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Mathematical details of the models

We consider individuals’ division of resources between a signaling trait and their own survival, or viability (after Holman 2012). Signalers vary in quality q ($0 \leq q \leq 1$), which could be any trait that is of interest to receivers but that cannot be observed directly. We assume that receivers attempt to judge quality by measuring a focal individual’s signal size s ($0 \leq s \leq 1$) relative to the mean signal \bar{s} in the rest of the population (excluding the focal individual). On the other hand, by producing a large signal, an individual also reduces its survival probability, given by $t(s, q) = 1 - s^{1+kq}$. Crucially, a given signal size may be equally costly for individuals of any quality ($k = 0$), or it may be differentially costly for low-quality individuals ($k > 0$; Fig. S1).

We first determine the optimal strategy for varying signal size with individual quality. This is the strategy that maximizes individual fitness (w , lifetime reproductive output), which we measure as the product of the individual’s relative signal size and its survival probability: $w = (s / \bar{s}) \cdot t(s, q)$. To find the optimal, quality-dependent signal size $s^*(q)$, we differentiate fitness with respect to signal size and evaluate at the population mean signal size. Solving $(dw / ds)|_{s=\bar{s}=s^*} = 0$ gives

$$s^*(q) = (2 + kq)^{\frac{-1}{1+kq}} \quad (\text{A1})$$

(plotted in figure 1a of the main text), and we have checked that this strategy does in fact represent a local fitness maximum. Consistent with previous models, Eqn. A1 shows that quality dependence in the optimal signal size ($ds^*/dq > 0$) requires that signaling is differentially costly for low-quality individuals ($k > 0$). In contrast, when there is no differential cost of signaling ($k = 0$), the model predicts that all signalers will express $s^* = 1/2$, irrespective of quality. In reality, given that signals no longer reflect quality at this point, we expect that receivers will ignore the signal trait, and so it may eventually be lost altogether.

Our main objective is to extend the optimal signaling model to include a simple mechanism for honest signaling that is consistent with the index hypothesis. Specifically, we suppose that an individual’s signal size is a function of two traits:

$$s(x, c) = x(1 - (1 - q)\exp^{-1/c}), \quad (\text{A2})$$

where x represents the maximum signal size that an individual is able to produce (the ‘signaling strategy’), and c imposes a causal, linear relationship between quality and signal size (‘quality dependence’; Fig. S2). Unlike the optimal signaling model, we do not suppose that individuals can vary their expression of x and c in response to quality. Instead, we assume that natural selection acts on genetic variation for both x and c , and our aim is to find

the joint evolutionarily stable strategy (ESS) x^*, c^* that best fits the distribution of signaler qualities in the population.

To model natural selection in this scenario, we explicitly assume a simple genetic basis for signal size. We assume that the signaling strategy and quality dependence are coded by alleles at a single locus and that there is no genetic correlation between the traits. Furthermore, we consider the fitness of a focal individual that carries mutant alleles for the traits x_m, c_m in an otherwise monomorphic population of individuals expressing x, c . The population mean signal size (excluding the focal individual) is therefore $\bar{s} = s(x, c)$, and the fitness of the focal mutant is

$$w(x_m, c_m, x, c) = \frac{s(x_m, c_m)}{s(x, c)} t(x_m, c_m, q), \quad (\text{A3})$$

where survival probability t is the same quality-dependent function given above. Under the assumption that mutant alleles differ only slightly from the resident population, the direction of selection for each trait is given by the following selection gradients:

$$\left. \frac{\partial w}{\partial x_m} \right|_{\substack{x_m=x=\hat{x} \\ c_m=c=\hat{c}}} \quad \text{and} \quad \left. \frac{\partial w}{\partial c_m} \right|_{\substack{x_m=x=\hat{x} \\ c_m=c=\hat{c}}}, \quad (\text{A4})$$

where \hat{x}, \hat{c} is the candidate ESS, defined as the point at which both selection gradients are equal to zero. To illustrate the evolutionary dynamics of the signalling strategy and quality dependence over time (as in figure 2 of the main text), we multiplied the selection gradients by the rate constants v_x and v_c (for the signalling strategy and quality dependence, respectively). We have also checked that equilibrium of the system is independent of these rates.

To analyze the joint evolution of the signalling strategy and quality dependence, we specify a simple distribution of individual qualities in the population. Specifically, in the main text, we consider a population with signallers that are either low or high quality ($q = 0$ or 1), each with probability $1/2$. In this case, the candidate ESS is:

$$\hat{x} = (k + 2)^{\frac{-1}{1+k}} \quad \hat{c} = 1 / \text{Log} \left[\frac{2}{2 - (2 + k)^{\frac{1}{1+k}}} \right] \quad (\text{A5})$$

(plotted in figure 2 of the main text). We have checked that this joint equilibrium is locally convergence stable, meaning that a nearby population will evolve toward the equilibrium (e.g., Christiansen 1991), and that it is indeed a local ESS that maximizes individual fitness. Substituting the equilibria from Eqn. A5 into Eqn. A2 gives the realized signal size at the ESS x^*, c^* (plotted in figure 1 of the main text).

More generally, we conjecture that when the distribution of individual qualities is more complex, the joint ESS x^*, c^* will be an approximation of the optimal strategy. As an

example, we numerically solved for the candidate ESS in a population with three possible levels of individual quality ($q = 0, 1/2, \text{ or } 1$, each with probability $1/3$). This is plotted in figure S3, which shows that when there is a differential cost of signalling ($k = 5$) the candidate ESS is indeed an approximation to the optimal strategy.

References

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Grafen, A. 1990. Biological signals as handicaps. *Journal of Theoretical Biology* 144:517–546.

Holman, L. 2012. Costs and constraints conspire to produce honest signaling: insights from an ant queen pheromone. *Evolution* 66:2094–2105.

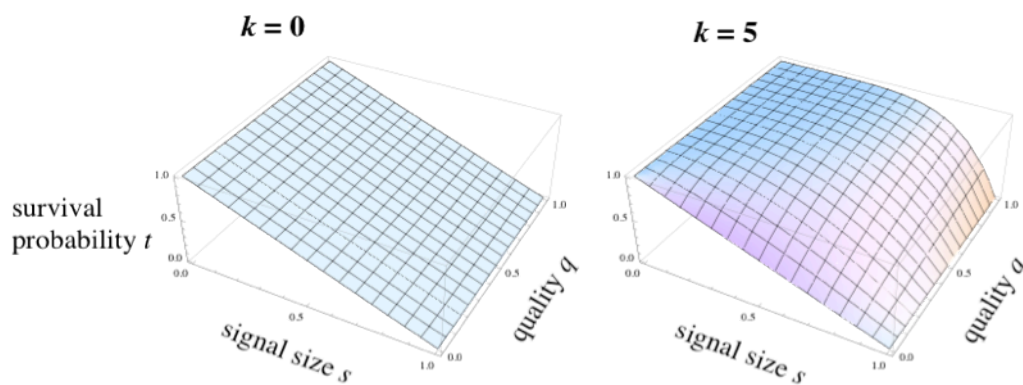


Figure S1. The effect of increasing the differential cost of signaling k on the survival probability of the signaler.

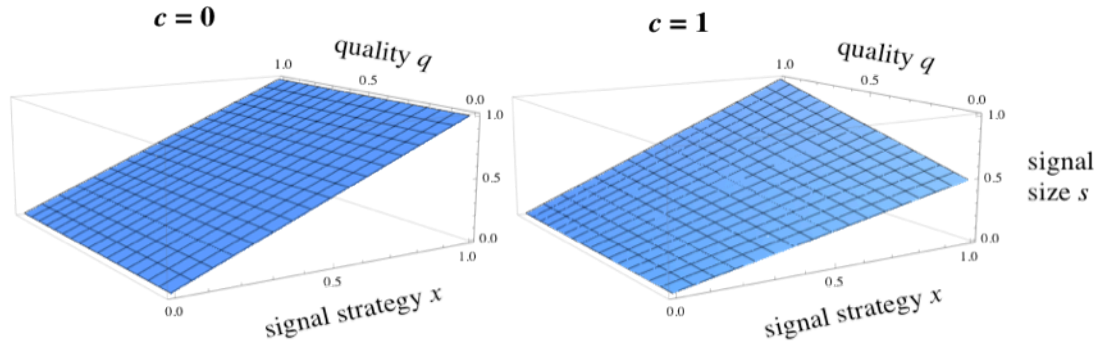


Figure S2. The effect of increasing quality dependence c on the realized signal size of an individual of quality q , expressing a given signaling strategy x .

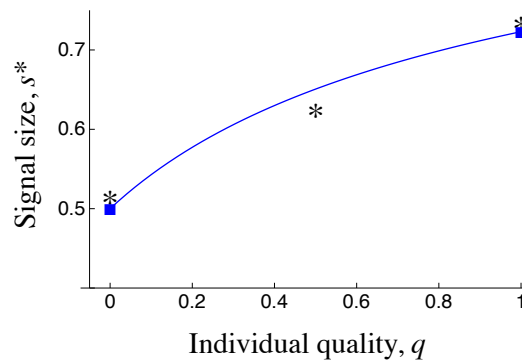


Figure S3. The optimal quality-dependent signal size (blue line) and the outcome of the joint evolution of signal size and quality dependence. Blue squares indicate the realized signal size in a population with two possible qualities ($q = 0$ or 1 ; replicated from figure 1a of the main text). Black asterisks indicate the realized signal size in a population with three possible qualities ($q = 0, 1/2, \text{ or } 1$). In all cases, the differential cost of signaling is $k = 5$, as in figure 1 of the main text.