

A general signalling theory: why honest signals are explained by trade-offs rather than costs or handicaps

Szabolcs Számadó^{1,2}, István Zachar^{3,4}, Dustin J. Penn⁵

¹Department of Sociology and Communication, Budapest University of Technology and Economics, Budapest, Hungary

²CSS-RECENS Research Group, ELTE Centre for Social Science, Budapest, Hungary

³Institute of Evolution, HUN-REN Centre for Ecological Research, Budapest, Hungary

⁴Department of Plant Systematics, Ecology and Theoretical Biology, Eötvös Loránd University, Budapest, Hungary

⁵Department of Interdisciplinary Life Sciences, Konrad Lorenz Institute of Ethology, University of Veterinary Medicine, Vienna, Austria

Handling editor: Max Reuter, Associate editor: Stephen Montgomery

Corresponding author: Szabolcs Számadó, Department of Sociology and Communication, Budapest University of Technology and Economics, Budapest, H-1111, Hungary. Email: szamado.szabolcs@tk.mta.hu

Abstract

Honest signals have long posed a challenge for evolutionary biologists to explain. Here, we propose a general Darwinian theory of signalling, signalling trade-off theory, to explain both honest and dishonest signalling based on recent theoretical and empirical developments. The leading explanation for honest signalling has been the handicap principle (HP), which argues that signals are honest because they are costly. We summarize the main reasons why the HP—and the related costly signalling paradigm—can be fully rejected. Instead, we propose an alternative and more general explanation for honest signalling. The acceptance of the erroneous HP was based on misinterpretations of early signalling models. These models contrary to common interpretations, show that signals are honest, not because they are costly (handicaps), but because cheating (deception) is costly. Deception is costly due to differential signalling costs or differential benefits, or more generally differential trade-offs (i.e., an antagonistic constraint between two functions). Trade-offs are the basis evolutionary life-history theory, and we argue that they are also central to explaining signal honesty and deception. Unlike costs, trade-offs can fully represent both aspects of an investment (marginal cost vs. marginal benefit) over different timescales arising in evolutionary analyses. We examine the alternative explanations proposed to explain honest signalling, such as indices and social punishment, and show that these hypotheses require trade-offs, despite being overlooked. We examine more recent theoretical models that demonstrate that signalling trade-offs maintain honesty, even without signalling costs (handicaps) at the evolutionary equilibrium. Moreover, we show that differential trade-offs are both necessary and sufficient to explain honest signals in cases with conflict of interest. Based on these advances, we argue that differential signalling trade-offs provide a general evolutionary explanation for both dishonest and honest signals and also unify earlier alternative proposals about signal honesty. Finally, we demonstrate that short-term investments under trade-offs at the proximate level (once considered handicap mechanisms) can result in long-term fitness benefits, which thus integrates proximate and evolutionary explanations for signal honesty. We also address how results from sexual selection studies (e.g., terminal investment) are consistent with our theory.

Keywords: animal communication, honest signalling, deception, life-history trade-offs, signalling trade-offs, costly signalling theory

Introduction

“No advantages in this world are pure and unmixed”
(Hume, 1758 p. 81)

Honest communication has puzzled scientists and laymen for centuries. Signals provide information that mediates social and sexual interactions (Maynard Smith & Harper, 1995, 2003; Searcy & Nowicki, 2006). However, signals can be unreliable and even deceptive, especially when there are conflicts of interest between senders and receivers (Brown et al., 2012; Casewell et al., 2017; Christy & Rittschof, 2011; Dalziel & Welbergen, 2016; DePaulo et al., 1996; Fischbacher & Föllmi-Heusi, 2013; Fujisawa et al., 2020; Wang et al., 2017). Signals provide information, but their function is to influence and persuade receivers rather than to inform per se (Dawkins & Krebs, 1978). Dishonest signals, it might seem, will spread and eventually become ignored, and then communication would

break down. Yet contrary to what is often suggested, signals need not be honest—not even on average—to be maintained (Számadó, 2000, 2008, 2017). So, how to explain the evolution of animal communication and why some signals are honest whereas others are dishonest?

Our main goals here are to summarize the problems with the conventional theory for honest signalling [handicap principle (HP)/costly signalling theory (Grafen, 1990; Zahavi, 1975)] and propose an alternative theoretical framework to explain both honest and dishonest signals [signalling trade-off theory (STOT)]. First, we summarize the main criticisms of the HP (Zahavi, 1975), the dominant theoretical paradigm for honest signalling, and we summarize the main reasons why this idea is erroneous and should be fully rejected (Penn & Számadó, 2020). Second, we explain why so-called “costly signalling” models (Godfray, 1991; Grafen, 1990) have provided valuable insights but have been mislabelled, misclassified,

Received January 24, 2025; revised October 12, 2025; accepted November 14, 2025

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and misinterpreted as supporting the HP (Penn & Számadó, 2020). Third, we argue that a new theoretical framework is needed to replace the handicap/costly signalling paradigm and one that is more general and can explain honest and dishonest signals—which have been ignored for too long. Fourth, we show that signalling models can be re-interpreted and subsumed with the general theoretical framework of evolutionary life-history theory, which is based on trade-offs—not just costs—at proximate and ultimate levels. We examine the differences between costs versus trade-offs and how trade-offs, unlike costs, are essential for explaining honesty under conflicts of interest. Moreover, we propose that signalling trade-offs provide a causal connection necessary to integrate signalling mechanisms at the proximate level and their adaptive functions. Finally, we show how trade-offs (or their lack) can potentially explain deception as well as honesty and provide predictions that can be tested. For terminology, especially terms in bold, see Glossary.

The handicap principle

“In order to be effective, signals have to be reliable; in order to be reliable, signals have to be costly” (Zahavi & Zahavi, 1997 p. XIV)

The **handicap hypothesis** has a complicated and confusing history, especially since several variations have been proposed, and each has a variety of interpretations (reviewed in Penn & Számadó, 2020). Zahavi introduced the term “handicap” as a metaphor for sexual displays that are costly and “obviously deleterious to the survival of the individual” (Zahavi, 1975, p. 211). To explain how apparently costly signals such as a peacock’s extravagant train evolve, he argued that they are selectively favoured not despite of their costs (or viability trade-offs), as Darwin proposed, but *because* they are costly. Their costs, Zahavi argued, function to demonstrate their reliability. Peacocks, he suggested “handicap themselves” with costly sexual signals to demonstrate their high quality to peahens (Zahavi, 1975, p. 206). Thus, the handicap hypothesis predicts that signals are honest and reliable because they are costly to produce and impose a **fitness** cost on the signaller. Zahavi also argued that signals are wasteful, as well as costly, because “by wasting one proves conclusively that one has enough assets to waste and more. The investment—the waste itself—is just what makes the advertisement reliable” (Zahavi, 1981, 1987; Zahavi & Zahavi, 1997, p. 229). His proposals were initially controversial but generated much interest in honest signalling and sexual selection.

The handicap hypothesis was initially criticized particularly for its upside-down Darwinian logic in which costs (and waste) are beneficial. In reply to critics, Zahavi argued that signals are different from other traits because they evolve under a non-Darwinian process of “signal selection” that favours waste rather than efficiency (Zahavi, 1981, 1987; Zahavi & Zahavi, 1997). He never explained how signal selection works, however. Furthermore, Zahavi maintained that his theory provides a general principle, which he dubbed the HP that explains all forms of communication. Thus, Zahavi made several different, albeit related proposals that became the **Handicap Paradigm** with its own terminology and theoretical framework to interpret models and empirical evidence (Penn & Számadó, 2020).

The HP became widely accepted and highly cited after it was reportedly validated by Grafen’s “strategic handicap” model (Grafen, 1990). In this model, males attract females with sexual signals that honestly reflect their quality due to two critical assumptions: (i) signal expression is condition-dependent and (ii) males in poor condition pay a higher fitness (viability) cost for signalling compared to high-quality males (“differential cost” assumption). Grafen interpreted his model as confirming the HP, including Zahavi’s argument that honesty requires wasteful as well as costly signals. Grafen’s model was generally viewed as placing Zahavi’s HP on “firm mathematical footing” (Hammerstein & Hagen, 2005) and his handicap interpretations and conclusions were widely accepted. The Zahavi-Grafen HP became the most-cited and most common textbook explanation for honest signalling. It was embraced in behavioural ecology (Johnstone, 1997), evolutionary anthropology (Bliege Bird et al., 2001; Hawkes & Bliege Bird, 2002; McAndrew, 2021), evolutionary psychology (Miller, 2011), and it continues to be cited (Krebs & Davies, 2009; Searcy & Nowicki, 2021).

Some authors—though not Zahavi or most others—subsequently changed their definition of the HP to match Grafen’s model, i.e., honesty is due to low-quality signallers paying higher costs than low-quality males [**strategic costs** (Maynard Smith & Harper, 1995, 2003)], while retaining Grafen’s handicap label and interpretations. Other honest signalling models were also interpreted as supporting the HP (Getty, 1998a; Godfray, 1991; Godfray & Johnstone, 2000), despite that differential benefits rather than costs, explain honesty (see below). Together, these models were labelled as the “**theory of costly signalling**” (Maynard Smith & Harper, 1995). Some questioned the logic of the HP, and some raised doubts about the generality of Grafen’s model (Barker et al., 2019; Bergstrom et al., 2002; Getty, 1998a, 1998b, 2006; Grose, 2011; Higham, 2014; Lachmann et al., 2001; Stibbard-Hawkes, 2019; Számadó, 1999, 2000, 2003, 2008, 2011; Számadó & Penn, 2015). Others argued that more empirical tests are needed to test costly signalling models, which were equated to the HP, or they questioned its falsifiability (Grose, 2011; Kotiaho, 2001). Until recently, however, no one ever challenged the handicap interpretations of these models or “costly signalling” theory.

The HP is dead

“There is no grandeur in this view of life, with its endless forms most wasteful and inefficient [...] It is time to usher the handicap principle off to an honourable retirement” (Getty, 2006 p. 87)

We have argued extensively that the Handicap Paradigm can be fully rejected (Penn & Számadó, 2020), and here we briefly summarize three of the main reasons for putting this idea to rest.

Theoretical models refute the HP

Several theoretical models demonstrate that the proposed handicap cost is both unnecessary and insufficient to explain honesty. That is, honest signals need not have realized costs at the evolutionary equilibrium (see **equilibrium cost**), as such costs, even if they exist, cannot maintain honesty (Bergstrom et al., 2002; Hurd, 1995; Lachmann et al., 2001; Számadó, 1999, 2011; Számadó et al., 2023). Therefore, signal costs

paid at the equilibrium, i.e., “handicaps,” are neither necessary nor sufficient to explain honest signalling (Getty, 1998b, 2006) [also see the fallacy of the HP (Számádó, 2011)].

These findings raise the question: how was Grafen’s signalling model (Grafen, 1990) interpreted as confirming the HP? The problem, as it turned out, is that Grafen misinterpreted his own model, as it is not a model of the HP (Penn & Számádó, 2020). He provided three claims to justify his handicap interpretation: (i) Signals are honest because they are costly to produce; (ii) costly signals evolve *because* of rather than *despite* of their costs; and (iii) honest signals require wastefulness. However, none of these assertions were shown, and his interpretation is an over-simplification of the model and a logical error, **affirming the consequent** (Penn & Számádó, 2020; Számádó et al., 2023). Honesty in his model arises due to signals being condition-dependent and having trade-offs in which low-quality signallers incur a higher marginal fitness cost for signalling compared to high-quality signallers (see Figure 1). More precisely, the **marginal cost** for low-quality males for producing a high intensity signal (i.e., deception) is greater than the marginal benefit gained by cheating at the honest equilibrium (Grafen, 1990; Hurd, 1995; Lachmann et al., 2001; Számádó, 1999; Számádó et al., 2023). Unlike the HP, signals in this model are thus efficient rather than wasteful, and honesty evolves because of the marginal cost of deception, not the magnitude of the absolute (realized) fitness cost of signalling at the equilibrium per se (Getty, 1998a, 1998b; Hurd, 1995; Lachmann et al., 2001; Számádó, 1999; Számádó et al., 2023).

Another model (Godfray, 1995) shows that honest signals of quality are also favoured if high-quality signallers obtain more benefits for signalling than low-quality ones (differential benefit assumption) (Getty, 1998a; Godfray, 1991; Godfray & Johnstone, 2000). Yet, remarkably, this model was also misinterpreted as a handicap model and a costly signalling model. Signals are honest in Grafen’s and Godfray’s “costly signalling” models, not because signals are wasteful or costly, but because honesty is beneficial, and deception has higher marginal fitness costs than benefits. Thus, the handicap hypothesis and the more general HP can be rejected on theoretical grounds alone.

The handicap paradigm confounds proximate and ultimate explanations

The predictions of the HP have always been unclear and controversial, as there is no consensus for how signalling costs might enforce honesty or how these predictions should be measured. Beginning with Zahavi (Zahavi, 1975), hormones, energetic demands, and other physiological costs, as well as fitness costs, for producing signals have been proposed to maintain honesty. These proximate mechanisms have often been confused with evolutionary or ultimate explanations of honest signals. Both types of explanations are necessary, but it is crucial to differentiate them. The proximate costs of signalling have been widely assumed to increase the **(ultimate) fitness cost** of signalling (and used as proxies for fitness costs). This assumption has led to fruitless debates over how high the energetic costs of signalling must be to support the HP (Kotiaho, 2001; Searcy & Nowicki, 2006). Signals shown to have metabolic, oxidative, immune, and other proximate costs have been labelled as “handicaps,” resulting in a gamut of various “handicaps,” including immunocompetence handi-

caps, revealing handicaps, vulnerability handicaps, and performance handicaps (Folstad & Karter, 1992; Hurd & Enquist, 2005; Vehrencamp, 2000). Labelling signals as “handicaps” does not explain them, and it gives the false impression that their function has been solved (see **nominal fallacy**).

Proximate investment is necessary for the development of any morphological feature or behaviour, which is selectively favoured for their fitness benefits and not because of the investment per se. Accordingly, any signal costs measured at the proximate level are better labelled as *investments* (Getty, 2006), which may increase their fitness costs, benefits, both, or neither. Signal investment may generate allocation trade-offs at the proximate level, which may or may not influence their fitness costs. A previous version of the HP, the **index signal hypothesis** (Maynard Smith & Harper, 1995, 2003), also confuses proximate versus evolutionary explanations (see below). The HP inspired much research into the metabolic and other proximate costs of signal production and allocation trade-offs, but it also generated much confusion about the differences between levels of explanation. This conceptual confusion is one more reason to reject the HP and the entire Handicap Paradigm (Penn & Számádó, 2020).

Empirical evidence does not support the HP

Despite decades of empirical research, there is no unambiguous evidence for the HP, whereas there are many contradictory (though widely ignored) findings. Part of the problem with empirical studies on honest signalling is due to confusing proximate versus ultimate explanations, as mentioned above. Many examples of signals that are both honest and costly have been found, but such results do not show that signals are honest *because* they are costly, i.e., **correlation is not causation**. There is no evidence that signal costs predict their reliability or that honest signals are wasteful and more costly than they need to be [in terms of fitness cost; i.e., “strategic costs” sensu (Maynard Smith & Harper, 1995, 2003)], as predicted by the HP (Penn & Számádó, 2020; Számádó, 2011). Numerous studies have failed to find support for the predictions of “costly signalling,” including signals used as the flagship examples of the HP (e.g., the peacock’s train (Askew, 2014; Thavarajah et al., 2016), bowerbird bowers (Borgia, 1993, 1996; Guimarães et al., 2017; McCullough & Emlen, 2013), deer antlers (Borgia, 1993, 1996; McCullough & Emlen, 2013), and offspring begging calls (McCarty, 1996) (see Moreno-Rueda, 2006 for review). There have been also an increasing number of findings that directly contradict the HP (see examples in Penn & Számádó, 2020; Számádó, 2011). Andersson’s (Andersson, 1982) classic experiment of manipulating tail lengths of male widow birds, and similar studies, demonstrate that large, conspicuous sexual signals are beneficial investments rather than wasteful handicaps (directly contradicting the predictions of HP), though this interpretation has been completely overlooked. Thus, the empirical evidence is sufficient to reject the handicap hypothesis, as well as the more general HP.

Thus, the HP can be fully rejected, and therefore, the many studies reporting evidence for this idea need to be re-evaluated and reinterpreted (for examples, see Számádó & Penn, 2015, 2018), and alternative explanations considered. Before presenting alternatives, we first summarize our criticisms of “costly signalling” theory. Most authors equate the HP and costly signalling theory [citing (Grafen, 1990; Zahavi,

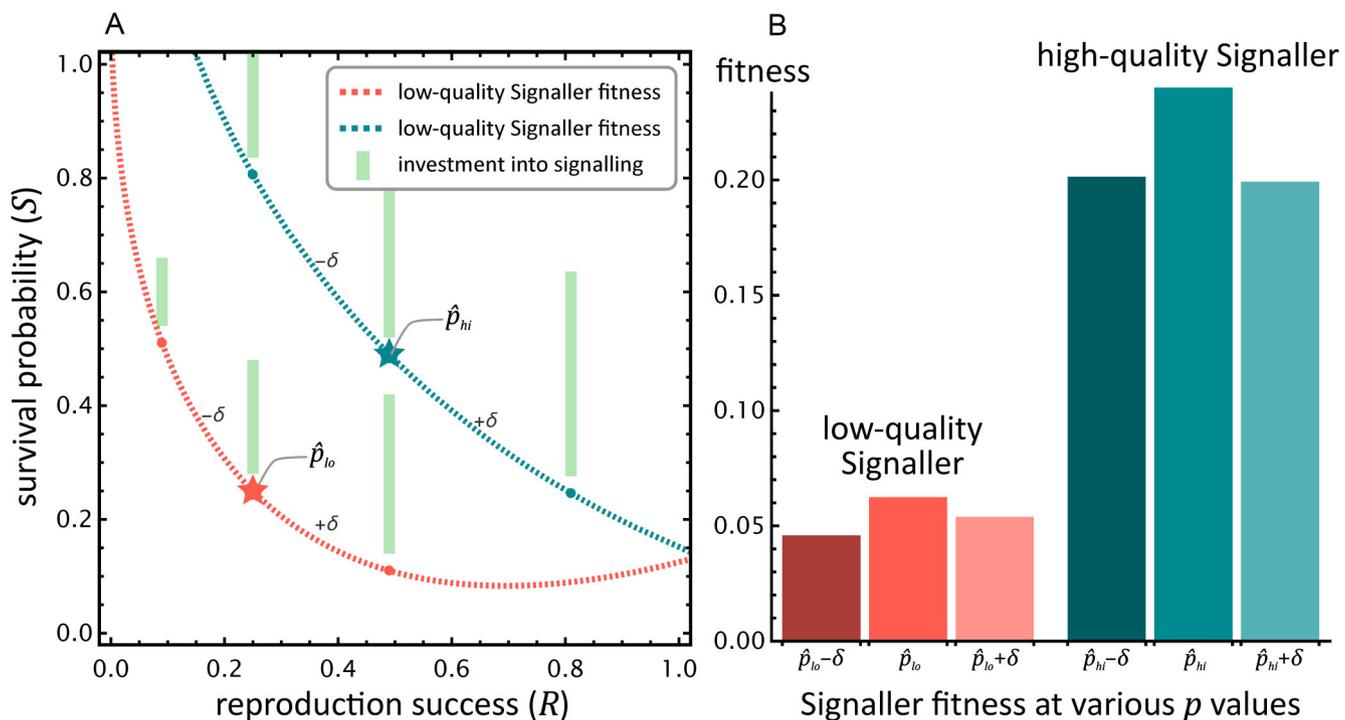


Figure 1. Honesty is explained by trade-offs rather than costs in Grafen’s classic “strategic handicap” model (Grafen, 1990). (A) Fitness w_S of high- and low-quality signallers (teal and red curves, respectively) confers different trade-offs between survival probability S and reproductive success R . Green bars indicate investment into signalling: we assume that the more the Signaller invests, the higher his signal intensity (a) will be, and the more amount of resource (p) he asks from the Receiver. Stars indicate the optima for the different signallers where fitness is maximized and the double-optimization problem of Signaller and Receiver is resolved. At the optimum, both Signaller and Receiver are at equilibrium, and the Receiver shares exactly what the Signaller asks for, \hat{p} . Note that the optimum is at different p values for low- and high-quality Signallers due to their different trade-offs ($\hat{p}_{lo} \neq \hat{p}_{hi}$). Points show out-of-optimum values, when the signal intensity is changed (to request a different amount of resource) with $\hat{p} - \delta$ (left) or $\hat{p} + \delta$ (right). (B) The same change δ in signal intensity yields different fitness changes for low- and high-quality Signallers. Bars show the actual Signaller fitness at the optima (middle) and out of optima (flanking) for low-quality (red) and high-quality (teal) individuals. Any deviation from the optimum trait value results in sub-optimal fitness. This marginal decrease of fitness when leaving the optimum maintains honesty at the equilibrium. There is no ultimate cost paid at the equilibrium as both reproduction and survival are a positive contribution to fitness, though there are proximate investments. Note that the same δ in signal intensity (and in requested resource amount p) yields a larger fitness change for a high-quality than for a low-quality Signaller. Parameters are: [$q_{lo} = 0.5$, $q_{hi} = 0.7$, $r = 2$, $\delta = 0.2$].

1975)], but some assume that the HP has been replaced with the more logical costly signalling theory. However, we are unaware of any attempt to clarify their differences. In the next section, we clarify what costly signalling theory is and what it is not and argue that this paradigm can also be rejected. We also show how honesty in these models is explained by signalling trade-offs rather than realized costs or handicaps, and we show how trade-offs—unlike signal costs—are both necessary and sufficient to account for honesty.

The misleading and mislabelled “Costly signalling” paradigm

“Grafen’s (1990) strategic signalling model is better understood as a life-history model in which individual differ in quality and optimally allocate resources into traits for survival versus sexual signalling due to their fitness trade-offs” (Penn & Számadó, 2020)

Here, we briefly summarize why previous “costly signalling” models (Godfray, 1995; Grafen, 1990) are more accurately labelled, classified, and interpreted as being based on trade-offs rather than costs and why a complete break from the handicap paradigm is needed.

To understand our arguments, we first address the differences between the terms *cost* and *trade-off*. *Trade-offs* are defined in at least six non-mutually exclusive ways in biology (Garland et al., 2022; Roff & Fairbairn, 2007)—and all of which regard trade-offs as constraints and none equate them to costs. In the broad, ordinary sense, a trade-off means one must give up something to obtain something else. In the narrow, mathematical sense, a trade-off is defined as a *relationship* between two or more functions in which one cannot be increased without reducing another. A *trade-off* implies a situation in which individuals must choose between different options (e.g., to what they should invest) that have different costs, different benefits, or both, or they may have the same costs or same net benefits, and which cannot all be maximized simultaneously. A trade-off between reproduction and survival is a well known example of a life-history trade-off (see the following sections for a more detailed discussion and examples). Signalling can have a variety of trade-offs, which are far more complex and interesting than their costs and although trade-offs often involve costs, they do not necessarily require any costs.

In theoretical models, functions represent the effects of traits and their trade-offs. For example, increasing signal intensity can increase the benefits, but it can also increase predation risk, just as increasing short-term reproduction can

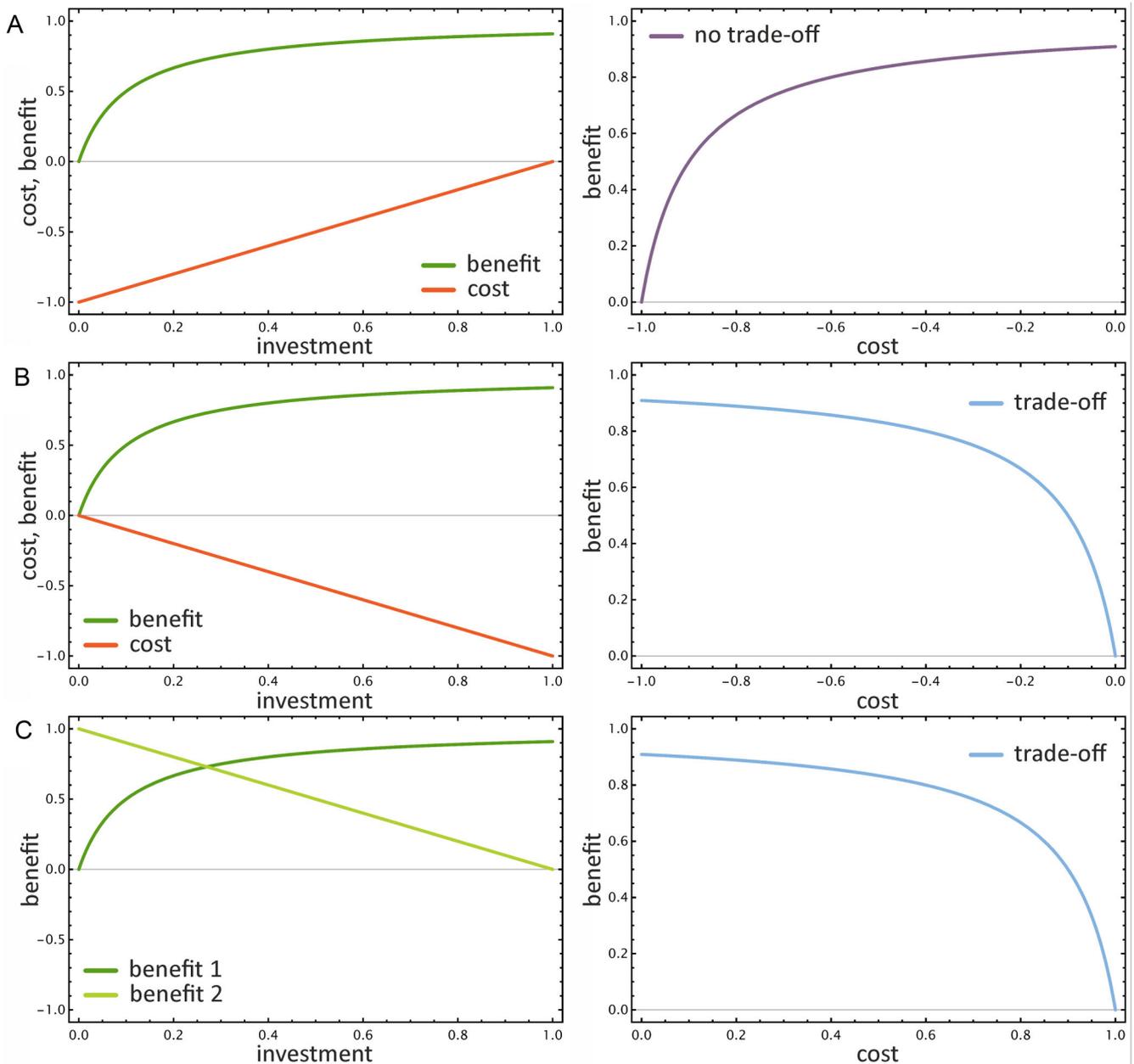


Figure 2. Benefits and costs can be represented either by two differently signed functions (left column): something is added or something is taken away, or as a trade-off curve (right column, showing the relation of the respective functions of the left column as a parametric plot of investment). The term *trade-off* represents an antagonistic relationship between two functions: one cannot be increased without decreasing the other. This implies that the increasing slope in one function (marginal benefit) corresponds to a decreasing slope in the other function (marginal cost). Note that a pair of cost and benefit functions does not necessarily imply a trade-off (A). If their slopes are the same sign then there is no trade-off between the two functions but rather a *congruence*, see (A) (left panel, red curve denotes cost, green denotes benefit function), without trade-off (A, right panel). (B) shows an example of a trade-off created by a cost (red) and a benefit (green) function. It is important to note that a trade-off may even exist between functions of the same sign (C): i.e., between two cost or two benefit functions (light vs. dark green). [Table 1](#) sums up the possible relationships for two functions.

reduce long-term survival (and future reproduction). While the term *trade-off* in casual discussions is often equated with *cost*, this is an over-simplification that differs from the formal definition above and has resulted in misunderstandings (see [Figure 2](#) for technical details). The terms *benefit* and *cost* represent functions with different signs (but no explicit relationship among them): something is gained or something is lost e.g., payoff or fitness. The term *trade-off*, however, represents an *antagonistic relationship between two functions*: one cannot be increased without decreasing the other, independent

of their signs. This constraint means that the increasing slope in one function (marginal benefit) corresponds to a decreasing slope in the other function (marginal cost). Note that a pair of absolute cost and absolute benefit functions does not necessarily imply a trade-off (first row in [Figure 2](#)). If their slopes are of the same sign then there is no trade-off between the two functions but rather a *congruence*. On the other hand, a trade-off exists whenever slopes are antagonistic, even between two benefit or two cost functions (third row in [Figure 2](#); see [Table 1](#) for possible combinations of signs and slopes).

Table 1. The relationships between absolute cost/benefit (sign) and marginal cost/benefit (slope) in case of two functions *f* and *g*.

		Function <i>f</i>				
		– sign (cost)		+ sign (benefit)		
		Marginal cost (– slope)	Marginal benefit (+ slope)	Marginal cost (– slope)	Marginal benefit (+ slope)	
Function <i>g</i>	– sign (cost)	Marginal cost (– slope)	Congruence	Trade-off	Congruence	Trade-off
		Marginal benefit (+ slope)	Trade-off	Congruence	Trade-off	Congruence
	+ sign (benefit)	Marginal cost (– slope)	Congruence	Trade-off	Congruence	Trade-off
		Marginal benefit (+ slope)	Trade-off	Congruence	Trade-off	Congruence

There can be congruence or trade-off between any combination of absolute cost and benefit. An absolute cost and an absolute benefit function can be congruent but they can trade-off, etc. A trade-off is defined by the slopes when the slopes are antagonistic. Consequently, there can be a trade-off relationship between two cost functions or two benefit functions. It follows that it is not correct to claim that absolute cost maintains honesty, because absolute cost per se does not imply a trade-off. Moreover, it is incorrect to claim that marginal cost maintains honesty because marginal cost in itself does not imply a trade-off either. Shading highlights the pattern when marginal cost vs. marginal benefit creates a trade-off.

Table 2. The different potential meanings of cost and benefit.

	Positive (+)	Negative (–)	Negative (–) <i>Handicap/costly signalling terminology</i> (Grafen, 1990; Falk et al., 2025)
Sign of the function	Benefit function	Cost function	Handicap
Slope of the function	Marginal benefit	Marginal cost	Handicap
Relation between two functions	Congruence	Trade-off	Handicap

The table shows three distinct levels where the term cost or benefit is defined (rows): sign of a function, (ii) slope of a function, and (iii) the relationship between two functions. The first two columns show the correct terminology for a positive or negative effect. Last column shows the misleading terminology of the HP/costly signalling paradigms for negative effects. Then becomes immediately clear how the term “handicap,” applied for all three levels, is confusing.

Table 3. The relationship between three paradigms: (i) the handicap principle (HP), (ii) costly signalling, (iii) Signalling trade-off theory (STOT) (columns).

Signalling theories and paradigms	Handicap principle (Grafen, 1990; Zahavi & Zahavi, 1997; Zahavi, 1975)	Costly signalling (Maynard Smith, 1991; Godfray, 1995; Johnstone, 1997; Lachmann et al., 2001; Bergstrom et al., 2002; Biernaskie et al., 2014)	Signalling trade-off theory ([Számadó et al., 2022, 2023] and here)
How is signalling honesty explained?	Zahavian handicaps (honest signals are favoured because they are costly and/or wasteful)	Differential marginal signal costs or differential signal benefits	Differential trade-offs in costs or benefits; equilibrium costs neither sufficient or necessary
How is dishonesty explained?	N/A	?	Natural outcome of diverging from the optimum
Allows Zahavian handicaps?	Yes, all signals are Zahavian handicaps (costly and honest because they are costly)	Yes, costly signalling models widely interpreted as Zahavian handicaps or only in terms of costs rather than trade-offs	No, there are no Zahavian handicaps (theoretically illogical and contradictory)
Is the theory (consistent with evolutionary theory (Is it Darwinian)?	No, assumes non-Darwinian wasteful traits	Yes	Yes
In what domain is the theory grounded?	Nowhere	Originally derived from economic signalling models, whereas in biology it is interpreted as part of the Darwinian framework	Darwinian, evolutionary life-history theory (allocation trade-offs based on condition-dependence)
Does the theory offer a link between proximate and ultimate level of explanations?	No	No	Yes
Key predictions & empirical support	High (wasteful) equilibrium cost. No empirical support	Differential marginal cost (or benefit). Some support for differential marginal cost, see (Kotiaho, 2001)	Differential trade-offs (costs or benefits). Plenty of support, e.g., (Creighton et al., 2009; Davies et al., 2023; Duffield et al., 2017; Farchmin et al., 2020; Fitzpatrick et al., 1995; Heinen-Kay et al., 2015; Hopkins et al., 2021; Számadó et al., 2022; White et al., 2022)

We compare these paradigms in the following questions (rows): (i) How does the paradigm explain honesty? (ii) How does the paradigm explain dishonesty? (iii) Does the paradigm allow Zahavian handicaps? Is the paradigm consistent with the Darwinian theory? (iv) In what theory is the paradigm grounded in? (v) Does the theory offer a link between proximate and ultimate level of explanations? (vi) Is there support for the prediction of the paradigm?

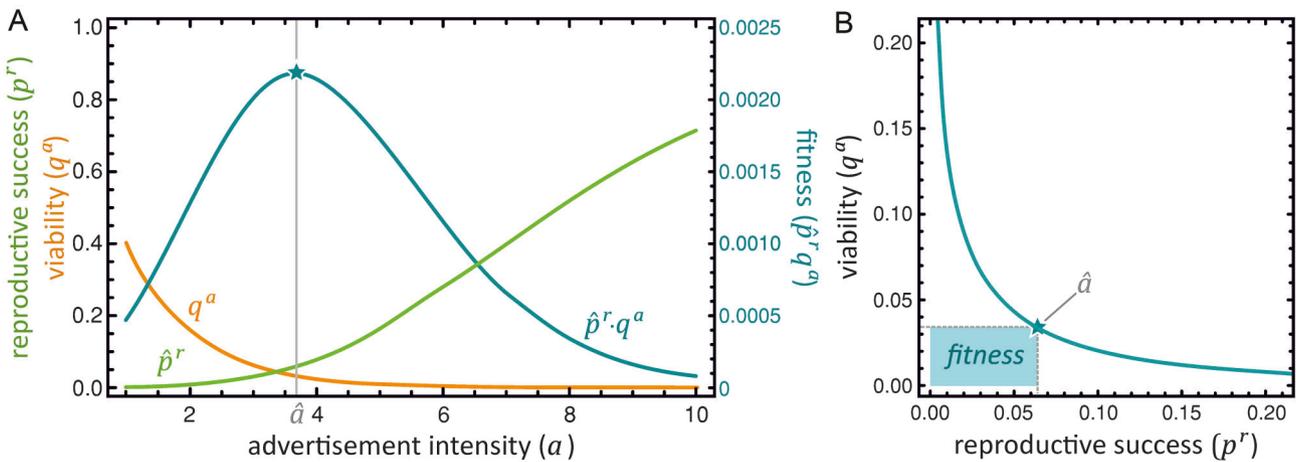


Figure 3. Grafen’s signalling model (Grafen, 1990, p. 522) is based on a life-history trade-off. (A) The components of the signalling male’s fitness are reproductive success p^r and viability q^a (green and orange curves, respectively, left y axis), which are multiplied to get the male fitness ($p^r q^a$, teal curve; right y axis). Since increasing advertisement intensity a adversely affects these two components, this is a model of trade-off. At the honest equilibrium, the Signaller fitness optimum must be where the Receiver’s fitness optimum is (grey line at $\hat{a} = 3.69$). (B) Plotting viability q^a against reproductive success p^r . The area of the rectangle gives the fitness at the optimum, and the star denotes the maximum fitness where the product of reproductive success and viability is the largest, corresponding to \hat{a} on the left panel. Parameters are $\{a_0 = 2, q_0 = 0.2, r = 3, q = 0.4\}$.

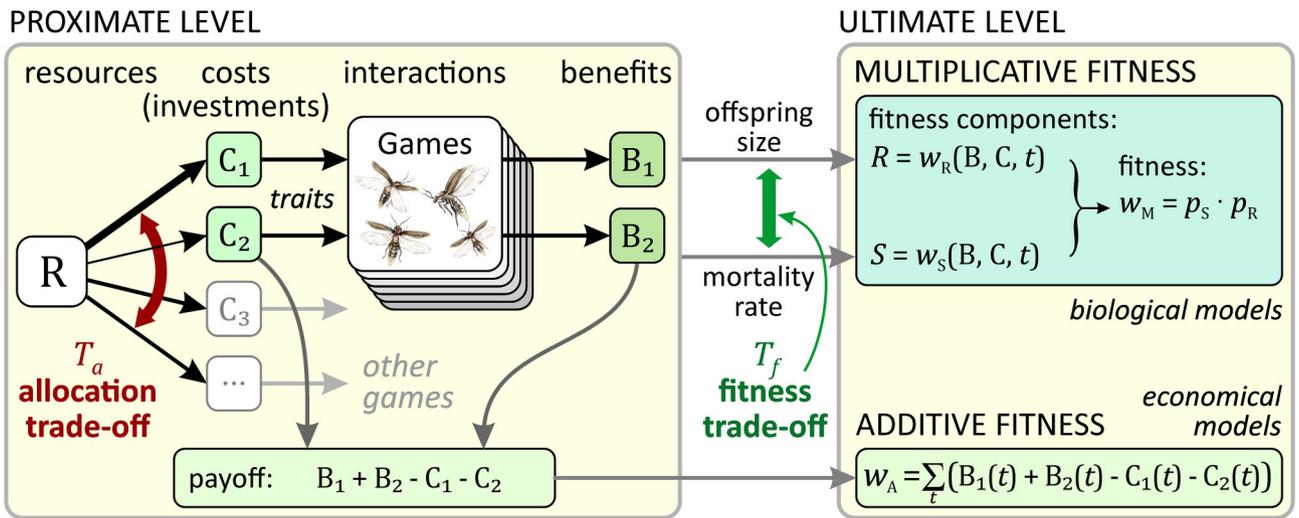


Figure 4. A simple model for how allocation trade-offs for signal investment at the proximate level can result in fitness consequences. The HP assumes that increased investment into signals (metabolic and other proximate “costs”) results in fitness costs, whereas it is generally expected that such investment will have trade-offs at proximate and ultimate levels. The relationship between allocation trade-offs at the proximate level and their fitness consequences has been neglected in “costly signalling” theory, however. Here, we assume that signallers face allocation trade-offs in the short-term (proximate mechanisms, T_a), and that they can invest energy, time, and other resources (costs, C_i) into the expression of a signal trait (plumage, begging, mate attraction, etc.). Expressed signals may then influence other individuals through interactions (signalling games). There are many other possible games, and not necessarily signalling ones. Interactions yield various immediate benefits (B), e.g., mating opportunities in sexual signalling or resources from begging calls. These benefits, if translated to the same quantity, can theoretically be summed to a payoff, which can be accumulated over time. The assumption of additive fitness models is that cumulative payoff correlates with the probability of the individual being selected by natural selection (w_A). This assumption holds for most interactions in human economic systems where both investment and profit are measured in the same monetary scale. However, biological interactions affect offspring size and mortality rate, which define the fitness components of biological signalling games: reproductive success (p_R) and survival chance (p_S), as probabilities. In multiplicative fitness models, these probabilities are multiplied to yield the fitness of individuals (w_M) that evolve by natural selection. Proximate-level allocation trade-offs (T_a) manifest as trade-offs between fitness components (T_f), though the exact relationship between T_a and T_f is not trivial.

In other words, having an absolute cost function is neither necessary nor sufficient condition to have a trade-off.

It is very clear from these definitions that biological costs (and benefits) can only represent one side of the effect of an event on fitness, ignorant of any restrictive relationship between two or more functions, i.e., ignorant of any potential trade-off. The crucial point is that cost and benefit functions

decompose net values (payoffs) into *two distinct quantities* (e.g., invested energy vs. reward), intuitively considered to be negative and positive, respectively, *without* actually defining any relationship between the two functions. Whereas a trade-off explicitly defines a relationship between two functions (e.g., reproductive chance and mortality, signal intensity and survival, etc.), where only one can increase if the other is

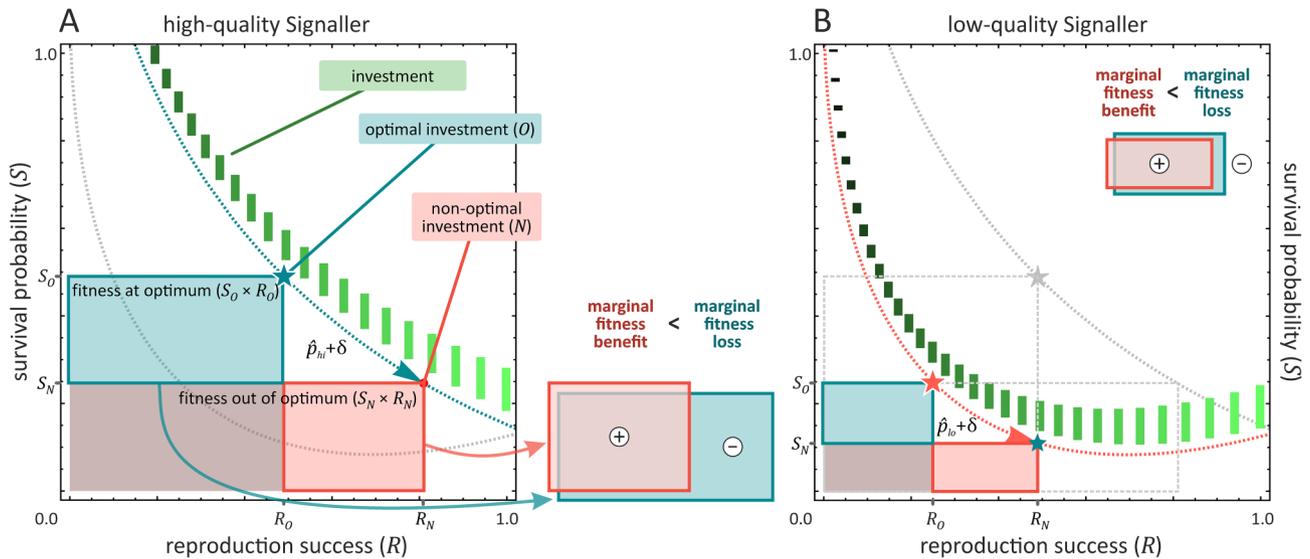


Figure 5. Relationship between proximate investment into sexual signal expression and fitness trade-offs for high-quality (A) and low-quality individuals (B) in Grafen's model (Grafen, 1990). Fitness curves show classic life-history trade-offs between investment into reproduction R and survival probability S . Individuals of different qualities are facing different trade-offs hence they invest differentially into signalling. Signal intensity (height of green bars) increases from left to right along the curve. Ultimate fitness is the multiple of R and S , measured by the area of the rectangles from the origo. At the optimum (star), the area and fitness are the largest; individuals of different qualities have different optima. When a signaller moves out of the local optimum by increasing signal intensity with δ (arrows on the trade-off curves), fitness is decreased ($S_N R_N < S_O R_O$). Note that by increasing signal intensity, the low-quality individual actually adopts the optimal strategy of the high-quality individual (teal star). The fitness decrease is not because of increasing signal cost but because the marginal cost paid (the area lost from the fitness rectangle, thick teal box) surpasses the marginal benefit gained (the area gained, thick pink box). The same result would happen if a signaller decreased signal intensity (i.e., moving to the left on the curve), proving that fitness optimum does not directly depend on signal cost (contrary to the main tenet of the HP). Parameters are: $\{q_{io} = 0.5, g_{hi} = 0.7, \delta = 0.2\}$.

decreasing. It is absolutely possible that a model with explicit cost and benefit functions has an implicit trade-off defined between these functions (see e.g., Hurd, 1995; Maynard Smith, 1991; Számadó, 1999), in which case it is a trade-off model. As a matter of fact, we claim that the models successfully explaining honest signalling are all based on trade-offs rather than costs (Számadó et al., 2023).

Thus, it is a confusing over-simplification to describe the trade-offs that maintain honesty in signalling models as “costs,” as it is the antagonistic relationship between fitness components that actually explains honesty. Signal honesty is explained by trade-offs rather than costs, and it is time to place signalling theory on the solid foundation of evolutionary life-history theory, a general framework for analysing adaptations, which is based on trade-offs (Roff & Fairbairn, 2007) rather than costs.

The problems with costly signalling paradigm

“One prominent mechanism for ensuring honesty is differential costs or benefits to a signal, also known as handicap mechanisms (Grafen, 1990; Maynard Smith, 1991; Zahavi, 1975).” (Falk et al., 2025)

“Costly signalling” models have provided important insights, but they provide an incomplete and misleading account of honest signalling for several reasons. First, costly signalling models continue to be misinterpreted and couched in terms of the erroneous HP (Penn & Számadó, 2020). For example, Biernaskie et al. argue, “The fundamental aspect of costly signalling theory is the potential cost of faking a dishonest signal. This applies to honest signals that incur a realized cost at equilibrium (i.e., traditional “handicaps”) and to honest signals with minimal realized costs (e.g., when the cost of dis-

honesty is socially imposed)” (Biernaskie et al., 2014). Falk et al. present a similar argument (Falk et al., 2025) (see quote above). Most authors continue to equate costly signalling theory and the HP, and the new insights provided by more recent theoretical and empirical developments presented above have been ignored (Table 2 summarizes how the HP/costly signalling paradigm is unable to differentiate between key concepts).

Second, costly signalling theory places undue emphasis on signal costs and ignores the differences between costs and trade-offs in its interpretations of models (see discussion above). The “costly signalling” paradigm emphasizes (marginal) costs, and yet one could alternatively place the emphasis on benefits and change the label to “beneficial signalling” theory (and it would be equally incorrect). Costly signalling models would not work without marginal costs, but they would not work without marginal benefits either. Emphasizing trade-offs resolves this apparent conundrum by giving equal weight to both marginal costs and marginal benefits of signals.

Third, many of the costly signalling models are formalized based on economic predecessors (Bergstrom & Lachmann, 1997, 1998; Lachmann & Bergstrom, 1998; Nöldeke & Samuelson, 1999; Spence, 1973). Yet, these models, including seminal models such as the Sir Philip Sydney game and its derivatives (Bergstrom & Lachmann, 1997; Hurd, 1995; Maynard Smith, 1991; Számadó, 1999), assume an additive utility/fitness function, which is completely unrealistic for most biological scenarios. Our aim is to place biological signalling games on a solid and general foundation of evolutionary life-history trade-off theory.

Fourth, costly signalling mistakenly equates proximate costs with fitness costs of signalling, whereas a trade-off

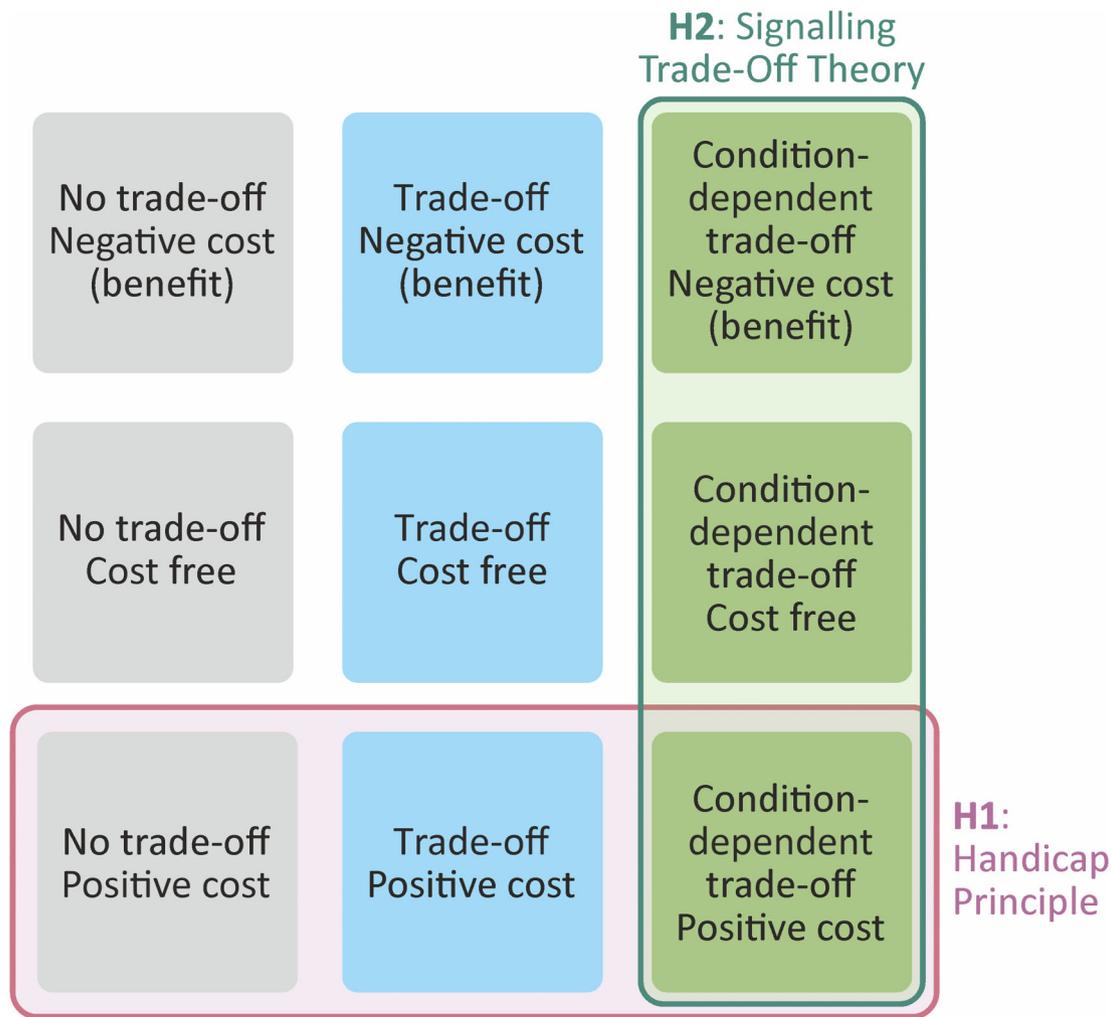


Figure 6. Comparing the predictions of the HP and STOT (after Számadó et al., 2022). Rows represent the manipulation of absolute signal cost in an arbitrary experiment: beneficial signals, cost-free signals, costly signals. Columns represent the manipulation of trade-off: no trade-off, same trade-off for everyone, condition-dependent trade-off (more favourable for high-quality signallers). H1: prediction of the HP, costly signals will be honest (in terms of absolute cost). H2: prediction of STOT: signals with condition-dependent trade-off will be honest. As is clear from this arrangement, HP and STOT can only agree in a subset of possible cases; otherwise, they give orthogonal predictions.

perspective allows the integration of signalling theory into the well-established theory of life-history evolution (e.g., increased investment into signalling is not a cost, but rather an investment that can have trade-offs at proximate and ultimate levels).

Fifth, costly signalling theory has almost entirely ignored dishonesty (especially costly deception), and assumed it must be rare somehow (Johnstone & Grafen, 1993; Maynard Smith & Harper, 1995). Therefore, a more general signalling theory is needed that can account for both honest and deceptive signals. We propose that deception arises when signalling trade-offs maintaining honesty are removed.

Thus, “costly signalling” theory has been a step in the right direction, but it is mislabelled and misinterpreted, and it is inadequate to account for honest and dishonest signalling (Table 3 compares the different paradigms). We do not advocate rejecting these models, and tossing out the baby with the bathwater, but a new paradigm is needed that provides a complete break from the HP. Below, we explain our proposal for how signalling theory is based on trade-offs rather than costs, though first we briefly summarize the origins of STOT.

Sexual signalling and life-history theory

“The budget of nature is fixed; but she is free to dispose of particular sums by an appropriation that may please her. In order to spend on one side, she is forced to economize on the other side.” (Darwin, 1872)

Darwin (Darwin, 1872; White et al., 2022) proposed that sexually dimorphic sexual signals evolve due to their sex-specific fitness trade-offs, and his idea has much support (Davies et al., 2023; Doorn & Weissing, 2006; Fitzpatrick et al., 1995; Heinen-Kay et al., 2015; Hopkins et al., 2021; White et al., 2022). Sexual conflict is based on the idea that males and females have different optima due to differences in trade-offs for sexual signals and other traits (Bonduriansky et al., 2008). Variation in sexual signals can be maintained by balancing selection on different alleles having antagonistic fitness trade-offs (Johnston et al., 2013). Recent theoretical models have examined dynamic changes in the trade-offs of sexual signals (Lerch & Servedio, 2023).

Trade-offs were first formally investigated in economics (e.g., see opportunity costs, analysed with production-

possibility frontier graphs and the Pareto front, which involves the optimization of multiple functions), and they have long been central to evolutionary theory (Garland et al., 2022; Kirkwood, 1977; Reznick et al., 2000; Roff, 1993; Roff & Fairbairn, 2007), not only life history theory (Stearns, 1989, 1992), but also sex allocation (Charnov, 1982), virulence evolution (Anderson & May, 1982), adaptive behaviour (Houston et al., 2023), aging (Kirkwood, 1977), and sexual selection. The main problem has been explaining examples when the expected trade-offs are not found or the counter-examples, such as apparent evidence that sexual signal expression is often positively rather than negatively correlated with longevity (Jennions et al., 2001).

Van Noordwijk and de Jong pointed out that positive correlation can manifest at the population level between traits that are actually traded off whenever there is individual heterogeneity in condition (due to differences in acquisition or allocation of resources), such as between reproduction and longevity; see “big houses big cars” (Jong, 1993; Laskowski et al., 2021; Noordwijk & Jong, 1986). Thus, many seemingly contradictory results can be explained by variation in individual condition or quality, which is a **condition-dependent trade-off** (see Box 1. for more details about sexually selected signals under condition-dependent trade-offs). Interestingly, signalling trade-offs may also explain sex differences in condition-dependent (phenotypically plastic) signal expression (Bonduriansky, 2007; Rohner & Blanckenhorn, 2018).

Box 1. Do sexual traits honestly signal male fertility?

It has been proposed that the expression of male secondary sexual traits provide honest indicators of males' fertility to potential mates, and that females use these traits to avoid mating with infertile males (Sheldon, 1994). This *phenotype-linked fertility* hypothesis predicts that pre- and post-copulatory traits are positively correlated (honest signalling). However, males are expected to face an allocation trade-off between investing into the development and maintenance of secondary sexual traits (courtship signals) versus primary sexual traits, such as sperm count and testes size (Simmons et al., 2017). This *sexual allocation trade-off* hypothesis predicts that pre- and post-copulatory traits show a negative correlation in their size or functions. Empirical evidence for these opposing predictions is mixed, as some studies find positive correlations, whereas others find a negative or no correlation between these traits (Mautz et al., 2013). The direction of the correlation between pre- and post-copulatory traits may be positive or negative depending upon on the degree of variation in the quality or condition of individual males or their access to resources that they can invest into competing sexual traits (Mautz et al., 2013; Tunj et al., 2018). Variation in male quality can potentially mask or even generate positive correlations among life-history traits [Y-model of resource allocation trade-offs (Noordwijk & Jong, 1986; Reznick et al., 2000)]. Males in good condition and with more resources are expected to be better able to invest into both primary and secondary sexual traits than males in poor condition, who might face trade-offs in sexual allocation. This hypothesis predicts an overall positive correlation between these traits (honest signalling), and a negative correlation among males in poorer condition, access to resources, or both (condition-dependent fertility indicator hypothesis) (Nicolakis et al., 2025). Thus, sexual signals may provide honest indicators of male fertility, and especially if there are condition-dependent trade-offs between primary versus secondary sexual traits. This hypothesis is consistent with honest

signalling theory (Grafen, 1990; Számadó et al., 2023), as well as life-history theory.

Box 2. Signalling models explained by signalling trade-offs

1. The strategic handicap is a signalling trade-off model

Grafen (1990) assumed sexual signals are condition-dependent and that signallers face a trade-off between investing into signals to enhance reproductive success versus survival (Grafen, 1990), which is a classic life-history trade-off. In his example model, male signaller fitness (w_S) is multiplicative, and defined as (Grafen, 1990, p. 522):

$$w_S = p^r \cdot q^a,$$

where q is signaller quality, a is the level of signal advertisement, p is the amount of resource provided by the receiver, and r is a constant determining reproductive success of the signaller. The trade-off is not visible in any of Grafen's figures, and therefore, we explicitly show the trade-off between the two fitness components, depending on advertisement level a , in Figure 3. Note that our figures are not recreations of any of Grafen's figures—he did not plot these relationships, which would have helped to avoid the handicap interpretation of his results. The “costly signalling” models of Godfray and Grafen illustrate the different approaches in modelling fitness, see Figure 1.

2. A general trade-off function exists for any fitness function without trade-off

Grafen assumed a particular trade-off, and consequently, and he calculated a single equilibrium optimum strategy for signallers $A(q)$ and receivers $P(q)$. It has since been shown that there is an infinite number of possible trade-offs that can ensure an honest equilibrium (Bergstrom et al., 2002; Lachmann et al., 2001; Számadó et al., 2023). For example, here we consider a signaller fitness function that lacks a trade-off (the benefit function B) and assumes that in honest equilibrium, a trade-off function t transforms the signaller's optimal decision to the receiver's optimum. We also introduce a particular receiver fitness function w_R , that meets the criteria set by Grafen (Grafen, 1990, p. 518):

$$B = p^r \cdot q, \quad w_S = B \cdot t, \quad w_R = q - (p - q)^2.$$

In the honest equilibrium, the signaller achieves optimal fitness when he asks for (by advertising \hat{a}) and gets the same amount \hat{p} the receiver is willing to share, and thus \hat{p} depends on \hat{a} . Hence, t must also depend on the receiver optimum \hat{p} . The general trade-off function is as follows (for its derivation, see Számadó et al., 2023):

$$t(q, p) = D(q) - \frac{w'_S(q, \hat{p})}{w_S(q, \hat{p})} \frac{D(q)}{w_S(q, \hat{p})} (p - \hat{p}) - \left(\frac{D(q)}{w_S(q, \hat{p})} \left(\frac{w''_S(q, \hat{p})}{2} - \frac{w'_S(q, \hat{p})}{w_S(q, \hat{p})} \right) + \varepsilon \right) (p - \hat{p})^2,$$

where $D(q)$ is an arbitrary function, and ε is positive. We then plot the multiplicative signaller fitness in Figures 4 and 5 as a parametric curve of the survival probability $S = q t$ times the reproductive success $R = p^r$ for a given quality q (as in Figure 3A). We assume (just like Grafen did) that signal intensity a increases with increasing proximate investment (height of green bars). Due to the trade-off, the simultaneous optimization of signaller and receiver strategies is ensured, and in the equilibrium, both receiver and signaller are expected to be at their respective optima. Furthermore, both the high-, and low-quality sig-

allers are at their respective optima (maximizing ultimate fitness), where they produce different but honest signals, and it is not worth cheating (Figure 1B). Figure 5 demonstrates that it is the marginal cost of deviating from such local optimum that maintains honesty and not the equilibrium cost of signals (see Számadó et al., 2023), contrary to the HP.

Getty (Getty, 2006) first showed how decisions about investment into sexual signal expression are similar to life-history allocation trade-off models, in which signalling is a component of reproductive effort and males invest into signalling depending upon their condition. He urged researchers to “stick with traditional life-history variables, viability, fecundity, and fitness, and focus on selection for efficient trade-offs,” rather than attempting to model or measure differential, marginal signalling costs (p. 87). Getty’s insights about how honest signalling theory can be integrated with life-history theory have largely been overlooked (though see Morehouse, 2014).

A general theory for honest signalling

“Evolutionary biological thought is firmly grounded upon the assumption that trait evolution is restricted or biased by fitness trade-offs” (Roff & Fairbairn, 2007)

We present the case for a general theory of signalling based on trade-offs by investigating the role of trade-offs in theoretical models and pointing out how alternatives to the HP and costly signalling models all depend on trade-offs, albeit at different levels. We also argue that a general signalling theory needs to explain deception as well as honesty, and that life-history trade-offs provide the foundation for a general and unifying theory of signalling.

Signalling trade-off theory: signalling trade-offs and condition-dependence provide a general theory of honest signalling

Theoretical models have repeatedly shown that honesty can evolve when there are condition-dependent fitness trade-offs between the marginal cost and marginal benefits of honest signalling (Bergstrom et al., 2002; Getty, 1998a, 1998b; Hurd, 1995; Lachmann et al., 2001; Számadó, 1999; Számadó et al., 2023) (see Higham, 2014; Számadó, 2011 for reviews). These models imply a **double-optimization**, i.e., to find the honest equilibrium, one must calculate the optimum strategy of the receiver and must transform the fitness function of the signaller such that optimal resource division is the same for both of them (Számadó et al., 2023). In theory, for any signaller fitness function, there exist an infinite number of trade-off functions that transform its optimum to coincide with that of the receiver fitness to yield honesty (Számadó et al., 2023).

We propose that honest signals are maintained by condition-dependent signalling trade-offs. Individuals produce signals that influence various inter- and intra-specific interactions, and these can be modelled as strategic games (see Figure 4). Individuals invest into traits (e.g., mate searching or conspicuous signals) that influence the outcome of these games, which may yield various benefits, but they also face trade-offs (e.g., time, energy, and resources at a proximate level). Natural selection maximizes fitness by optimizing al-

location to fitness components that are under trade-offs (e.g., survival vs. reproduction). Fitness trade-offs are thus consequences of proximate allocation trade-offs, or in other words allocation trade-offs describe how proximate investments are translated to ultimate fitness benefits (see Figure 5 for an example).

Honesty means that condition (state) is inferable from a signal, which requires that individuals of different condition (or quality) signal differently, and this is expected whenever individuals face different trade-offs (see Figure 5). When individuals of different quality have the same trade-off, they share the same optimum too, and hence they invest identically resulting in dishonest (pooling) equilibrium (where both honest and dishonest individuals share the same signal, thus will be undistinguishable for a receiver). *Differential investment into the signalling trait* (i.e., honest signalling) only evolves when signallers of different qualities face different fitness trade-offs, obtaining therefore different fitness returns from the same proximate investment. In other words, trade-offs define the “exchange rate” of the investment of individuals into different fitness gains (currencies). While both high and low quality signallers are at their respective optima (honest equilibrium), high quality individuals enjoy a more favourable exchange rate (a better trade-off) than low quality ones (Számadó et al., 2023), and they can invest more into signalling [see also efficiency principle (Getty, 1998b)]. Thus, the same investment by a high-quality signaller yields a larger fitness increase than by a low-quality signaller.

Empirical evidence for signalling trade-offs

The importance of trade-offs for explaining honest signalling has recently been supported by empirical evidence in an experimental signalling game (Számadó et al., 2022). This study demonstrated that condition-dependent trade-offs can account for honesty among humans, whereas equilibrium (realized) signal costs (handicaps) cannot. Honesty was observed in all experimental treatments with a condition-dependent signalling trade-off *regardless of the immediate cost of equilibrium signals* (costly, cost-free or beneficial). Moreover, even signals providing immediate benefits can maintain honest signalling, as long as there is a condition-dependent trade-off (Számadó et al., 2022, 2023). Consequently, traits with condition-dependent trade-offs need not be harmful, wasteful, or even costly for honest individuals at the equilibrium. In other words, honesty is maintained by the fact that different types of signallers face different trade-offs. The *differential investment* (or differential proximate cost) is the result of such differences in trade-offs.

These trade-offs might be obvious in some contexts [e.g., a trade-off between mating success versus survival (Darwin, 1872; Poulton, 1890; White et al., 2022) or between present versus future offspring], while obscure in others [e.g., in gossip (Wu et al., 2021), reputation systems, market advertising, public relations, and modern social media]. Despite their obscurity, signalling trade-offs potentially govern honesty in humans and non-human species, and both in the biological and the economical contexts: every signalling model that has an honest equilibrium to our knowledge also requires a signalling trade-off and thus, identifying and understanding these trade-offs is central to explaining honest and dishonest signals.

Integrating alternative explanations for honest signalling

“In modern Darwinism, Darwin’s contrasts between sexual selection’s extravagance, its trade-offs, its harmfulness, and natural selection’s utility, its efficiency, its benefits all melt away. All adaptations are compromises; a trade-off between mating and predation is no different in principle from a trade-off between foraging and predation.” (Cronin, 1991 p. 242)

There are three alternative explanations for honest signals under conflicts of interest, which are viable (unlike the HP) (i.e., strategic, index, and conventional signals). Here, we examine each of these hypotheses and show how these all involve trade-offs at various levels, even though they were all originally interpreted as versions of the HP or costly signalling (Penn & Számádó, 2020).

First, so-called “costly signalling” models explain honesty through strategic signalling trade-offs (Számádó et al., 2023), and though most continue to equate them with the HP (Dawkins, 1990; Godfray, 1991; Grafen, 1990), some reject the HP and view these models as an alternative. As we argue above, Grafen’s signalling model (Grafen, 1990) is identical to life-history models in which there are allocation trade-offs between increasing sexual signal expression (reproductive effort) versus survival; and yet there is a positive relationship between these two traits in the population because there is variation in individual quality and trade-offs are condition dependent, i.e., high-quality individuals are better able to invest into both traits despite their trade-offs than low-quality males (Getty, 1998a, 1998b, 2006; Höglund & Sheldon, 1998). Figure 3 shows the trade-off in Grafen’s model (based on his equations). This figure was not in Grafen’s paper, though it would have helped to reveal the differences between the model’s implicit trade-off-nature and the erroneous handicap interpretation (see Box 2 for a more detailed explanation). A related model later showed how offspring begging calls can be honest indicators of hunger (Godfray, 1991) due to a life-history trade-off between the survival of current versus future offspring (but it was also generally misinterpreted as a model of the HP). Several proximate mechanisms have been proposed to explain how honest signal expression is regulated through endocrine signals that allocate investment of energy and resources into sexual signalling versus other traits [e.g., immunocompetence handicap hypothesis (Folstad & Karter, 1992), oxidative handicap hypothesis (Alonso-Alvarez et al., 2006, 2008)]. These ideas were also originally equated to the HP, but they are logical and consistent with life-history allocation trade-offs (Morehouse, 2014; Wedekind & Folstad, 1994), even if the proximate mechanisms are controversial and unresolved (Roberts et al., 2004).

Second, honesty is often suggested to be explained by inescapable physical constraints that make signals impossible to fake (index signal hypothesis) (Maynard Smith & Harper, 1995, 2003). For example, the roars of red deer stags were proposed to honestly reflect their size due to an anatomical constraint (formant dispersion of the vocal tract) (Clutton-Brock, 2009). Such signals were originally interpreted as “revealing handicaps,” but were then re-labelled as “indices” and reinterpreted as an alternative to the HP (e.g., Maynard Smith & Harper, 1995, 2003). Purported examples of physical constraints remain untested, and it is difficult, if not impossible to determine whether individuals are unable to fake a signal or

whether they perceive greater marginal potential costs than their marginal potential benefits. The roars of red deer may be honest indicators of size due to condition-dependent allocation trade-offs (see Box 1). The problem is that the index hypothesis provides a proximate explanation (developmental and physiological constraints), which has been mistakenly pitted against ultimate explanations, such as selective trade-offs (e.g., Hill et al., 2023). If an honest signal cannot be faked due to a proximate constraint at some point in time, then it begs the question how such constraints have evolved and are maintained, and it does not explain why deception does not evolve. Evolutionary versions are based on vague speculations about genetic, developmental, phylogenetic, or other constraints on adaptation. Hypotheses about constraints, trade-offs and adaptations are not mutually exclusive alternatives: index signals provide a proximate explanation (Biernaskie et al., 2014, 2018; Holman, 2012), and evolutionary explanations for such constraints require the analyses of traits constrained by trade-offs (Sinervo & Basolo, 1996).

Third, signals can be honest due to social punishment or other negative trade-offs inherent in social interactions (Enquist, 1985; Számádó, 2003, 2008, 2011). Such signals, which are sometimes labelled “conventional signals” (Dawkins & Guilford, 1991), are produced in the context of competition for limited resources (food, mating opportunities). Initially, these signals were also misinterpreted as handicaps or “vulnerability handicaps” (Grafen, 1990; Hurd & Enquist, 2005; Vehrencamp, 2000; Zahavi & Zahavi, 1997). Punishment (e.g., from rivals) can generate a trade-off for sexual signals, just as attracting predators and parasites is also a trade-off. Theoretical models all describe a condition-dependent trade-off between viability and resource acquisition, where strong (high quality) individuals are better off by investing in resource acquisition (hence signalling), whereas weak individuals are better off by investing in viability (Enquist, 1985; Számádó, 2003, 2008, 2011)—the eponymous criteria of a life-history trade-off.

Thus, the proposed alternative hypotheses for honest signals are all based on life-history trade-offs, albeit at different levels of biological organization.

Signalling trade-offs and the evolution of deception

“[In cuttlefish, Sepia plangon] males deceive rival males by displaying male courtship patterns to receptive females on one side of the body, and simultaneously displaying female patterns to a single rival male on the other, thus preventing the rival from disrupting courtship.” (Brown et al., 2012)

Unfortunately, deception has been ignored by honest signalling theory. Zahavi never addressed deception, other than to assert that signals should be honest and cheat-proof (Zahavi & Zahavi, 1997), and he ignored counter examples of costly deception. Yet, dishonest signals exist and require an evolutionary explanation. Although some proponents of the HP acknowledged their existence, cheating has been too often depicted as a rare, marginal behaviour (Johnstone & Grafen, 1993; Maynard Smith & Harper, 2003; Searcy & Nowicki, 2006). Examples of dishonest signals abound in nature, such as Batesian mimicry (Joron, 2009), sexual mimicry (Dominey, 1980; Gross & Charnov, 1980) and predatory mimicry (Lloyd, 1965). Deceptive signals do not evolve be-

cause they have no costs. They may be quite costly (e.g., the broken-wing display attracts predators to the signaller), but their benefits outweigh their costs (Gómez-Serrano & López-López, 2014; Whoriskey, 1991).

Here, we propose that a lack of signalling trade-offs may explain dishonest sexual signals. We predict that signals can be dishonest when they lack condition-dependent trade-off regardless of their costs or apparent extravagance (e.g., deceptive signals can be quite elaborate and conspicuous). For example, when trade-offs that enforce honest signals are removed, individuals with low survival chances are expected to increase their investment into sexual signals (Creighton et al., 2009; Duffield et al., 2017; Farchmin et al., 2020; Kokko, 1997). This **terminal investment** hypothesis is supported by theoretical models, though one suggests that terminal investment is only beneficial at the end of lifespan; when death is imminent (the authors recognized the importance of life history theory for sexual signalling, but signalling trade-offs were interpreted as handicaps) (Proulx et al., 2002). The terminal investment hypothesis is supported by many but not all empirical studies (Kuczynski et al., 2015).

Various forms of mimicry offer several further examples. If edible and toxic butterfly species face the same trade-off when producing a given wing pattern, then both can produce it, one being dishonest (Joron, 2009); if both males and females face the same trade-off when producing a morphotype, then both can produce it [e.g., males mimicking females (Dominey, 1980; Gross & Charnov, 1980)]. Thus, dishonesty is the expected outcome when signalling trade-offs are not condition-dependent.

Predictions of the theory

Here, we summarize the predictions of the theory.

- Honest signalling is maintained by condition-dependent trade-offs, not by absolute cost and not by marginal cost (Számádó et al., 2022, 2023).
- Signal honesty will often have nothing to do with their immediate costs but instead will be maintained by trade-offs between two competing benefits.
- Most explanations for honesty are proximate, and we predict that they can be explained by trade-offs, potentially at different levels.
- We predict that dishonest signals are also costly—and just as costly as honest signals. Moreover, we predict that they are maintained by trade-offs or by a loss of trade-offs that otherwise keep them honest (e.g., terminal investment).

Testing the predictions

To illustrate how to test our predictions, we refer to the experiment by Számádó et al. (2022). Számádó in a simple lab experiment tested the behaviour of human subjects in a signalling game similar to the Sir Philip Sydney game (Maynard Smith, 1991). Players were randomly assigned as signallers or receivers, and they were randomly matched up in pairs. Additionally, signallers were randomly assigned “low” or “high” quality. Signallers could send a signal to request a resource from the receiver (the signal could be low or high intensity). The receiver could either give the resource to the signaller or deny it. The value (benefit) of the resource was the same in all experimental treatments. Absolute cost and marginal cost of

the high intensity signal were manipulated across treatments to create the following conditions in terms of absolute cost for high quality signallers: (i) costly signal where high-quality signallers had to pay to use the high intensity signal, (ii) cost-free signal where the use of the high intensity signal was cost free (i.e., zero) for high-quality signallers, (iii) beneficial signal where high-quality signallers received a payment independent of the receiver’s response. Marginal cost of the signal was also manipulated, given that the marginal benefit was fixed it created the following conditions in terms of trade-offs: (i) no trade-off where switching from low to high quality signal had no fitness consequences, (ii) trade-off where switching from low to high quality signal had consequences (decreased fitness) but the same way for all signallers, (iii) condition-dependent trade-off where switching from low to high quality signal had consequences (decreased fitness) but it was more severe for low-quality signallers (i.e., high-quality signallers had more favourable trade-offs). All possible combinations were tested (see Figure 6). The HP predicts that costly signals in terms of absolute cost will be honest (Figure 6H1). Signalling trade-off theory predicts that signals with condition-dependent trade-offs will be honest regardless of the absolute cost (or benefit) of the signal (Figure 6H2). The latter is supported by the experimental results of Számádó et al. (2022): signals with condition-dependent trade-offs are honest, while costly signals (without condition-dependent trade-offs) are not (for all possible test combinations of the experiment, see Figure 6).

We strongly suspect that if STOT had been made earlier, that researchers could have avoided spending years of empirical studies that focused on measuring the costs of signals (especially proximate costs or investment), and would have instead focused on trade-offs (e.g., measuring the costs that come with benefits, and negative relationships between different benefits).

Concluding remarks

Explaining the evolution of honest and dishonest signals presents challenging problems. Although Zahavi’s HP helped to call attention to the problem of explaining costly and honest signals, the signalling models used to support this idea have been misinterpreted (Penn & Számádó, 2020). The HP/costly signalling theory provides an excellent example of the ongoing *theory crisis* in the biological and social sciences (Nakagawa et al., 2025). The theory crisis has been generated by researchers attempting to test hypotheses based on theories that are verbal and vague, which allows many possible interpretations (*researcher degrees of freedom*). Furthermore, even when hypotheses are formally evaluated in mathematical models, they are often poorly described and misinterpreted, so that the actual theoretical predictions are not evaluated in empirical tests, generating an *interpretation crisis*.

Here, we briefly recapitulate our conclusions. (i) First, equilibrium signal cost (handicap) is neither necessary nor sufficient condition of honest signalling (Lachmann et al., 2001; Számádó, 1999, 2011; Számádó et al., 2023). (ii) Second, advocates of the HP have misinterpreted classic sexual selection trade-off models as “costly signalling” models (Grafen, 1990; Godfray, 1991), while all are based on life-history trade-offs, and none show the necessity of equilibrium cost. (iii) Cost is not sufficient in itself to maintain honesty (be it equilibrium or marginal cost) as a cost function does not specify a

relation between different fitness components. It is a trade-off function that specifies an antagonistic relation, and honesty is maintained by such condition-dependent antagonistic relation. (iv) Research on the HP confused correlation with causation: honest and costly signals exist in nature (costly in terms of proximate investments), yet these signals are not honest because they are costly but because trade-offs guarantee that honest individuals are the most efficient (Getty, 1998b; Lachmann et al., 2001; Számadó, 1999; Számadó et al., 2022, 2023). (v) Lastly, the HP confused proximate investment with ultimate fitness cost. Proximate investment (time, energy, resources, etc.) is a necessity of life, and when this investment is returned as increased fitness, it cannot be a waste, handicap, or even fitness cost. Animals (and humans) invest in the short-term to accrue fitness benefits on the long run. Table 3 provides a summary of the differences between the three competing paradigms for signalling theory: HP, costly signalling, and STOT.

Our emphasis on signalling trade-offs versus costs thus is not merely a semantic quibble because there is crucial mathematical distinction between the underlying concepts and crucial evolutionary distinction in what they predict. As we suggest, theoretical models show that honesty can be explained by signal trade-offs, but not signal costs per se; and early models were misinterpreted because they confused these concepts (e.g., it was assumed that a trade-off due to a differential benefit supports the costly signalling or handicap theory) (Godfray, 1991; Johnstone, 1997). Moreover, empirical studies have focused on measuring (mostly proximate) signalling costs, while this is insufficient to determine trade-offs—as this would require measuring both marginal benefits and marginal costs of signals (Lachmann et al., 2001; Számadó, 2011).

The HP is the only theory in modern biology to our knowledge that is anti-Darwinian. Zahavi argued that signals evolve *because* and not despite of their costs and that the HP is based on signal selection, a non-Darwinian process that favours wastefulness rather than efficiency (Zahavi & Zahavi, 1997). This claim is mind-boggling, and it is puzzling that the HP continues to be cited, despite the lack of theoretical or empirical evidence. The main problem is due to the handicap labels and interpretations of “costly signalling” models. The role of trade-offs is well established in the evolution of development, morphology, physiology, and behaviour, but not in animal communication. Roff and Fairbairn (Roff & Fairbairn, 2007) argue that evolutionary theory is “Evolutionary theory has long been grounded on the assumption that trait evolution is restricted and biased by fitness trade-offs (Roff and Fairbairn 2007 and references within). (Charnov, 1989; Futuyma, 1998; Houston & McNamara, 1999; Roff, 2002; Reznick et al., 2000; Stearns, 1992; Stephens & Krebs, 1986).” All recent theoretical and empirical results on signalling support this perspective (Fromhage & Henshaw, 2022; Számadó et al., 2022, 2023). The time is long overdue to reject the HP/costly signalling paradigm and integrate STOT into the framework of life history evolution.

Since the handicap hypothesis (and HP) can be rejected, an alternative theory is needed, we propose the STOT. Every signalling model that has an honest equilibrium under conflict of interest also assumes a signalling trade-off. The presence or absence of condition-dependent, life-history trade-offs can account for both honest and dishonest signals. Signalling trade-offs readily translate short-term investments into long-term fitness benefits, thus provid-

ing the exchange rate between different currencies and between proximate investments and fitness benefits. Signalling trade-offs potentially govern honesty in humans and non-human species, both in biological and economical contexts—though they may not be obvious. We predict that such condition-dependent trade-offs will be found in every honest communication system. Identifying and understanding these trade-offs is crucial for explaining honest and dishonest signals.

Such a change of paradigm will provide the following benefits: (i) It will demonstrate a complete break away from the HP; (ii) it will help to integrate marginal costs and marginal benefits into theory; (iii) it will help to integrate different timescales and proximate and ultimate explanations, as well as better clarify their differences; (iv) it will ground signalling theory in well-established life-history evolutionary theory—rather than continued relation to economic signalling models, based on utility; and (v) it will readily apply to explaining the evolution of dishonest as well as honest signals (vi) it will get rid of the misleading terminology of HP and costly signalling. To achieve a complete paradigm change, much more work needs to be done. We need to re-evaluate the past three decades of research on honest signals in the light of signalling trade-offs. We need to experimentally test the predictions of signalling models and particularly fitness trade-offs in vivo and in vitro, in humans and non-humans (microbes, plants, fungi, animals). We need to integrate research on proximate signal mechanisms with their evolutionary consequences by focusing on how trade-offs at the proximate level influence fitness and vice versa. Finally, the integration of theoretical models on the evolution of honest and dishonest signals is needed. The HP has dominated Signalling Theory for more than three decades, which is the longest non-Darwinian detour in the history of modern biology. It is high time to reintegrate Signalling Theory with modern evolutionary biology.

Glossary

Affirming the consequent (fallacy of the converse): A logical fallacy due to inverting a conditional statement so that the conclusion becomes the premise. For example, Jill got sunburnt in Egypt; Jack has sunburns too, but it is fallacious to conclude that he too was in Egypt. The HP argues that honesty is maintained by costs; but just because a signal involves costs and it is honest does not mean that honesty evolved because of these costs.

Benefit: Positive effects on individual survival, reproductive success, or both (fitness benefit), or any changes in the performance of an adaptive physiological or other mechanism (proximate benefit).

Cheating: Producing dishonest or deceptive signals (see dishonest signal), and the functional definition neither requires nor implies intentionality.

Condition-dependence: Phenotypic plasticity in the expression of signals or other traits that depend upon an individual's condition (quality), i.e., nutritional state, health, etc. Adaptive condition-dependence is often called “strategic.”

Cost/costly: A term used in several very different ways, and especially: (1) Proximate costs refer to the energetic or resource investment into trait expression (regardless of their fitness effects). (2) Fitness costs refer to reduction in survival or reproductive success, which depend upon the evolution equilib-

rium: (see Equilibrium cost). In theoretical models, costs describe a single function, whereas the term trade-offs describes a relation between functions.

Costly signalling theory: Hypotheses and theoretical models aim to explain the selective maintenance of honest signals by differential marginal costs and differential marginal benefits, but are usually mistakenly interpreted as models of the HP (see Penn & Számadó, 2020).

Differential benefit/cost: When signallers of different quality face or realize different benefits/costs.

Dishonest: A signal that is not reliably correlated with an attribute of a signaller (e.g., with quality or identity), and includes deception, in which signals mislead receivers to give responses favourable for the signaller but detrimental for the receiver; conscious intentionality is neither necessary nor implied.

Double-optimization problem: Situations in which a signaller and receiver's signalling strategy vary and depend upon each other's strategy, and therefore, require finding the optima of both parties.

Equilibrium cost: The realized fitness cost of signalling at the evolutionary equilibrium, whereas the out-of-equilibrium cost is a reduction in fitness due to deviating from the equilibrium. Such costs can be calculated in additive fitness models (economics), but it does not make sense in multiplicative models (evolutionary biology). Also see marginal cost.

Fitness: Measures of individual survival (viability or longevity) or reproductive success, though there are various ways to measure Darwinian fitness. It is not a measure of physical fitness, though they may be correlated. Contrary to what is often stated, signals rarely if ever can provide "fitness indicators," as an individual's longevity and lifetime reproductive success are still unknown.

Handicap: Originally, this term referred to a signal with a survival or viability cost (at the evolutionary equilibrium), but then it acquired a new meaning (see Zahavian handicap). The term *cost* is usually interpreted to include either or both proximate and ultimate costs. We recommend avoiding this confusing term.

Handicap hypothesis: Zahavi's proposal that signals need to be costly (or wasteful) in order to be honest. There are many different versions, but this is the generic version, which is usually used.

Handicap principle (HP): Widely used in the loose sense as a synonym for the handicap hypothesis, but in the strict sense, it refers to Zahavi's broader claim that his handicap hypothesis is a general scientific principle that explains honest signals.

Handicap paradigm: Terminology and interpretations of signals and signalling models and empirical data based on the HP.

Honest signal: A signal that is consistently correlated with an attribute of the signaller, such as their condition, status, identity, or resources (versus dishonest signal, see above) and does not require any intentionality by the signaller (see signal).

Index signal hypothesis: The prediction that honesty is due to inescapable physical constraints that make deceptive signals impossible regardless of the potential benefits (Maynard Smith & Harper, 1995, 2003).

Hybrid equilibrium: An evolutionary equilibrium in which low quality signallers use a mixed strategy giving both low- and high-quality signals, and receivers respond with a mixed strategy as well: with probability p , they respond positively

to signals and with probability $1 - p$ they reject them. Such mixed equilibria are expected to evolve when the marginal cost of producing a high-quality signal for low-quality individuals is not high enough to support a separating equilibrium (Zollman et al., 2013).

Life history theory: Analytical framework used to study the evolution of life cycles, which typically focuses on trade-offs between survival and reproduction, including mechanisms and strategies to allocate investment into survival (growth and repair) versus reproduction (number and quality of offspring). A key postulate is that adaptive allocation mechanisms evolve under certain trade-offs and other constraints that limit evolutionary trajectories.

Marginal cost: The cost to increase the intensity or expression of a signal, which can be represented and approximated by the rate of change of the cost function, $C(x)$, defined as the derivative of the cost function $C'(x)$.

Nominal fallacy: A logical error in which it is erroneously assumed that giving a label to a phenomenon explains it.

Potential cost of cheating: The potential fitness cost paid by dishonest signallers (cheaters) if they produce a dishonest signal. It is the marginal cost of cheating. This cost is not paid by honest signallers or when all individuals are at the honest equilibrium.

Proximate cost: Investment of time, energy, or any other resource (such as pigments) into the expression or function of a signal or other trait. Not to be confused with ultimate fitness cost.

Proximate explanations: How biochemical, cellular, physiological mechanisms within individuals work or function. Not to be confused with ultimate or evolutionary explanations for these mechanisms.

Quality: See condition.

Reliable signal: See honesty.

Sexual selection: A type of natural selection due to differential or any non-random mating success (which promotes genetic survival, even sometimes even if it reduces individual survival).

Signal: Any behaviour or structure produced (by a signaller) that functions to transmit information and alter the behaviour of other organisms (receivers) in a way that benefits the signaller. In contrast, *cues* transmit information inadvertently, which may benefit receivers but not signallers. Dishonest signals may benefit the signaller only.

Signal cost: Costs of producing signals either at the proximate or ultimate explanation. The energetic and other proximate costs of signalling have often been confused with the fitness costs of signalling, though they are not equivalent (e.g., signals that require a high investment may have large energetic costs but can still evolve because they have low fitness costs or none). Moreover, increasing signal costs (investment) at the proximate level can increase their benefits at the ultimate level.

Signalling trade-off: A type of constraint that prevents the simultaneous maximization of two or more traits in the context of signalling interactions, e.g., attracting mates versus attracting parasites and predators (see Darwin, 1872; Poulton, 1890).

Signalling trade-off theory (STOT): A general theory proposed here to account for both honest and dishonest signals at equilibrium due to trade-offs depending on signaller condition. The aim is to integrate proximate and ultimate explanations for honest signals, including models previously interpreted as costly signalling or handicaps, i.e., equilibrium fitness costs of signals.

Strategic cost: Signal cost paid on top of the efficacy cost of signals to maintain reliability. The term was introduced (Maynard Smith & Harper, 1995, 2003) as a reinterpretation of the HP by omitting the term “handicap.”

Terminal investment: Increased mating or reproductive effort once individuals face reduced chances of survival (e.g., due to age, health, predation risk). The terminal investment hypothesis predicts that once the trade-offs maintaining honest signalling are removed, cheating can become beneficial.

Trade-off: A type of constraint in which an increase into the investment into the expression or function of one trait results in decreased expression or function of one or more other traits and thus preventing the simultaneous maximization of these traits. Trade-offs can occur with proximate mechanisms (e.g., requiring allocation of energy and resources between different traits), and at ultimate levels (e.g., traits that enhance one fitness component, but reduce another, i.e., “selective trade-offs”). The term is also used to refer to a situation in which a decision or strategic choice requires weighing the available options to find the optimal solution to allocate time, energy, or other limited resources.

Ultimate fitness cost: Negative effects on individual survival or reproductive success (fitness cost).

Ultimate explanations: The explanations of how traits (biological structures, functions, behaviours, etc.) evolve. Not to be confused with proximate explanations.

Zahavian handicap (usually just “handicap”): A hypothetical signal that is honest because it is costly at the evolutionary equilibrium, and evolves because and not despite of its costs, unlike all other traits.

Data availability

The manuscript has no new data.

Author contributions

Szabolcs Számadó (Conceptualization [lead], Funding acquisition [equal], Visualization [supporting], Writing – original draft [lead], Writing – review & editing [equal]), István Zachar (Conceptualization [supporting], Funding acquisition [equal], Visualization [lead], Writing – original draft [supporting], Writing – review & editing [equal]), and Dustin J. Penn (Conceptualization [equal], Funding acquisition [equal], Writing – original draft [equal], Writing – review & editing [equal])

Funding

The authors acknowledge support from the Austrian Science Fund (FWF) (P28141-B25 and P36446-B) and the Human Science Program (RGP0003/2020) (D.J.P.).

Acknowledgments

We would like to thank two reviewers their insightful critiques, Thomas Getty, Sarah Zala and Lutz Fromhage for their comments on an earlier version of the paper.

Conflicts of interest

The authors declare that they have no competing interests.

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Received January 24, 2025; revised October 12, 2025; accepted November 14, 2025

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