Body postures and patterns as amplifiers of physical condition

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The question of why receivers accept a selfish signaller's message as reliable or 'honest' has fuelled ample controversy in discussions of communication. The handicap mechanism is now widely accepted as a potent constraint on cheating. Handicap signals are deemed reliable by their costs: signallers must choose between investing in the signal or in other aspects of fitness. Accordingly, resources allocated to the signal come to reflect the signaller's fitness budget and, on average, cheating is uneconomic. However, that signals may also be deemed reliable by their design, regardless of costs, is not widely appreciated. Here we briefly describe indices and amplifiers, reliable signals that may be essentially cost free. Indices are reliable because they bear a direct association with the signalled quality rather than costs. Amplifiers do not directly provide information about signaller quality, but they facilitate assessment by increasing the apparency of pre-existing cues and signals that are associated with quality. We present results of experiments involving a jumping spider (*Plexippus paykulli*) to illustrate how amplifiers can facilitate assessment of cues associated with physical condition without invoking the costs required for handicap signalling.

Keywords: signalling; handicap; index; amplifier; spider; Salticidae

1. INTRODUCTION

The forces influencing signal design have been the topic of considerable controversy throughout the past three decades. In particular, debate has focused on how signals are designed to reliably or 'honestly' convey information about signaller quality. This ongoing debate has identified three basic constraints that can support honesty as the most common policy: convention, handicap and design. Conventional signals (symbols and icons) exist only in cooperative environments, where the sender and receiver both benefit from the receiver making an appropriate choice of action and cheating offers no incentive (Maynard Smith 1994; Maynard Smith & Harper 1995; Hasson 1997). The two other mechanisms of reliable signalling, handicaps and design, inhabit the 'choice-based signalling environment' where the interests of senders and receivers may not be in close accord (Hasson 1994, 1997). In the choice-based signalling environment, signals are designed to repel receivers if being chosen is detrimental (e.g. rivals, predators) or attract receivers if being chosen is beneficial (e.g. mates, pollinators).

Handicap signals are costly to produce and these costs are directly responsible for signal reliability. A trade-off between investment in signalling and other components of fitness leads signallers to optimize signal intensity (Zahavi 1975, 1977, 1987; Grafen 1990; Hasson 1997; Getty 1998). Individuals with small budgets cannot afford costly signals. For example, Kotiaho *et al.* (1998) found that courtship 'drumming' by male wolf spiders bears costs of massive energy expenditure that is linked with increased mortality. They suggest that these costs dictate drumming rate; spiders having a bigger budget can afford a higher drumming rate. This trade-off is the essence of a handicap signal. Spiders with small budgets could drum at higher rates but are deterred from doing so because the

costs of increased drumming rate would not be adequately balanced by social benefits.

Like handicaps, indices are reliable indicators of their bearer's quality but, unlike handicaps, their reliability is not based on investment strategies of signallers. Instead, their reliability rests on a direct and incorruptible link with the quality of interest to receivers (Hasson 1997). Indices are well portrayed by Maynard Smith & Harper's (1995) example of a tiger reaching up and scratching a tree trunk, thereby signalling its size to subsequent passers by. The maximum height at which scratches are left is defined by physical limits on how high an animal can reach, not costs associated with scratching height. Similarly, a cat arching its back and erecting its fur may demonstrate its size to rivals as an index signal because the maximum attainable profile is dictated by the cat's true size (Hasson 1997). Returning to the example of Kotiaho *et al.* (1998), if the rate of drumming by wolf spiders is set by maximum ability, rather than optimized trade-offs, then drumming rate is an index rather than a handicap. As with handicaps, receivers interpret a more intense index (e.g. higher scratch, taller arch) as indicating a superior signaller.

Amplifiers are a class of reliable signals that alone are not indicators of signaller quality but, through their design, they improve the receiver's ability to assess pre-existing cues and signals (Hasson 1990, 1991, 1997; Hasson *et al.* 1992). For example, colours and patterns that contrast with a background might amplify apparent differences in cues of body size and proportion (Hasson 1991). No amount of amplification will make the bearer seem bigger but any amount will make actual size easier to ascertain. Similarly, the narrow frame of colour outlining a butterfly's wing makes damage to the edges more apparent (Zahavi & Zahavi 1997). These body patterns need not be costly to be informative. The evolution of amplifiers is driven by the benefits to high-quality signallers that make their status unambiguously apparent to

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assessors (Hasson *et al*. 1992). Ideally, amplifiers are cost free and may be fully expressed by all members of a population (although, if condition-dependent, correlation between degree of amplification and signaller quality may arise later; Hasson *et al*. 1992).

Despite their logical robustness and broad applicability (Hasson 1990, 1997; Hasson *et al*. 1992), many researchers appear to have misunderstood or overlooked the potential explanations offered by signals made reliable by design. Maynard Smith & Harper (1995) recognized this shortcoming and accepted indices into the fold as bona fide signals, but did not consider amplifiers. Other theoreticians and empiricists have continued to assume that costs are a prerequisite of reliable signalling (e.g. Johnstone 1995; Zahavi & Zahavi 1997; Getty 1998; Kotiaho *et al*. 1998; Thornhill & Gangestad 1999). The present paper is intended to increase general awareness of signals deemed reliable by design rather than costs. As illustration, we provide a practical example of how amplifiers may increase the apparency of cues associated with body condition in a jumping spider (Araneae: Salticidae) without invoking the investment required for handicap signalling.

Salticids differ from other spiders by possessing remarkably acute vision (Blest *et al*. 1990) that permits them to visually discriminate amongst prey and conspecifics from as far as 30 cm (Jackson & Blest 1982; Harland *et al*. 1999). They are heavily reliant on their acute vision during intraspecific interactions, all studied species having characteristic displays (Crane 1949; Richman 1982). The display repertoire of many species contains elements in which the abdomen is presented prominently to conspecifics. In the case of *Plexippus paykulli*, males raise their bodies and lower their abdomens, exposing the abdomen's ventral surface to their prospective mate or rival directly beneath the 'face' (figure 1; Jackson & McNab 1989*a*). On its ventral surface, the spider's abdomen has a dark central 'patch' surrounded by pale 'margins' that extend up the lateral surfaces (figures 1 and 2). These patterns are absent in juveniles and females, who do not partake in courtship at all and have only rudimentary agonistic repertoires (Crane 1949; Jackson & McNab 1989*a*). The correlated emergence of contrasting body patterns and highly ritualized intraspecific communication suggests a signalling role for these adornments.

How might abdominal exposure and patterns function in signalling? Like many other animals, spider contests and courtship appear energetically demanding (Watson & Lighton 1994; Kotiaho *et al*. 1998). Salticid interactions typically involve a great amount of 'dancing', accompanied by abdominal vibrating and leg waving (Crane 1949; Richman 1982) and there is evidence that females of one salticid, *Phidippus johnsoni*, discriminate against males that fail to dance (Jackson 1981). Body condition of males may be relevant to females as an indicator of heritable foraging prowess, metabolic competence or health. Hence, quality as rivals or mates probably varies with energy stores ('condition') and this is a quality that should be of interest to interacting conspecifics. In nature, spiders often suffer suboptimal nutrition and an individual spider's poor condition is evident in its diminished abdominal dimensions (Anderson 1974; Forster & Kavale
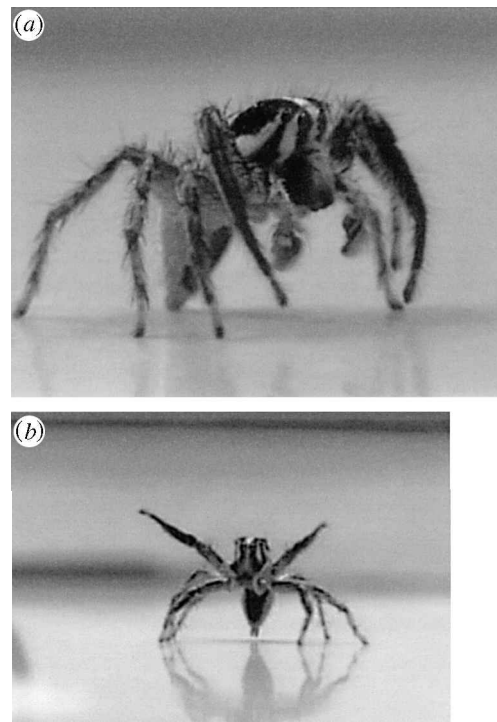
Figure 1. *P. paykulli* male (*a*) in a 'hunch' posture, displaying to a conspecific rival and (*b*) in a 'raised body' posture, displaying to a conspecific female. For details of display definitions and interaction sequences, see Jackson & McNab (1989*a*).

1989; Wise 1993). Other spider body parts are constrained by a rigid external skeleton and do not change with condition. In nature, we have collected *P. paykulli* with abdomens ranging from plump and taught to thin and shrivelled suggesting that this species is subject to highly variable condition. This variation sets the stage for the evolution of assessment and decision-making systems ('biases'), and signals that exploit them (Hasson 1999). Exposure of the abdomen might serve as an amplifier, facilitating assessment of abdominal dimensions and hence condition. Along with variation in abdominal size, our casual observations lead us to suspect that, compared with emaciated conspecifics, 'plump' spiders have distinctly wider abdominal margins but similar width patches (figure 2). If a spider's condition is more evident as variation in margin width than in overall abdominal dimensions, then abdominal patterns may also be interpreted as amplifiers of abdominal dimensions and associated energy reserves. We here present data that support this idea and hence illustrate how an amplifier can reliably reveal quality without invoking a costly handicap.

2. MATERIAL AND METHODS

(a) *Spiders in nature*

Forty-seven *P. paykulli* males were collected from nature around Rehovot, Israel, between March and September 1997. Within 6 h of collecting, each spider was weighed to the nearest microgram on a Sartorius RD2400 electronic balance. Immediately afterwards, the spider was transferred to a syringe with a clear cover-slip fastened to the end. The spider was gently pressed flat against the cover-slip so that the ventral surface was presented for video recording (Panasonic GP-US502E sVHS,
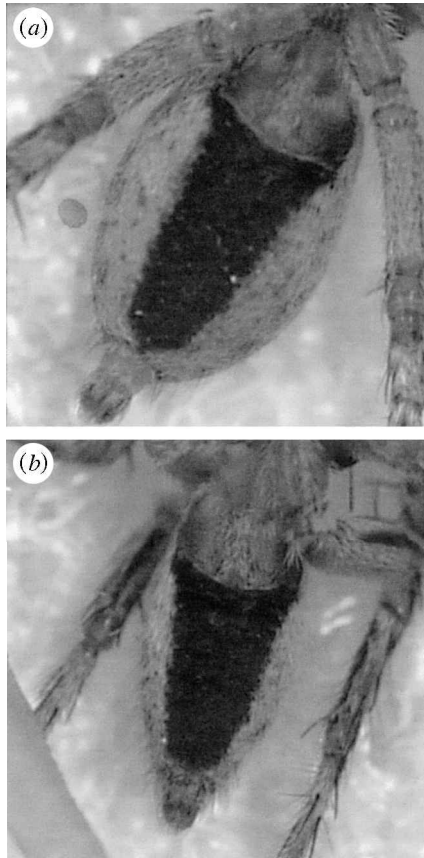
Figure 2. Images taken from video recordings of a representative spider on (*a*) the day after feeding and (*b*) after 20 days without food in the laboratory.

Sigma *f* 2.8 50 mm macro lens). Recorded images were transferred to a computer (Power MacIntosh AV 7600) for scaling and measurement in NIH Image, a public domain program from United States National Institutes of Health. Measurements included (i) length of patch along midline, (ii) width of patch at patch length midpoint, and (iii) width of abdomen at patch length midpoint (figure 2). Margin width was later determined as abdomen width minus patch width. As a general measure of body size, we used distance between the outer margins of the posterior medial eyes (hereafter, 'size'). This measure is close to the maximum carapace width, a popular measure of spider size (Jakob *et al.* 1996; Taylor & Jackson 1999). Because the carapace is heavily sclerotized, its dimensions do not vary with condition.

(b) *Effects of food deprivation in the laboratory*

The investigation of spiders in nature only considers variation between individuals. This second experiment was primarily intended to illustrate how variation in condition within a group of spiders is correlated with changes in abdominal dimensions. A secondary objective is to make some estimate of spider condition in nature in terms of equivalent days of deprivation in the laboratory.

Seventeen *P. paykulli* males were selected at random from our laboratory population. After *ad libitum* access to house fly (*Musca domestica* L.) adults, pupae and larvae as prey for two weeks, the spiders were transferred to clean cages and, for 20 days, were given no further sustenance. At 0, 2, 4, 8, 12, 16 and 20 days after feeding ceased, we assessed their weight and abdominal dimensions as for the spiders collected in nature.

3. RESULTS

(a) *Spiders in nature*

Each of the body dimensions measured was positively associated with size (table 1). Variance in patch width is most completely accounted for by size; patch length and abdominal width are intermediate, and margin width bears by far the weakest relationship with size. Hence, a greater proportion of variation in margin width must be accounted for by variation from other sources, such as condition.

After removing size effects (table 1), there is significant correlation between residual weight and residuals in each of the abdominal dimensions (table 2). Abdominal width, margin width, and patch length are of similar absolute variability (residual s.d.) and bear similar degrees of correlation with residual weight (table 2). However, margin width bears a coefficient of variability that is approximately two and a half times that of abdominal width and patch length, and three times that of patch width. Clearly, an assessor paying attention to margin width may more readily detect variation in condition than it would by instead paying attention to any other abdominal dimension.

(b) *Effects of food deprivation in the laboratory*

Over the 20-day period of food deprivation, spiders steadily lost weight and all abdominal dimensions varied accordingly; patches became shorter, abdomens became narrower, patches became narrower and the margins became narrower (figures 2 and 3). However, a change in patch width was minute in comparison with the change in margin width such that almost all of the change in abdominal width was accounted for by the sharp decline in the pale margins (figures 2 and 3). Comparing the relationship between size and weight of spiders collected in nature with spiders after varying latencies since feeding in the laboratory suggests that, on average, spiders in nature are in a condition similar to after 20 days without sustenance under laboratory conditions (figure 4).

4. DISCUSSION

(a) *Information of patterns*

Our results are consistent with the possibility that abdominal patterns of *P. paykulli* males function as amplifiers of differences in abdominal width, and therefore condition. By providing the patch as a (size-dependent) landmark defining the limits of a region of little interest to an assessor of condition, attention is focused on the region of greatest sensitivity to changes in body condition. The margins alone account for almost all of the variation in abdominal width and, being smaller, offer a far greater coefficient of variability than does overall abdominal width (table 2). Hence, a given absolute change in abdominal dimensions is associated with a greater, and therefore more apparent, proportional change in margin width. Naturally, this system requires some constraint on the relationship between body size and patch dimensions to prevent cheats that evolve narrower patches to give the appearance of better condition. One possibility is that, along with other features (e.g. face width, leg length), patch width serves simultaneously as a signal of size. This

Table 1. *Relationships between spider size (distance between outer margins of posterior medial eyes) and each of the assessed parameters*

	equation	r^2	$F_{1,46}$	p
weight (mg)	$291.3 - 321.6 \times \text{size} + 96.7 \times \text{size}^2$	0.91	226.992	< 0.001
patch length (mm)	$-1.778 + 1.850 \times \text{size}$	0.49	42.335	< 0.001
abdominal width (mm)	$-1.265 + 1.589 \times \text{size}$	0.43	33.081	< 0.001
patch width (mm)	$-0.695 + 0.935 \times \text{size}$	0.55	54.500	< 0.001
margin width (mm)	$-0.570 + 0.654 \times \text{size}$	0.13	6.365	0.015

Table 2. *Residual s.d. and residual coefficient of variation ($CV = (\text{residual s.d.}/\text{predicted mean}) \times 100$) for spiders of sizes 2.0, 2.2 and 2.4 mm in each of the residual abdominal dimensions and their Pearson correlation with residual weight*

(Chosen spider sizes are close to 10 percentile, median and 90 percentile of the wild population. All residuals and predicted means are from equations in table 1.)

		CV (%)				
	s.d. (mm)	2.0 mm	2.2 mm	2.4 mm	r_{47}	p
patch length	0.23	11.8	9.9	8.6	0.69	< 0.001
abdominal width	0.22	11.5	9.9	8.7	0.72	< 0.001
patch width	0.10	8.6	7.4	6.5	0.32	0.028
margin width	0.21	28.1	23.8	20.7	0.61	< 0.001

is consistent with the patch's limitation to a region that changes little with condition. Hence, any attempt to appear of better condition through a narrower patch might make the bearer appear smaller.

It is important to note that abdominal markings, which are established at the final moult to adulthood, are not themselves indicators of quality; all individuals apparently possess these markings more or less in accord with their body size. Actual pigmentation patterns, which make up the amplifier, do not change with condition. This precludes interpretation as handicap or index signal. Assessment is facilitated only because this fixed amplifier shows up changes in abdominal dimensions. Because they are fixed upon their development at the final moult to adulthood, patches such as those on the abdomen of *P. paykulli* cannot be condition-dependent amplifiers. On the other hand, behavioural amplifiers such as abdominal exposure may be condition dependent, with high-quality individuals tending towards greater amplification (e.g. more frequent or prolonged abdominal exposure).

(b) Abdominal exposure and patterns in other salticids

Abdominal exposure is amongst the most common display elements in the interactions of salticids from diverse geography, taxonomy and lifestyle. Like males of *P. paykulli*, many other salticids raise their bodies and point their abdomens downward during interactions, exposing the abdomen's ventral surface to rivals or potential mates (*Corythalia canosa*, Jackson & McNab 1989*b*; *Maevia inclemens*, Clark & Uetz 1993; *Trite planiceps*, Taylor & Jackson 1999). Some other species hold the abdomen upward (*Gertschia noxiosa*, Crane 1949; *Myrmarachne lupata*, Jackson 1982; *Marpissa marina*, Jackson *et al.* 1990; *Asemonea tenuipes*, Jackson & McNab 1991) or to the side (*Ashtabula*

furcillata, Crane 1949), similarly exposing characteristic abdominal surfaces to conspecifics. In the literature, these behaviours have consistently been referred to as displays, but little thought has been given to the kind of information that might be conveyed. Many salticids resemble *P. paykulli* in that the abdomen is marked with strongly contrasting patterns that might aid in the resolution of abdominal dimensions, and thereby condition. Overall, amplification of physical condition is a compelling hypothesis.

(c) Patterns as amplifiers of condition in other animals

Similar examples of physical condition amplified by postures and body patterns may be common throughout the animal kingdom (see Hasson 1991). Many visually competent animal species possess characteristic body patterns and thereby offer assessors a standard that might be used to compare different individuals. For example, the medial line and vertical bar displays used during contests of *Nannacara anomala*, a cichlid fish, may amplify both size and condition (Hurd 1997). Zahavi & Zahavi (1997, pp. 48–49) present one especially pertinent example. A student researcher was reportedly able to discern a water-buck's condition from behind by assessing a white patch on their rump. On healthy animals the patch was round but on emaciated animals, the white patch had the shape of a pointed ellipse because of the atrophied hind leg muscles. They suggest that rump patches function in communication of physical condition to predators, rivals and mates, all of which should be interested in this quality. Characteristically, the Zahavis interpret this and similar signals as handicaps (in particular, see Zahavi 1978), but we instead choose this as an excellent illustration of the amplifier mechanism. To be a handicap, maintaining the
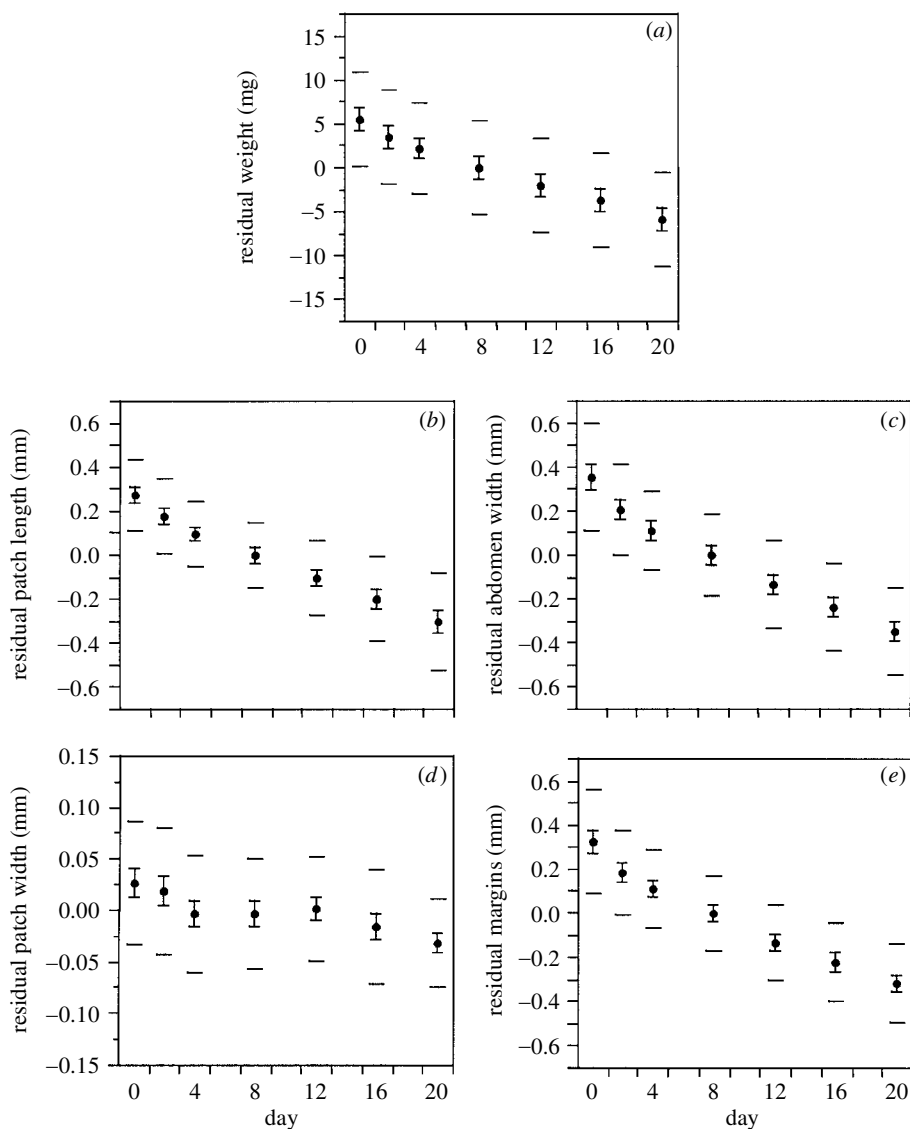
Figure 3. Variation in residual dimensions (after removing size effects) over 20 days of food deprivation in the laboratory. Circles are means, connected lines are standard errors and disconnected lines are standard deviations. Patch length, abdominal width and margin width span similar scales whereas patch width spans a much smaller scale (compare *y*-axes).
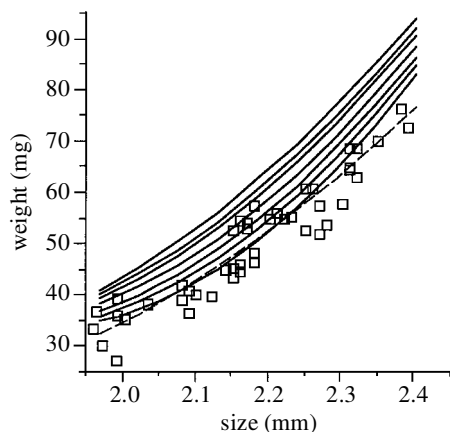

Figure 4. Relationship between size and weight for spiders collected in nature (dashed line and data points) and in the laboratory experiment after 0, 2, 4, 8, 12, 16 and 20 days without sustenance (solid lines descending from 0 days at top to 20 days at bottom). On average, spiders in nature are of a condition similar to that reached after approximately 20 days without sustenance in the laboratory.

patch 'roundness' should be costly such that only healthy animals can afford the cost of a round patch. However, the actual pigmentation patterns on the hair and hide do not change with condition and the patches are not themselves the source of any obvious short-term maintenance cost. The patches are effectively fixed and cost free and therefore cannot possibly be maintained as handicap signals (or indices). Instead, by providing a landmark on a region subjected to variable changes in hide tension as condition changes (lateral tension changes mostly at the bottom of the patch as muscle mass diminishes), they simply increase the apparancy of (i.e. amplify differences in) muscle mass. It is conceivable that individual water-buck sometimes dedicate resources to hind leg muscle mass specifically for signalling purposes and this signalling component would be open to interpretation as a handicap. However, this handicap is quite separate from its amplifier, which maintains identical function regardless of whether the amplified quality remains unmodified as a cue or has been modified as a signal.

The fact that signal reliability may be maintained by costly handicaps is not in question here. However, we dispute the common assumption that costs are a prerequisite of reliable signalling. The conclusions reached in science depend on the questions asked and so adherence to hypotheses based only on any single mechanism is surely a poor test of individual cases. Hence, design-based alternatives to the handicap mechanism of honest signalling should be considered, even if only so that they are equally exposed to disproving.

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