $\boldsymbol{q} = (q_1, \dots, q_n)$. I assume that the components of this vector are independent, discrete random variables, adopting values evenly spaced between 0 to 1, with frequency distribution $f(q_i)$. Various choices of f have been explored, but the results presented below are based on the bell-shaped distribution shown in figure 1. Other distributions yield qualitatively similar results.

3. Mate quality cannot be directly observed; instead, passive mates advertise their qualities to active mates, employing signals of varying levels of intensity. Again, to avoid unnecessary complication, I assume that there are only two distinct signal dimensions. The advertising levels of a passive mate will be denoted a_1 and a_2. I assume that a_1 and a_2 are discrete variables, adopting values evenly spaced between 0 and $a_{\max}$. The functions $A_1(\boldsymbol{q})$ and $A_2(\boldsymbol{q})$, which together will be referred to as the advertising or signalling strategy, specify the levels of advertising used by a signaller of true qualities $\boldsymbol{q}$ (these functions are initially unknown, and are determined from the evolutionarily stable strategy (ESS) conditions).

4. Active mates cannot assess the advertising levels of a passive mate with perfect accuracy; they are prone to errors of discrimination. The perceived advertising levels of a passive mate will be denoted p_1 and p_2. I assume that p_1 and p_2 are independent, discrete random variables, adopting values evenly spaced between $p_{\min}$ and $p_{\max}$. The probability that a passive mate is perceived as advertising at level p_i in signal dimension i when actually advertising at level a_i is given by the function $P_i(p_i;\, a_i)$. Various choices of P have been explored, but the results presented below are based on a quartic function defined as follows

$$P_i(p_i;\, a_i) = \frac{\left(\dfrac{p_i - a_i}{\alpha_i}\right)^4 - 2\left(\dfrac{p_i - a_i}{\alpha_i}\right)^2 + 1}{\sum\limits_{p'} P(p';a_i)},$$

$$a_i - \alpha_i < p_i < a_i + \alpha_i \quad (1)$$

$$P_i(p_i;\, a_i) = 0,\ p_i \leqslant a_i - \alpha_i,\ p_i \geqslant a_i + \alpha_i$$

which is shown in figure 2. This error distribution is symmetrical, with mean equal to the true advertising level, a_i, and satisfies condition (3*b*) of Johnstone & Grafen (1992*b*), which requires that the higher the true advertising level of a signaller, the more likely he is to be perceived as advertising strongly (other error distributions that share these properties yield qualitatively similar results). The half-width of the function, and hence the degree of error, is given by the parameter α_i.

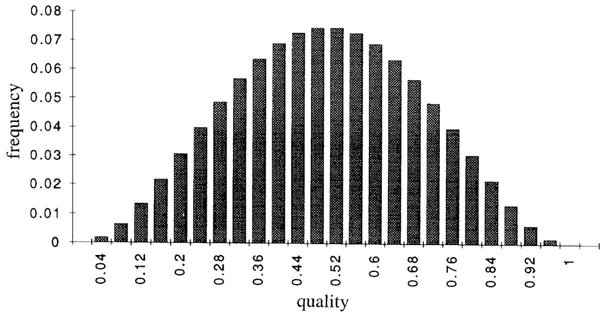

Figure 1. Probability distribution of passive mate qualities (for the case where there are 25 discrete categories).

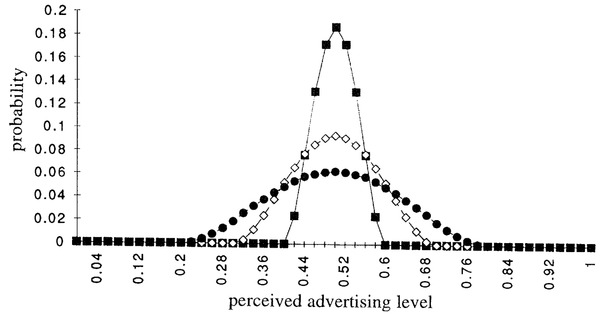

Figure 2. Probability that a passive mate is perceived as advertising at a given level in signal dimension i when actually advertising at a level of 0.5 in that dimension, for a range of different values of α_i. The three curves are for values $\alpha_i = 0.1$ (filled squares), $\alpha_i = 0.2$ (open diamonds) and $\alpha_i = 0.3$ (filled circles).

5. While searching, an active mate encounters passive mates one at a time, at random, and must decide in each case whether to mate or to continue searching. This decision is made on the basis of the potential partner's pair of perceived advertising levels. A choice strategy therefore consists of a set M of pairs of perceived advertising levels that will elicit mating. The set is initially unknown but, like the male advertising strategy, is determined from the ESS conditions. The fitness gain from mating depends on the qualities of the passive mate chosen, as specified by the function $V(\boldsymbol{q})$, while searching for and locating a new potential partner incurs a fitness cost c. For the case $n = 1$, where passive mates vary in only one quality, the fitness gain from mating is simply equal to this quality; for $n > 1$, two different functions V were explored:

$$V(\mathbf{q}) = (1/n)\sum_{i=1}^{n} q_i$$

$$V(\mathbf{q}) = \sqrt[n]{\prod_{i=1}^{n} q_i}.$$

In the former case, the fitness value of a passive mate is equal to the arithmetic mean of its qualities, in the latter case to the geometric mean. No recall of previously encountered passive mates is possible, and there is no fixed limit to the number of passive mates that may be sampled (see Real 1990 for analysis of a similar sequential search model, with direct assessment of quality rather than signalling).

6. The fitness of a passive mate in the context of the model depends on its qualities and its levels of advertising, and on its expected mating success, s. It will be denoted $U(a_1,a_2,\boldsymbol{q},s)$. Various choices are made for U, but they all take the form

$$U(a_1,a_2,\boldsymbol{q},s). = s - g_1(a_1,\boldsymbol{q}) - g_2(a_2,\boldsymbol{q}) \quad (2)$$

where g_1 and g_2 are functions satisfying the requirements for the existence of a one-dimensional signalling equilibrium when there is no error (Grafen 1990). The assumption is thus made that the cost of each signal is independent of the level of the other.

3. THE SOLUTION PROCEDURE

An equilibrium solution to the model comprises a signalling strategy and a choice strategy, such that the signalling strategy maximizes passive mate fitness given the choice strategy, while the choice strategy maximizes active mate fitness given the signalling strategy. For each set of parameters investigated, equilibria were found using an iterative procedure (similar to that described by Johnstone 1994): beginning with an initial signalling strategy, $A_1(\boldsymbol{q})_0$, $A_2(\boldsymbol{q})_0$, the choice strategy M_0 that represents the best reply is found using the methods described in Appendix 1. The optimum signalling strategy in a population adopting both this choice strategy and the initial signalling strategy is then obtained using the methods described in Appendix 2. This optimum signalling strategy, denoted $A_1(\boldsymbol{q})_{0r}$, $A_2(\boldsymbol{q})_{0r}$, together with the initial signalling strategy, $A_1(\boldsymbol{q})_0$, $A_2(\boldsymbol{q})_0$, is used to calculate a new strategy, $A_1(\boldsymbol{q})_1$, $A_2(\boldsymbol{q})_1$, where

$$A_1(\boldsymbol{q})_1 = (1-\lambda)A_1(\boldsymbol{q})_0 + \lambda A_1(\boldsymbol{q})_{0r},$$
$$A_2(\boldsymbol{q})_1 = (1-\lambda)A_2(\boldsymbol{q})_0 + \lambda A_2(\boldsymbol{q})_{0r}.$$

This procedure is then repeated to generate $A_1(\boldsymbol{q})_2$ and $A_2(\boldsymbol{q})_2$, $A_1(\boldsymbol{q})_3$ and $A_2(\boldsymbol{q})_3$ and so on, until convergence. The value of λ, although never greater than 1, is adjusted according to the form of the convergence; λ is increased if convergence is directional and decreased if it is oscillating. If convergence is slow, the solution procedure can first be performed using a coarse grid of strategies, with only a few discrete qualities and signal intensities, and this equilibrium used as a starting point for a higher resolution application. The whole iterative process is carried out in this way a number of times, starting from a different initial strategy in each case, in order to locate all possible equilibria. The results described below were obtained by starting from initial strategies of the form $A_i(\boldsymbol{q}) = xq_i^y$, using several different values for x and y.

In some cases, particularly at lower resolutions, the use of a discrete model to approximate a continuous one may prevent the solution procedure from converging to a unique equilibrium. It may instead settle down to indefinite oscillation between two closely similar strategies, in which the advertising levels specified for signallers of certain qualities differ by a single step. Alternatively, two closely similar equilibria may be found, again differing by a single step for signallers of certain qualities. Increasing the resolution with regard to advertising level may lead to a unique solution in such cases, as it provides a closer approximation to a continuous model and allows these signallers to adopt an intermediate level. However, because an increase in the resolution of the analysis entails an increase in the amount of computation required, it has proven impossible to locate unique equilibria for some sets of parameter values. Consequently, where the solution procedure oscillates between two closely similar strategies (or two closely similar equilibria were found), the average of the two is given as the solution.

4. RESULTS

In this section, I describe the range of signalling equilibria obtained for various sets of parameter values. I first consider one-dimensional and multi-dimensional signalling equilibria for the case in which there is a single quality ($n = 1$), assuming that the signalling cost functions $g_i(a_i,q)$ take the form

$$g_i(a_i,q) = a_i^m/k_i q$$

with the values of k_1, k_2 and m varying from one example to another. In this case, multiple signals (if they are used) serve to enhance the accuracy of assessment of a single quality (the 'backup signal' hypothesis). I then move on to consider the case in which there are two qualities ($n = 2$), assuming that the signalling cost functions $g_i(a_i,\boldsymbol{q})$ take the form

$$g_i(a_i,\boldsymbol{q}) = a_i^m/k_i q_i,$$

i.e. that the cost of the first signal depends only on the first quality, and the cost of the second signal depends only on the second quality. In this case, multiple signals can potentially provide information about different qualities (the 'multiple message' hypothesis', see Johnstone 1995*b*). For both situations, k_1 and k_2 determine the efficiency of each signalling dimension, with a high value of k_i indicating that signal i is relatively efficient and cheap to produce, whereas m determines whether costs increase linearly with signal strength, or at an accelerating or decelerating rate.

In all cases, advertising levels increase in increments of 0.025 from 0 to a_{max}, which is always much greater than the maximum advertising level employed (so that the equilibrium obtained does not depend on the particular value used). Quality increases in increments of 0.04 when $n = 1$, and in increments of 0.05 or 0.125 when $n = 2$ (doubling the number of qualities necessitates a lowering of resolution in order to keep the amount of computation within feasible limits). The half-widths of both error functions, α_1 and α_2, are fixed at a value of 0.5. Varying signalling costs (the values of k_1 and k_2), however, has an equivalent effect to varying the degree of error; the results obtained depend on the cost required to produce a noticeable difference in advertising level, which is determined by both parameters together.

(a) One-dimensional signalling equilibria

I begin by describing the range of one-dimensional equilibrium signalling rules (those in which only one signal is used) that were found, when passive mates

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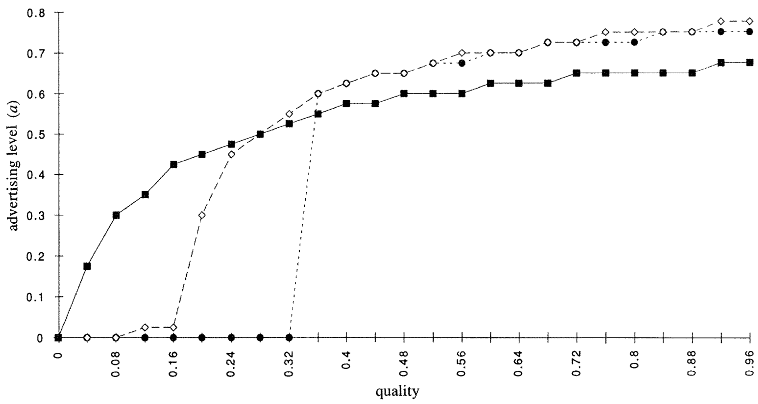

Figure 3. One-dimensional equilibrium signalling strategies (with a single quality) for different values of m (which determines whether signalling costs increase at an accelerating rate, and if so, how strongly). Other parameter values are $c = 0.05$, $k = 1.5$, $\alpha = 0.5$. The three curves are for values $m = 1$ (filled circles), $m = 2$ (open diamonds), $m = 3$ (filled squares).

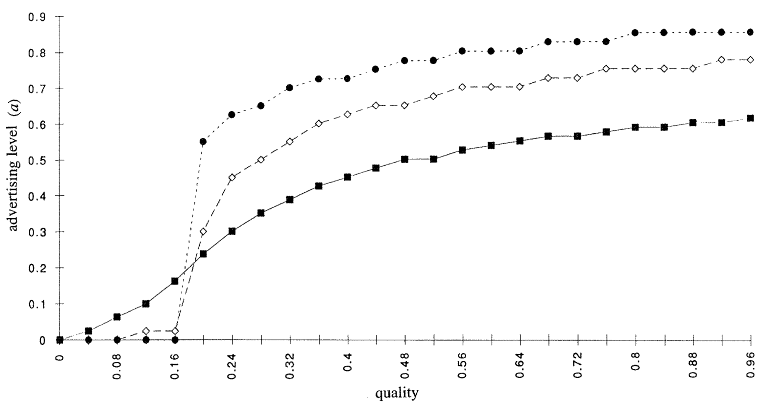

Figure 4. One-dimensional equilibrium signalling strategies (with a single quality) for different values of k , which determines the magnitude of signalling costs. A high value of k indicates an efficient, relatively low-cost signal. Other parameter values are $c = 0.05$, $m = 2$, $\alpha = 0.5$. The three curves are for values $k = 1$ (filled squares), $k = 1.5$ (open diamonds), $k = 2.5$ (filled circles).

vary in a single quality. Such equilibria were obtained for a wide range of parameter values, even where the width of the error distribution is substantially greater than the range of advertising levels used, so that even the best and the worst signallers cannot be clearly distinguished.

Figure 3 shows three such rules for different values of m(other parameter values being specified in the figure legend). The results are similar to those of Grafen & Johnstone (1993) and Johnstone (1994) in that when advertising costs are not strongly accelerating (for the cases $m = 1$ and $m = 2$ in the figure) the equilibria feature discontinuities, with signallers below a threshold quality failing to advertise at all, whereas those above advertise at a level significantly above zero. Moreover, as Johnstone (1994) found, strongly accelerating costs tend to 'smooth out' such discontinuities; the transition from the 'initial flat' to higher advertising levels is less abrupt when $m = 2$ than when $m = 1$, and for the case $m = 3$, advertising level increases smoothly with quality. This effect, however, is reduced when advertising costs are low: figure 4 shows three equilibrium signalling rules when $m = 2$, for different values of k, and reveals that the discontinuity is more marked with lower signalling costs (note that a high value of k indicates an efficient, low cost signal).

The major difference between the results of this model and those of Johnstone (1994) is that only a single equilibrium was found for each set of parameter values, even in those cases where the equilibrium featured a sharp discontinuity. By contrast, the latter study found multiple equilibria in such cases, differing in the proportion of signallers that advertised at a level above zero (with higher advertising levels among this group when the proportion was smaller). This difference appears to result from the incorporation of a concrete model of receiver choice in this study: the proportion of passive mates advertising at levels above zero now depends on the cost of choice to active mates. Figure 5 shows three equilibrium signalling rules for different values of c (when $m = 2$), and demonstrates that a reduction in choice costs leads to a reduction in the proportion of signallers advertising at levels above zero, an increase in advertising levels among this group, and a more marked discontinuity following the 'initial flat'.

(*b*) *Backup signals*

I now turn to the possibility of multi-dimensional signalling equilibria (those in which both signals are used) when passive mates vary in a single quality. Here

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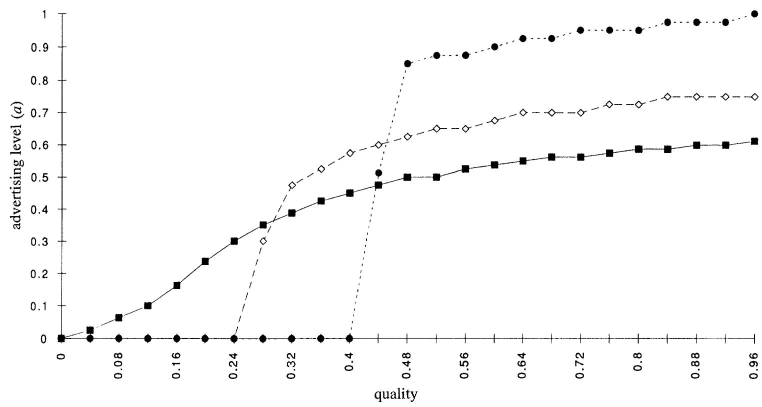

Figure 5. One-dimensional equilibrium signalling strategies (with a single quality) for different values of c (which determines the cost of choice to active mates). Other parameter values are $k = 1$, $m = 2$, $\alpha = 0.5$. The three curves are for values $c = 0.05$ (filled squares); $c = 0.03$ (open diamonds), $c = 0.015$ (filled circles).

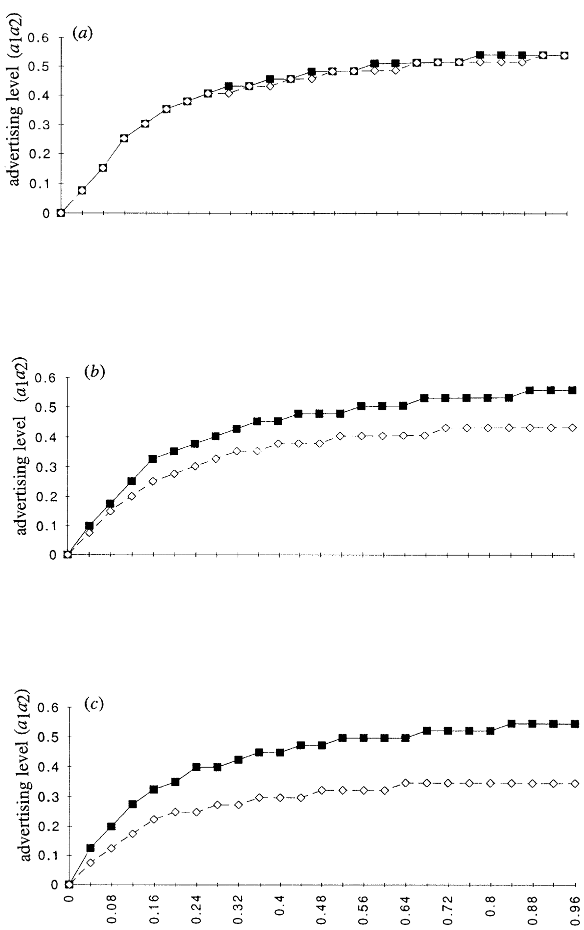

Figure 6. Two-dimensional equilibrium signalling strategies (with a single quality) for: (*a*) $k_2 = 1$; (*b*) $k_2 = 0.75$; (*c*) $k_2 = 0.6$. Other parameter values are $k_1 = 1$, $c = 0.05$, $m = 3$, $\alpha_1 = \alpha_2 = 0.5$. In each case filled squares denote a_1; open diamonds denote a_2.

again, the value of m, which determines whether or not signal costs are strongly accelerating, has a major influence on the results obtained. For high values of m (greater than approximately 1.8 for the parameter values given in figure 6), multiple signal equilibria were found, in which investment was biased towards the more efficient signal dimension, but not to the exclusion of the other. Figure 6 shows three equilibrium signalling rules for different values of k_2 but a constant value of k_1. As the cost of the second signal increases (i.e. as k_2 decreases), signallers invest less in that signal dimension and more in the other, but both signals continue to be used. For lower values of m, by contrast, no multiple signal equilibria were obtained, even when the cost of both signals was the same. The iterative solution procedure, starting from a wide range of different initial signalling strategies, always led to a one-dimensional signalling equilibrium (or to a non-signalling equilibrium).

Where multiple signal equilibria were found, the relation between quality and each signal was similar to that for one-dimensional equilibria, though lower advertising levels were adopted when both signals were employed. Figure 7 shows one-dimensional signalling equilibria compared with multiple signal equilibria (in which both signal dimensions are equally costly, i.e. $k = k_1 = k_2$) for three different values of k, and reveals that the drop in advertising levels resulting from the use of multiple signals is greater when signal costs are lower.

(*c*) *Multiple messages*

Finally, I consider the possibility of multiple signal equilibria when passive mates vary in two qualities, and the cost of each signal depends on a different quality. Once again, for high values of m (i.e. for strongly accelerating signal costs) multiple signal equilibria were found in which individual signallers employed both signal types. Figure 8 shows a stable signalling rule of this kind, for the case in which the fitness value of a passive mate equals the geometric mean of its qualities. The figure reveals that at equilibrium, the level of each signal is influenced by both qualities, even though the cost of each depends on only one quality (see Johnstone 1995 *b*). This result also holds for the case in which the fitness value of a passive mate equals the arithmetic mean of its qualities.

In contrast to the above, for low values of m, signallers possessing a given set of qualities use only a single display type at equilibrium. However, different signallers may use different display types, i.e. the equilibrium features alternative signalling strategies.

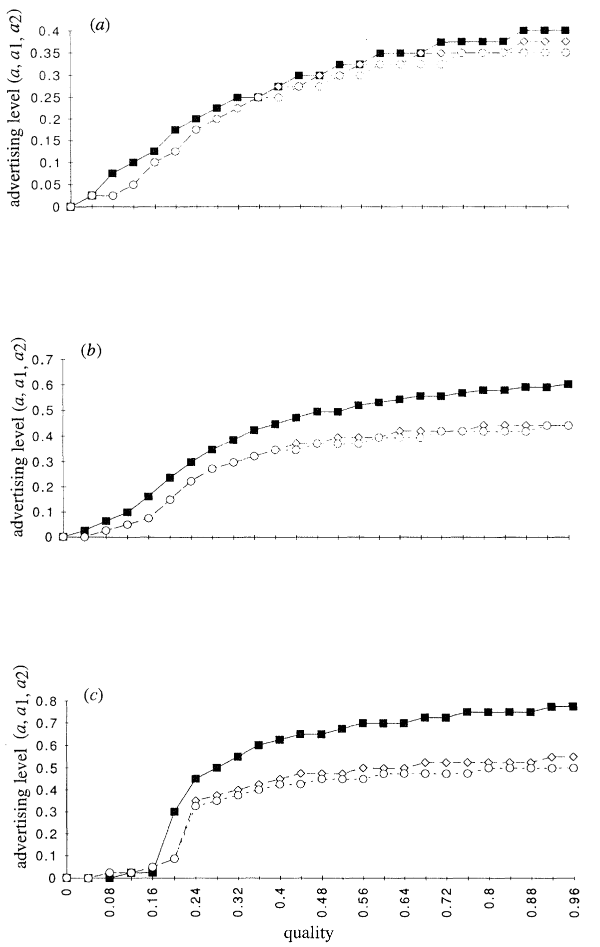

Figure 7. One- and two-dimensional equilibrium signalling strategies (with a single quality) for: (*a*) $k = k_1 = k_2 = 0.75$; (*b*) $k = k_1 = k_2 = 1$; (*c*) $k = k_1 = k_2 = 1.5$. Other parameter values are $c = 0.05$, $m = 3$, $\alpha = \alpha_1 = \alpha_2 = 0.5$. In each case filled squares denote a; open circles denote a_1 and a_2.

These results hold whether the fitness value of a passive mate is equal to the arithmetic or the geometric mean of its qualities. Figure 9 shows a stable signalling rule of this sort (when fitness value equals the geometric mean quality), in which passive mates who excel in the first quality employ only the first display type, whereas those who excel in the second quality employ only the second display type (individuals that excel in both qualities also employ only one or the other, depending on which of their qualities is greater). As the figure reveals, low values of m also lead to sharp discontinuities in the signalling strategy (as was the case with only a single quality), with many passive mates failing to signal at all, but those individuals who do signal displaying an advertising level significantly above zero.

5. DISCUSSION

(*a*) *Single signals*

Models of signalling have shown that honest, costly advertisement of quality can be stable (Grafen 1990; Godfray 1991), even when receiver assessment of signals is imperfect (Johnstone & Grafen 1992*b*; Johnstone 1994). Previous models of error-prone signalling have, however, concentrated on the evaluative element of the response to signals, ignoring the way in which the receiver chooses to use the information acquired (Johnstone & Grafen 1992*b*; Johnstone 1994). Selection is simply assumed to favour accurate assessment without specifying precisely why. This approach allows one to draw general conclusions about information transfer in many different signalling contexts (Grafen 1990), but it overlooks a potentially important aspect of communication. The analysis described above, by contrast, incorporates a concrete model of receiver behaviour, with active mates sampling signallers sequentially (at some cost to themselves), and attempting to select a high quality individual from among those encountered.

The incorporation of costly choice does not eliminate the possibility of stable signalling, but it does appear to restrict the range of signalling equilibria. Johnstone (1994) found that under error-prone conditions, many different equilibria were possible for a single set of parameter values. These equilibria all featured discrete groups of non-advertising and strongly advertising signallers (when signalling costs were not strongly accelerating), but ranged from those in which only the very best signallers advertised at a very high level, to those in which a large proportion of signallers advertised at a lower level. Here, only one equilibrium was found for each set of parameter values, the proportion of signallers advertising at a level above zero depending on the costs of choice to active mates.

The reason for this difference is that the benefits to be gained from display in this model are fixed by the costs of choice. In the earlier, evaluative model (Johnstone 1994), a signal that was used by only the very best signallers indicated a very high quality and thus yielded large benefits, but a signal used by a larger proportion of signallers indicated a lower mean quality, and consequently yielded smaller benefits. Both high cost/high benefit equilibria (with a few signallers advertising at a high level) and low cost/low benefit equilibria (with more signallers advertising at a lower level) were possible for a single set of parameter values. In this model, however, active mates will accept any partner attributed a quality above some critical threshold that is determined by the costs of choice (a general prediction of sequential choice models, see e.g. Real 1990). Consequently, a signal used by a smaller proportion of signallers need not bring larger benefits than one more widely employed, if both indicate sufficient quality to elicit mating. Only a single equilibrium is therefore possible for a given set of parameter values, with the proportion of signallers advertising at levels above zero dependent on the acceptance threshold of active mates, and hence on the costs of choice.

(*b*) *Multiple signals*

Although the possibility of one-dimensional signalling equilibria is now well established (see above), the stability of multiple signals has received much less attention. This analysis suggests that multi-dimensional signalling equilibria, in which individual signallers employ more than one display, do exist in cases

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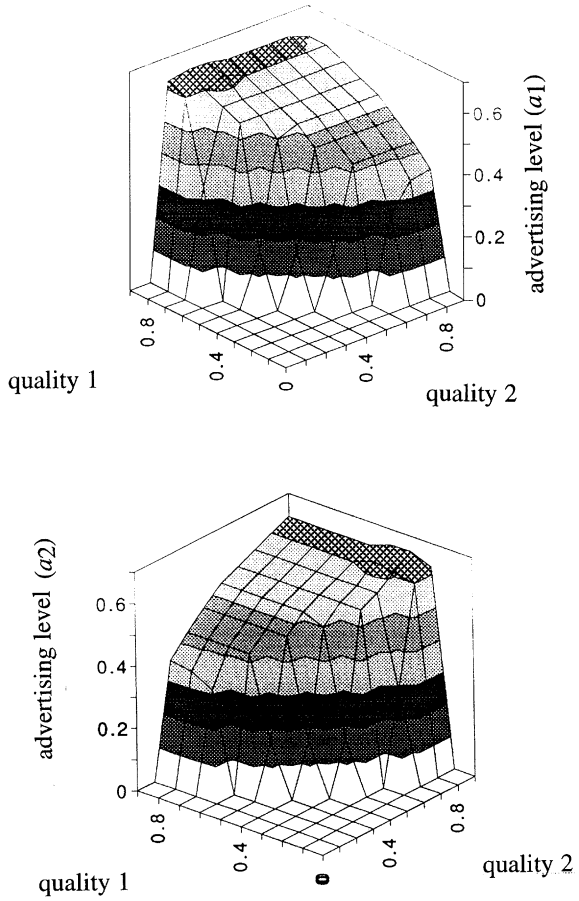

Figure 8. Two-dimensional equilibrium signalling strategy with two qualities (and the cost of each signal dependent on a different quality), when signalling costs are strongly accelerating. Parameter values are $c = 0.05$, $k_1 = k_2 = 1$, $m = 3.5$, $\alpha_1 = \alpha_2 = 0.5$, $V(\boldsymbol{q}) = n\sqrt{\prod_{i=1}^{n} q_i}$.

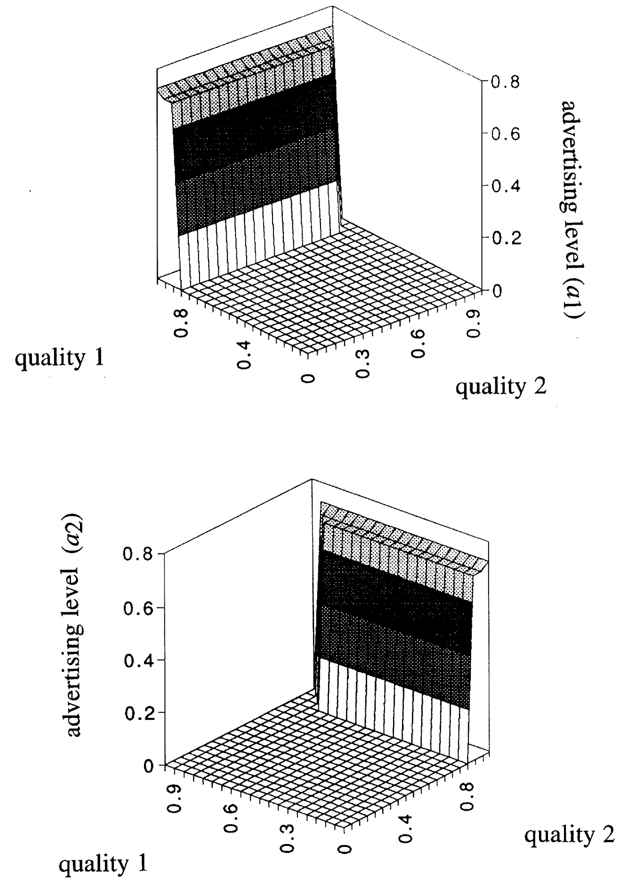

Figure 9. Two-dimensional equilibrium signalling strategy with two qualities (and the cost of each signal dependent on a different quality), when signalling costs are not strongly accelerating. Parameter values are $c = 0.05$, $k_1 = k_2 = 1$, $m = 1$, $\alpha_1 = \alpha_2 = 0.5$, $V(\boldsymbol{q}) = n\sqrt{\prod_{i=1}^{n} q_i}$.

where signalling costs are strongly accelerating. Under other circumstances, however, the use of multiple signals is not likely to be stable. This general result holds whether individual displays provide information about the same or different qualities. In the latter case, however, one-dimensional equilibria may feature alternative signalling strategies, with different signallers employing different display types.

Strongly accelerating costs favour the use of multiple displays because they make it more difficult for high-quality signallers to distinguish themselves from inferior individuals within a single signalling dimension. Raising the level of one display component becomes more and more costly, so that it pays to 'spread the load' over a number of signal types. By contrast, when signal costs are not strongly accelerating, there is no pressure of this sort. Increased investment in one signal dimension at the expense of others is reinforced by stronger preferences in receivers, because any increase in the range of advertising levels employed makes a signal more informative, and hence a better guide to quality. The end result is that only one, highly exaggerated signal will be preferred at equilibrium.

It is interesting to compare the above findings with those of the few previous theoretical studies of multiple signal use. Schluter & Price (1993) and Iwasa & Pomiankowski (1995) have both analysed quantitative genetic models of sexual selection in which females may evolve mating preferences for multiple sexual ornaments. The former study suggested that with two male traits to choose from, females should prefer the one with greater honesty × detectability, and ignore the second. Multiple displays, in other words, were predicted to be unstable except under the unlikely circumstances that all were equally effective indicators of condition. The latter study, which considered a wider range of cost functions for female preference, suggested that multiple preferences (and multiple ornaments) could be stable if there were negative interactions between choice costs, so that the overall cost of choice was not greatly increased by a female using additional male traits in her assessment of potential partners. Where joint costs were high, however, this model also predicted that honest advertisement using multiple signals would not be stable (although it has been shown that multiple sexual ornaments can evolve under these circumstances via Fisherian runaway evolution: see Heisler 1985; Tomlinson & O'Donald 1989; Pomiankowski & Iwasa 1993).

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(*c*) *Backup signals versus multiple messages*

A major difference between this model and previous analyses of multidimensional signalling is that it considers the case in which signallers may differ in more than one quality, and different signals may thus provide different kinds of information: the 'multiple message' hypothesis. The results suggest, however, that although the backup signal and multiple message hypotheses have been presented as alternative explanations for the evolution of multiple displays (Møller & Pomiankowski 1993; Johnstone 1995*b*), it may, in fact, be hard to distinguish between the two. At a multiple signal equilibrium, even where the cost of each particular signal depends on a different quality, there need no one-to-one relation between individual qualities and the level of individual signals. A given signal, in other words, may reflect many different qualities, and a given quality may influence numerous different signals. Such multivalent relations arise because an active mate's decision as to whether or not she will accept a potential partner is based on assessment of all his perceived advertising levels. Consequently, the benefit to be gained by advertising strongly in one dimension depends on whether the signaller can also afford to advertise strongly in other dimensions as well (see Johnstone 1995*b*).

The only circumstances under which different signals are likely to provide information about different aspects of quality are those in which active mates express idiosyncratic preferences, e.g. for complementary genes (Wedekind 1992, 1994*a*,*b*). Under these circumstances, an active mate needs to obtain information about each of a potential partner's various attributes in order to determine how well they complement her own. However, although a signalling system of this kind may be possible (see e.g. Wedekind 1992), it seems likely that in most cases, a high quality will be desirable to all passive mates, as assumed in this model. Consequently, we should not be surprised to find that there is considerable overlap in the information conveyed by different aspects of male sexual displays in nature (for examples, see Johnstone 1995*a*).

Even if the 'multiple message' hypothesis is problematic, however, allowing for multiple qualities in signalling models can shed new light on the process of signal change over evolutionary time. Schluter & Price (1993) have previously pointed out that where multiple signals are unstable, the handicap principle provides a possible explanation for population divergence in display (and hence, perhaps, for speciation). Small environmental differences can change the relative detectability of two display types, and hence trigger a switch in use between populations. The present study provides additional support for this idea, as it shows that where the cost of different displays are influenced by different qualities, alternative signalling strategies may emerge even within a single population. Moreover, a change in the relative importance of different qualities to females, or in the extent of variation in different qualities, could also drive a change in display use.

(*d*) *Empirical applications*

The first problem in testing the predictions of this or any other model of multiple signal evolution is to identify those displays that involve several distinct components. This is not as simple a task as it might seem, since signals that appear distinct to a human observer may not be distinguished by their intended receivers. For example, Clark & Uetz (1993) have shown that although male jumping spiders of the species *Maevia inclemens* exhibit extreme dimorphism, with the two male morphs differing in both appearance and courtship behaviour, they present females with images that are almost identical in height and visual target area. Although females do possess two distinct male recognition templates, some of the most strikingly different aspects of the male courtship displays thus give rise to similar images. Equally, receivers may respond to several, independently varying aspects of what appears to human observers as a single display. The preference of female swallows (*Hirundo rustica*) for both tail length and tail symmetry in males (Møller 1994) provides a good example.

Having identified those displays that do involve multiple components, one can attempt to determine the benefits receivers gain by responding to them. In the context of sexual display, it will be of particular interest to determine whether multiple sexual ornaments provide useful information about male quality, or whether preferences for them are arbitrary. As discussed above, Iwasa & Pomiankowski (1995) suggest that multiple sex traits are more likely than single ornaments to be arbitrary products of Fisherian runaway evolution. Moreover, even though the Fisher process cannot be invoked in signalling contexts other than mate choice, other variants of the 'unreliable signal' hypothesis can be advanced. For example, multiple displays could have evolved to exploit pre-existing sensory biases in receivers (Ryan 1990; Ryan & Rand 1993).

At present, there is insufficient evidence to resolve this issue: Møller & Pomiankowski (1993), in a comparison of avian taxa with and without apparent multiple feather ornaments, found that ornament size was significantly negatively correlated with asymmetry in the latter but not in the former, and interpreted this as evidence that single ornaments are expressed in a condition-dependent manner whereas multiple ornaments are not. However, although these results provide some support for the 'unreliable signal' hypothesis, evidence based on correlations between measures of quality and display can be problematic (see Johnstone 1995*a*). Furthermore, a number of studies of individual multiply-ornamented species suggest that their sex traits do reflect condition. For example, female pheasants (*Phasianus colchicus*) show preferences for male spur length, which is related to age, condition and viability (Koubek & Hrabe 1984; von Schantz *et al.* 1989; Goransson *et al.* 1990; Wittzell 1991), and for display activity, which has been experimentally linked to parasite load (Hillgarth 1990; Johnstone 1995*a* lists other examples of this kind). More studies of multiple sexual displays are therefore necessary.

The other major issue to be resolved is what factors favour the evolution of multiple over single displays, or vice versa. This model suggests that multiple displays will only be stable where signalling costs are strongly accelerating. It would therefore be of great interest to investigate the costs incurred by display in multiply ornamented (and in singly ornamented) species. At present, there is insufficient evidence to test the model's prediction because few experimental studies have been able to assess the costs of display (see Evans & Thomas 1992; Møller & de Lope 1995 for exceptions).

(*e*) *Further modelling possibilities*

There are many aspects of multiple signal use that remain to be explored, although this model could easily be modified to address some of these issues. First, there is the possibility of idiosyncratic preferences, and their consequences for signal evolution (Wedekind 1992, 1994). As mentioned above, it seems likely that such preferences will favour the evolution of multiple signals that each provide information about a different quality, but it remains to be seen under what conditions such a signalling system can be stable. It would also be interesting to look at constraints on preference, for instance by imposing a fixed time limit on the period of female choice. Second, it may often be the case that the level of one display component influences the costs of another, a possibility that is not considered in this model. Evans (1993), for example, suggests that the asymmetry of a bird's tail will influence the cost to the bearer of tail elongation, acting as a phenotypic 'tax' that enforces honest advertisement. Third, it is also possible that one display component influences the ease with which another can be assessed, or facilitates direct assessment of quality, i.e. acts as an 'amplifier' (Hasson 1989; 1991). Both this and the previous possibility could have significant consequences for multiple signal evolution, which remain to be examined.

I thank Andrew Pomiankowski, Lisa Thomas, James Deutsch and two anonymous referees for helpful comments and discussion. This work was carried out during tenure of a Junior Research Fellowship at St. Catharine's College, Cambridge.

APPENDIX 1

Each step of the iterative solution procedure described above in the main text requires the calculation of a choice strategy that is the optimal response to a given signalling strategy. This calculation is carried out using the techniques of stochastic dynamic programming (Houston *et al.* 1988; Mangel & Clark 1988; Mangel & Ludwig 1992).

Let $V(t,p_1,p_2)$ denote the expected future fitness gain of an active mate who, having previously rejected t - 1 potential partners, has just encountered a passive mate with perceived advertising levels p_1 and p_2. If we assume that each active mate can assess no more than some large number T of passive mates, then we can easily determine $V(T,p_1,p_2)$, the expected future fitness gain of an active mate who has just encountered its T^{th} and final potential partner, because the optimum decision for such an individual is always to mate. This value is simply equal to the expected quality of the passive mate, which can be calculated from its perceived advertising levels, in conjunction with the signalling strategy $A(q)$, the distribution of passive mate qualities $f(q)$, and the error function $P(p;a)$

$$V(T,p_1,p_2) = \mathrm{E}(q\,|\,p_1,p_2) = \frac{\sum_q q f(q)\, P[p_1 A_1(q)]\, P[p_2;A_2(q)]}{\sum_{q'} f(q')\, P[p_1;A_1(q')]\, P[p_2;A_2(q')]}. \tag{3}$$

At earlier stages of searching, expected future fitness gain is given by

$$V(t,p_1,p_2) = \mathrm{Max}\Big\{\mathrm{E}(q\,|\,p_1,p_2), \tag{4}$$
$$\frac{\sum_q\sum_{p_1}\sum_{p_2} f(q)\, P[p_1;A_1(q)]\, P[p_2;A_2(q)]\, V(t+1,p_1,p_2)}{\sum_{q'}\sum_{p'_1}\sum_{p'_2} f(q')\, P[p'_1;A_1(q)]\, P[p'_2;A_2(q)]} - c\Big\}$$

which is the expected fitness obtained by maximizing over the two possible actions available. The first term in the above expression represents the fitness consequences of mating, the second the fitness consequences of continuing to search.

Equation (4) can be solved numerically using a backwards optimization procedure. A fitness matrix is first created by filling in at $t = T$, for each possible pair of values p_1 and p_2, the fitness obtained from equation (3). This matrix is then used to determine, again for each pair of values p_1 and p_2, the fitness consequences of each possible action at the previous search step, and hence both the optimal decision and the expected future fitness gain at that stage and state. The same procedure is repeated for the previous search step, and so on until convergence on a steady choice strategy. This strategy represents the optimum choice policy with an infinite time horizon, and is independent of T.

APPENDIX 2

Each step of the iterative solution procedure described above in the main text also requires the calculation of the signalling strategy that is optimal in a population adopting a given choice strategy and a given signalling strategy. This is achieved simply by calculating, for each value of q, the fitness consequences of adopting each possible pair of advertising levels a_1 and a_2, and selecting those values that yield the highest fitness.

The fitness consequences, for a particular value of q, of adopting a particular pair of advertising levels a_1 and a_2, can be obtained from equation (2) provided that the expected mating success s obtained by advertising at those levels is known. The value of s (assuming a 1:1 population sex ratio) is given by

$$s = \frac{\sum_{(p_1,p_2)\in M} P(p_1;a_1)\, P(p_2;a_2)}{\sum_q f(q) \sum_{(p'_1,p'_2)\in M} P[p'_1;A_1(q)]\, P[p'_2;A_2(q)]}$$

where $A_1(q)$ and $A_2(q)$ represent the population-wide signalling strategy, and M the population-wide choice strategy (i.e. the set of pairs of perceived advertising levels that elicit mating). This expression simply represents the probability that a female will accept a male advertising at levels a_1 and a_2, divided by the mean acceptance probability for all males in the population.

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(*Received 3 July 1995; accepted 24 August 1995*)

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