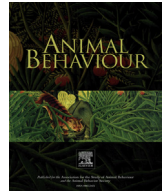




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Social costs are an underappreciated force for honest signalling in animal aggregations

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Animals in social aggregations use signals of quality or motivation to attract mates and intimidate rivals. Theory indicates that honesty can be maintained in these signals if the costs of signalling affect low-quality individuals more than they affect high-quality individuals. Considerable research has focused on identifying the nature of those costs and their ability to maintain honest signals. Much of this research, particularly in recent years, has focused on receiver-independent physiological costs of signal production. Less research attention has been paid to receiver-dependent costs that might arise from conspecific responses to signals. Here we survey the literature on these different types of costs, focusing in particular on case studies from a diversity of taxa. We find that signals often do carry significant physiological production costs, but this is not universal, as many signals appear to be physiologically inexpensive to produce. More importantly, very few studies have tested the key prediction that physiological production costs differentially affect low-quality individuals over high-quality individuals. In contrast, research from a diversity of taxa indicates that signals such as coloration and vocalizations often affect agonistic interactions, which in turn affect the production of signals, and that deceptive signallers receive more aggression than do honest signallers in at least some systems. Social costs are a plausible but understudied mechanism for maintaining honest signalling.

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Communication, which involves the exchange of information via a signal between a signaller (sender) and a receiver that leads to a response by the receiver, is a fundamental and ubiquitous characteristic of life (Bradbury & Vehrencamp, 2011). Prime examples come from aggregations of animals that come together to forage or breed: males on leks produce complex courtship signals to advertise their suitability to potential mates (e.g. Barske, Schlinger, & Fusani, 2015; Krakauer et al., 2016; Laird, Clements, Hunter, & Taylor, 2016), females in communally breeding groups often signal group membership and kinship (e.g. Gamboa, Reeve, & Pfennig, 1986; Riehl & Stern, 2015; Tibbetts & Dale, 2007), and breeders in nesting colonies signal their quality to intimidate rivals (e.g. Poston, 1997; Price, Earnshaw, & Webster, 2006; Tibbetts & Dale, 2004). For such signals to be evolutionarily stable, both the signaller and the receiver must benefit from the receiver's response to the signal (Searcy & Nowicki, 2005), which in turn requires that the signal be honest, at least on average (Johnstone & Grafen, 1993).

Take, for example, males using a complex physical display to signal their quality (among other things; Hill, 2015) to females on a lek: females would be selected to ignore the display if it did not provide accurate information about male quality, and males would be selected to drop the display if females did not respond to it. Accordingly, a fundamental issue for understanding communication is the identification of the factors that maintain signal honesty.

The simplest signalling scenario comes from cases where both the signaller and the receiver benefit from the accurate exchange of information, i.e. mutualism where the interests of the signaller and receiver align (Faser, 2012; Higham, 2014; Maynard Smith & Harper, 2004). For example, animals in aggregations often use a suite of signals to warn others about approaching predators (Manser, 2001; Templeton, Greene, & Davis, 2005). The receiver benefits from these 'alarm calls' by gaining information about an impending threat, and in many cases the signaller also benefits by warning close kin (e.g. Sherman, 1977) and reducing the likelihood that the predator will be successful (e.g. Sherman, 1985; Wheeler, 2008). In such cases we expect the signalling system to be stable, and even to evolve further to increase the quality and quantity of information exchanged (e.g. Templeton et al., 2005). Even so, signallers sometimes give and benefit from deceptive alarm calls (Flower, Gribble, & Ridley, 2014).

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Such deceptive signalling can be maintained if the costs to the receiver of not responding to the signal are high, but even then receivers will be selected to ignore the signal if it becomes too unreliable or ineffective (Doerr & Endler, 2015; Laidre & Johnstone, 2013; Leighton, 2014; Searcy & Nowicki, 2005).

Cases where the fitness interests of the signaller and the receiver do not fully overlap are more challenging to explain. A lek-breeding male, for example, will benefit from exaggerating his own quality if such exaggeration leads to a better position in the lek (e.g. through intimidating rivals) or to higher mating success (e.g. through successful courtship with females). Similarly, in cooperatively breeding groups, helpers may sometimes benefit from inaccurately signalling the amount of alloparental care they are willing to provide (Boland, Heinsohn, & Cockburn, 1997; Canestrari et al., 2010; Doutrelant & Covas, 2007), because helpers are often more closely related to their own future offspring than they are to the young being raised (Hamilton, 1964). Yet courtship, aggressive and cooperative signals persist, and appear to be generally honest, at least on average. What are the mechanisms that ensure this honesty?

Zahavi (1975, 1977) was among the first to suggest that signals can be 'handicaps' that carry costs, and that these costs may be central to maintaining honest signalling. Although initially criticized (e.g. Kirkpatrick, 1986; Maynard Smith, 1976), Zahavi's handicap hypothesis eventually gained wider acceptance, particularly after theoretical models eventually emerged to show that the mechanism is both plausible and compelling (e.g. Godfray, 1991; Guilford & Dawkins, 1991; Isawa, Pomiankowski, & Nee, 1991; Johnstone & Grafen, 1992; Maynard Smith, 1991; Pomiankowski, 1987). Particularly important were models by Grafen (1990) and Johnstone (1995a, 1997) that made explicit a fundamental assumption of Zahavi's model: costs (or 'handicaps') can maintain honest signalling if those costs have differential effects on high- and low-quality individuals (but see Getty, 1998). That is, selection will act against exaggerated signals of quality if the costs of signalling at a particular level are higher for low-quality individuals than they are for high-quality individuals.

The early theoretical work demonstrated the importance of differential costs to maintaining honest signalling, and consequently research has turned to understanding the nature of those costs. A number of different types of costs have been proposed. For example, because ornamental signals used in courtship often make males more conspicuous (Endler, 1980; Zeh & Zeh, 1988) or less mobile (Balmford, Thomas, & Jones, 1993), it is possible that ecological costs such as increased predation or reduced foraging limit elaboration of such signals and maintain honesty. However, studies examining the predation costs of ornamental signals have produced mixed or equivocal results (Götmark & Hohlfalt, 1995; Götmark & Olsson, 1997; Olsson, 1993; Stuart-Fox, Moussalli, Marshall, & Owens, 2003), and in particular there is little evidence that, for any given level of ornament expression, higher-quality individuals are better able to evade predators than are low-quality individuals (i.e. differential costs; but see Møller & de Lope, 1994).

Although ecological costs of signals have an intuitive appeal that was recognized by Darwin (1871), more recently other types of costs have been proposed as being particularly important to the evolution of honest signals. First, the physiological mechanisms that lead to signal expression may carry costs, for example through correlated effects on other physiological processes. If so, then such physiological costs can maintain honesty if those costs are higher for low-quality individuals than they are for high-quality individuals (Alonso-Alvarez, Bertrand, Faivre, Chastel, & Sorci, 2007; Folstad & Karter, 1992). Alternatively, if signals increase the likelihood or intensity of aggressive interactions with conspecifics, and low-quality individuals suffer higher costs than do high-quality

individuals from such interactions, then social costs can maintain honesty (Johnstone & Norris, 1993; Tibbetts & Dale, 2004; Tibbetts, 2014). Indeed, social costs have been proposed as being important to the evolution of 'badges of status' among individuals in foraging flocks (Chaine, Roth, Shizuka, & Lyon, 2013; Rohwer, 1975, 1977, 1982), and might also be important to signalling in breeding and other social aggregations as well (Tibbetts & Dale, 2004; Tibbetts, Crocker, & Huang, 2016).

In recent years, rapidly improving methodologies have allowed integrative biologists to examine the mechanisms of signal production in some detail (e.g. Fusani, Barske, Day, Fuxjager, & Schlinger, 2014; Fuxjager, Longpre, Chew, Fusani, & Schlinger, 2013, 2015; Riede, Forstmeier, Kempnaers, & Goller, 2015), and as a result physiological costs have become a major focus of work on honest signalling. Indeed, research on physiological costs has eclipsed work on other costs that might maintain honest signalling (Fig. 1) to such an extent that one might infer that physiological costs are the primary factor maintaining honest communication. Although physiological costs may be important, our view is that it is premature to conclude that physiological costs are the primary factor maintaining honest signalling, and we instead suggest that social costs are more important and prevalent than previously suspected.

Here we outline several key predictions of the physiological cost and social cost hypotheses. The intent is not to develop the hypotheses themselves, as this has been done elsewhere (e.g. Hill, 2011; Tibbetts, 2014). Nor do we offer a detailed classification of the different types of costs, because this also has received attention (e.g. Higham, 2014; Searcy & Nowicki, 2005). Rather, our intent is to

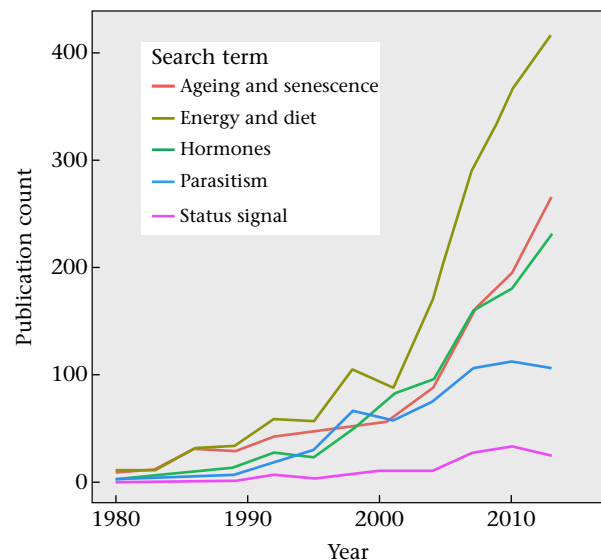


Figure 1. Publications on costs of signalling over time. Plotted are the number of publications in each of the categories from 1979 to 2016 from a select subset of animal behaviour, evolutionary biology and physiological journals. We used a subset of journals as some of the search terms (specified below) routinely returned hundreds or thousands of entries from neurobiology journals; these articles were not relevant to signalling in animal aggregations and were removed by using a more relevant subset of journals. The plot was generated using the frequency polygon function in ggplot in R and publications were binned in 3-year intervals. The search terms that composed each of the categories were as follows: status signal ('social cost', 'socially enforced', 'badge of status', 'badges of status', 'social punish*', 'status signal*', 'retaliation'), age ('age*', 'senesc*'), energy and diet ('energ', 'nutri*', 'diet*', 'oxida*'), hormones ('androgen', 'testosterone', 'corticoster', 'cortisol', 'juvenile hormone', 'serotonin', 'octopamine'), parasitism ('parasit*'). In addition to the search terms listed above that were specific to the categorical searches, we also included general search terms that were required of each paper; these general search terms were ('social*' or 'sexual*') and ('signal*' or 'ornament*').

clarify the predictions that can be used to test these hypothesized costs, and therefore resolve which type of costs are most important to maintaining honest signalling. We then review some of the available evidence in light of those predictions, focusing on instructive case studies that underscore ideas about the costs maintaining honest signalling. From this review we conclude that physiological costs may be important in the maintenance of honest signals in some cases, but that they may not be as general an explanation for honest signalling as frequently assumed. Rather, the social consequences of dishonest signalling appear to be important in many cases. This may be particularly so for animals communicating in aggregations, where signals of status and/or individual identity should be favoured by intense competition for resources (e.g. food or breeding sites) and frequent interactions with conspecifics that often are unfamiliar (Whitfield, 1987). Indeed, comparative analyses have indicated that such signals are often associated with colonial breeding and/or group foraging during the nonbreeding season (Dey, Valcu, Kempenaers, & Dale, 2015; Tibbetts & Safran, 2009). Although this hypothesis was first proposed by Rohwer (1975, 1977) decades ago, it has received relatively little research attention since (Fig. 1). We conclude by arguing for a more holistic approach that utilizes strong-inference to examine possible social mechanisms that may enforce honest signalling.

PREDICTIONS OF THE HYPOTHESES

Physiological, or Receiver-independent, Costs

The production of a signal, such as a vocalization or conspicuous colour patch, depends on several inherent, or receiver-independent mechanisms, and this hypothesis suggests that those mechanisms carry fitness costs for the signalling individual. Such costs might arise, for example, if the signal production has pleiotropic effects on other physiological processes (Ducrest, Keller, & Roulin, 2008; Wittkopp & Beldade, 2009) or utilizes resources that could otherwise be used for self-maintenance. For example, in birds and other vertebrates, a number of male sexual signals – such as song production (Ball, 1999; Enstrom, Ketterson, & Nolan, 1997), coloration (Blas, Pérez-Rodríguez, Bortolotti, Viñuela, & Marchant, 2006; Eens, Van Duyse, Berghman, & Pinxten, 2000; Vandenbergh, 1965) and courtship displays (Chastel et al., 2005; Day, McBroom, & Schlinger, 2006; Hutchison, 1970) – depend on the androgen testosterone for development or full expression. At the same time, testosterone has several demonstrated pleiotropic effects that can potentially reduce fitness, such as increased energy consumption (Buchanan, Evans, Goldsmith, Bryant, & Rowe, 2001), increased signalling or activity levels that can attract predators (Hughes, Kelley, & Banks, 2012; Marler & Moore, 1989; Zuk & Kolluru, 1998), and physiological effects such as reduced immunocompetence and antioxidation activity (Alonso-Alvarez et al., 2007; Buchanan, Evans, & Goldsmith, 2003; Fuxjager, Foutopoulos, Diaz-Uriarte, & Marler, 2011). It is therefore reasonable to hypothesize that these negative pleiotropic effects of testosterone underlie honesty in some testosterone-dependent traits, and similar arguments can be made for other physiological costs of signal production (e.g. physiological stress; Bortolotti, Mougeot, Martínez-Padilla, Webster, & Piertney, 2009).

A challenge to this hypothesis is that testosterone itself is not a 'cost' per se, but rather a chemical signal within the organism; whether the hormonal signal induces a fitness cost for the organism will be mediated by the social and ecological environment (Higham, 2016). This also will hold for other hormones (Beehner & Bergman, 2017). Indeed, the physiological mechanisms involved in signal production themselves can evolve, and would be expected to do so such that correlated effects of signal production become less costly, and accordingly less able to maintain honesty (see

Wedekind & Folstad, 1994). If, for example, production of a plumage signal requires high levels of testosterone, which suppresses immune function to negatively affect fitness, then selection should strongly favour those individuals that can produce the plumage signal with lower amounts of testosterone, for example through increased tissue-specific sensitivity to testosterone via increased receptor density (e.g. Fuxjager et al., 2015). Similarly, if testosterone suppresses parental care in a manner that negatively affects fitness, then selection should favour individuals that decouple signal production and/or parental care from testosterone (Hau, 2007). Such dynamics are similar to selection in 'green beard' traits (Dawkins, 1976) where selection is expected to break the association between cost and benefit so that the signal loses the cost while maintaining the benefit (Gardner & West, 2010).

Signalling systems that rely on physiological costs to maintain honesty should only occur where selection cannot decouple signal production from costly physiological processes. In such cases, signals maintained by unavoidable physiological costs may best be considered 'index signals'; that is, signals that are causally linked to individual quality, such that they cannot be 'faked' (Bradbury & Vehrencamp, 2011; Maynard Smith & Harper, 2004). For example, the growth of some male signals, such as beetle horns, appears to be regulated by the insulin pathway, which is highly conserved and regulates growth overall, such that low-nutrition individuals cannot grow large horns (Emlen, Warren, Johns, Dworkin, & Lavine, 2012; see also Kuo et al., 2012) despite the fact that these traits appear not to be costly (e.g. McCullough, Weingarden, & Emlen, 2012). Similarly, the expression of some signals of quality may be inextricably linked to basic cellular processes (Hill, 2011). Moreover, it is likely that costly signals evolve to become index signals due to the costs of dishonesty (Biernaskie, Grafen, & Perry, 2014).

Despite these concerns, the physiological costs (i.e. receiver-independent) hypothesis makes several testable predictions (Table 1). One is that the mechanisms of signal production should negatively affect other traits, such as other behaviours (e.g. activity levels, parental care), immune function, or other important physiological processes. This prediction has been the focus of much of the research shown in Fig. 1, and by and large the prediction has held true in many systems: the mechanisms of signal production often do appear to have negative effects on other traits. Testosterone, for example, often does appear to suppress behaviours like parental care (e.g. Ketterson, Nolan, Wolf, & Ziegenfus, 1992; Peters, Cockburn, & Cunningham, 2002), as well as the immune system (Mougeot, Irvine, Seivwright, Redpath, & Piertney, 2004; Oppliger, Giorgi, Conelli, Nembrini, John-Alder, 2004; Peters, 2000) and antioxidation (Alonso-Alvarez et al., 2007; von Schantz, Bensch, Grah, Hasselquist, & Wittzell, 1999), in many vertebrates. However, and importantly, this is not universally the case: testosterone appears to have little effect on parental care and aggression (e.g. Lynn, Hayward, Benowitz-Fredericks, & Wingfield, 2002; Trainor & Marler, 2001; Van Duyse, Pinxten, & Eens, 2000) or on immune/antioxidation function (e.g. Hasselquist, Marsh, Sherman, & Wingfield, 1999) in some systems, pointing to the possible evolutionary malleability of these effects. Moreover, evidence for immunosuppression by testosterone comes mostly from correlational studies, whereas evidence from experimental studies is ambiguous (Roberts, Buchanan, & Evans, 2004).

Two other predictions of the physiological costs hypothesis appear to have received less attention. First, the negative effects on other traits must impose a fitness cost if they are to maintain honest signalling. Although it may seem intuitive that the effects outlined above will likely have negative fitness consequences, this may not hold true in many cases, and the connections between physiological effects and fitness have not been made in most studies. For instance, a suppressed immune system may not necessarily lead to

Table 1
Predictions of the receiver-dependent and receiver-independent cost hypotheses

Questions to ask when differentiating the factors maintaining signal honesty	Receiver dependent	Receiver independent	Source
Can signals be cheap to produce?	Yes	No, signal production is costly (although relatively less so for high-quality individuals)	Dawkins & Krebs, 1978
Is there a cost of the signal if no one sees it?	No, not necessarily	Yes	Rohwer, 1975; Tibbetts & Dale, 2004
Does production cost depend on the form of the signal?	No (connection between signal and information is arbitrary)	Yes (high-quality signals are necessarily more costly than low-quality signals)	Hurd & Enquist, 1998; Maynard Smith & Harper, 2004; Tibbetts, 2013
What happens to Trojan horses (undersignalling)?	Longer/harder aggressive interactions (or other social costs)	Reduced physiological costs, potentially leading to improved condition	
What happens to bluffers (oversignalling)?	Receive disproportionate aggression (or other social costs) from conspecifics	Reduction in physiological condition and/or other vital processes (e.g. immunocompetence)	

disease (see discussion in Zuk & McKean, 1996), and females will often compensate for reduced male parental care (e.g. Harrison, Barta, Cuthill, & Székely, 2009; Saino & Møller, 1995). Second, and critically, if physiological costs are to explain honest signalling, then the costs of signalling must differentially affect low-quality individuals more than high-quality individuals (Grafen, 1990). This is because the costs of signalling at a high level must outweigh the benefits for low-quality individuals but not for high-quality individuals, if honest signalling is to be stable. If differential costliness does not hold, physiological costs of signal production will not prevent low-quality individuals from signalling at a high level (i.e. bluffing), regardless of whether those costs are low or high (Higham, 2014). Consider, for example, increased activity levels that might be induced by the high levels of testosterone needed to produce some signal of quality. Increased activity may attract the attention of predators, but if high- and low-quality individuals are equally able (or unable) to escape a predator's attack, then the costs (and benefits) of signalling are equal across individuals of varying quality, and all individuals should signal at the level that maximizes the payoff (i.e. benefit – cost) independent of quality. Such differential costs are a critical prediction of the physiological costs hypothesis, yet this prediction appears to have been tested very rarely: in our survey of the literature (Fig. 1, Supplementary Table S1) we found very few studies that demonstrate differential physiological costs of signal production (but see Kotiaho et al., 1998; Møller & de Lope, 1994; Roberts & Peters, 2009).

Social, or Receiver-dependent, Costs

Social costs of a signal are incurred when conspecifics, such as other members of a social group, respond to the signal in a way that leads to fitness costs for the signaller, for example if males are aggressive to other males that signal high dominance or quality (Senar, 1999; Tibbetts, 2013). For the signal to persist, the fitness benefits of signalling must outweigh those costs, which can lead to honest signalling of quality if the fitness costs are differential and scale to individual quality. Under this hypothesis, the costs of signalling are receiver dependent, in the sense that the signal is not costly to produce in the absence of those receivers (Searcy & Nowicki, 2005). Thus, social costs can explain the evolution of 'conventional' signals of quality that appear arbitrary and cheap to produce (Higham, 2014; Hurd, 1997; Lachmann, Számadó, & Bergstrom, 2001). Indeed, these receiver-dependent costs are often 'potential costs', in that they typically are not realized unless the receiver punishes a signaller, and so will not be costly to produce under most conditions of honest signalling (Higham, 2014; Számadó, 2011).

The responses of conspecific receivers can maintain honest signalling via two different mechanisms. First, honest signalling

could arise if conspecifics detect and 'punish' individuals that falsely signal. In this scenario, receivers use other cues to assess degree of incongruence between signalled quality and actual quality (or motivation), punishing those individuals with greater incongruence, but signals persist because they lower the overall costs of competition, on average, for both signaller and receiver (Caryl, 1982; Maynard Smith, Harper, & Brookfield, 1988; Moynihan, 1982). Originally developed to explain signalling in winter foraging flocks of birds, this 'incongruence hypothesis' (Rohwer & Rohwer, 1978) predicts that level of signalling is correlated with individual quality, and critically that aggression received from conspecifics is correlated with a mismatch between level of signalling and individual quality. Second, honesty also could arise if conspecifics are aggressive towards any individual signalling high quality, but low-quality individuals suffer higher fitness costs from this aggression than do high-quality individuals (Tibbetts, 2014). This seems particularly likely to apply in signals of dominance, where dominant individuals should be likely to respond to challengers. The predictions of this 'king-of-the-hill hypothesis' are very similar to the incongruence hypothesis, except that aggression towards signallers is correlated with the degree of signal expression, independent of the actual quality of signaller, rather than with the mismatch between the signal and the signaller's actual quality.

One strength of these receiver-dependent costs hypotheses is that the mechanism to maintain honesty is itself under positive selection, because individuals in a population should be selected to challenge others, at least in some contexts (Parker & Ligon, 2002; Tibbetts & Izzo, 2010; Tibbetts, 2008). For example, high-ranking individuals should be 'on guard' for challenges from below, and low-ranking individuals should seek to increase their own rank by testing higher-ranking individuals, as increases in dominance are often associated with fitness benefits (Bell et al., 2014; Thompson, Donaldson, Johnstone, Field, & Cant, 2014). Accordingly, social mechanisms maintaining signal honesty are expected to be maintained by selection, in contrast with the physiological costs hypothesis, where selection should favour production of signals via less costly mechanisms (see above).

CASE STUDIES

In this section we present evidence from three systems that highlight one or more important points about receiver-dependent costs. The taxonomic breadth of these systems suggests that social costs may be more widespread than previously considered.

Australian Fairy-wrens

In many bird species, males use bright plumage, as well as song and postural displays, to court females and repel rival males (Ligon,

1999). For example, in the red-backed fairy-wren, *Malurus melanocephalus* (Maluridae), males are cryptic brown in coloration and resemble females during the nonbreeding season, but acquire a conspicuous red and black nuptial (alternate) plumage just prior to the breeding season (Rowley & Russell, 1997). This nuptial plumage is only loosely associated with age: males older than 2 years and also some younger males acquire the red-black plumage during the breeding season, whereas other young males moult back into the cryptic brown plumage during the prenuptial moult (Webster, Varian, & Karubian, 2008). Some of these young brown males are nonbreeding helpers on their natal territory, but others establish their own territories and breed despite having brown female-like plumage. Breeding males in red-black plumage sire more offspring, particularly extrapair offspring, than do those in brown plumage (Webster et al., 2008). This raises the question: why don't all breeding males acquire the red-black plumage during breeding?

Plumage colour in red-backed fairy-wrens appears to be an honest indicator of male condition, as males acquiring red-black plumage are in better condition than those acquiring brown plumage during the prenuptial moult (Lindsay, Webster, Varian, & Schwabl, 2009), and experimental manipulation of body condition prior to moult affects the plumage acquired during moult (Barron, Webster, & Schwabl, 2013). Moreover, in contrast to many other passerines (Kimball & Ligon, 1999; Kimball, 2006), acquisition of the nuptial plumage type is regulated by the androgen testosterone in red-backed fairy-wrens and other malurid wrens (see Peters, Astheimer, Boland, & Cockburn, 2000): males moulting into red-black plumage have much higher levels of circulating testosterone than do males moulting into brown plumage (Lindsay et al., 2009), and experimental implants of testosterone induce males to moult into red-black plumage (Lindsay, Webster, & Schwabl, 2011). These results suggest that testosterone may be the physiological link between male condition and plumage type, as young males in poor condition may not be able to handle the costs of high testosterone levels.

Experimental and observational studies of red-backed fairy-wrens in the field, however, do not support the hypothesis that physiological costs constrain the acquisition of red-black plumage (although it is possible that they affect the timing of moult; see Cockburn, Osmond, & Double, 2008). First, levels of circulating androgens are not correlated with body condition (Barron et al., 2013). Second, all males, regardless of plumage type, elevate androgen levels strongly in response to experimental injection of gonadotropin-releasing hormone (GnRH), and there are no differences in induced androgen levels between brown males and red-black males (Barron, Webster, & Schwabl, 2015). Third, although experimental manipulation of condition in the field affects the probability that young males will moult into red-black plumage, those manipulations do not affect androgen levels (Barron et al., 2013). Finally, experimental manipulations of social context (see below) show that brown-plumaged males elevate testosterone levels when conditions are appropriate (Karubian, Lindsay, Schwabl, & Webster, 2011). Taken together, these results strongly suggest that brown-plumaged males can and do handle elevated levels of testosterone, and so the costs that maintain honest signalling in this system are likely coming from somewhere else.

In contrast to results for the physiological costs of nuptial plumage coloration, results strongly implicate a role for social interactions in maintaining honest plumage signalling in this system. First, simulated territorial intrusions show that red-black males receive much more aggression from conspecifics, particularly from other adult males in red-black plumage, than do brown males or females (Karubian, Silllett, & Webster, 2008). Second, experimental manipulations of social status during the breeding season show that brown males that start the breeding season as helpers rapidly

increase androgens when they obtain a breeding position (Karubian et al., 2011). Importantly, these same experiments also showed that these increased androgens also affect plumage signals: when feathers were plucked from brown males that had become breeders, about half of those males grew in red/black feathers instead of brown feathers (Karubian et al., 2011). These results strongly support the hypothesis that brown males are capable of elevating androgen levels, and also developing red-black plumage, but that they do not do so unless they are in the proper social context. Under this hypothesis, those males who breed in brown plumage do so because they were not in the proper social context to elevate androgens prior to moulting, but then subsequently obtained a breeding position after moult (Webster et al., 2008, 2010). Our current working hypothesis is that social interactions prior to the breeding season affect androgen levels (see Oliveira, 2004), which in turn affect the likelihood that a young male will obtain red-black plumage (see Webster et al., 2010). As such, androgens would be acting as a regulator that integrates information from external cues (social interactions with other individuals) and internal cues (physiological condition) to affect sexual plumage signals (sensu Dey, Dale, & Quinn, 2014; Rubenstein & Hauber, 2008; Tibbetts et al., 2016).

Chameleons

Chameleons are perhaps best known for their ability to rapidly change colour as a means of camouflage (Stuart-fox, Moussalli, & Whiting, 2008; Stuart-Fox, Whiting, & Moussalli, 2006). However, all species of chameleons change colour during social interactions (Nečas, 1999), and recent comparative evidence indicates that pressure for conspicuous social signals may have driven the evolution of colour displays in some chameleon groups (Stuart-Fox & Moussalli, 2008). For example, detailed examination of the colourful signals used by veiled chameleons, *Chamaeleo calytratus*, has shed light on the specific aspects of colour change used by chameleons to mediate aggressive, competitive interactions. In this species, brightening serves as a signal of general aggression (Ligon & McGraw, 2013; Ligon, 2015) and darkening serves as a signal of submission (Ligon, 2014). Although the specific physiological mechanisms of colour change in this species have not been investigated (but see Teyssier, Saenko, van der Marel, & Milinkovitch, 2015), and although colour change is frequently an energy-dependent process (e.g. requiring pigment translocation by motor proteins; Ligon & McCartney, 2016; Nilsson Sköld, Aspögren, & Wallin, 2013), rapid colour change probably does not carry strong physiological costs (Nilsson Sköld et al., 2013; but see Rodgers, Gladman, Corless, & Morrell, 2013). In contrast, experimental evidence indicates that colour change does carry social costs: chameleons with experimentally manipulated coloration (bright versus dark) that did not match their contest behaviour (aggressive versus not aggressive) received higher levels of physical aggression than did honestly signalling controls (Ligon & McGraw, 2016).

In contrast to the other visual signals that we discuss, colour change in chameleons is a dynamic signal that can change rapidly. In this respect, the colourful signals of veiled chameleons (and possibly other colour-changing organisms) are similar to postural and behavioural signals used by many animals to mediate aggressive encounters (Enquist, 1985; Hurd & Enquist, 2001; Hurd, 2004; Molles & Vehrencamp, 2001). As with other such conventional strategic signals, the flexibility of colour change allows individual chameleons to change their own signalling strategies across time and contexts. However, because signals must be honest on average to remain stable over evolutionary time (Johnstone & Grafen, 1993), most chameleons are expected to signal honestly most of the time (but see Számadó, 2000). This is exactly what has been found in this

study population (Ligon, 2015), although most individuals did signal dishonestly at some point, highlighting the need for further work investigating the context specificity of optimal signalling strategies (Botero, Pen, Komdeur, & Weissing, 2010). Regardless, the results of the experimental manipulation (Ligon & McGraw, 2016) clearly indicate significant social costs of signalling dishonestly in this system, with conspecific aggression providing the kind of checks and balances needed to maintain stable signals over evolutionary time.

Social Wasps

Perhaps the best-studied system with respect to social costs enforcing signal honesty is the paper wasp *Polistes dominulus*. As with other primitively eusocial wasp species, *P. dominulus* foundresses emerge from diapause and establish nests either singly or with other foundresses (Reeve, 1991). When individuals found nests with other conspecifics, a dominance hierarchy is established whereby the dominant queen becomes the primary reproductive individual within the group. *Polistes dominulus* females signal dominance using a visual pigment signal on their clypeus (face) (Figure 1A in Tibbetts et al., 2016): more broken facial patterns of black pigment on the face are associated with increased dominance (Tibbetts & Dale, 2004; Tibbetts & Izzo, 2010). However, the black facial signal represents <1% of black coloration present on the body, and likely does not entail high production costs (Tibbetts & Dale, 2004). The facial markings on *P. dominulus* wasps therefore represent a signal that is possibly maintained by social costs. Indeed, research has demonstrated that wasps receive more aggression if their facial patterns are manipulated in a way that oversignals ('bluffs') relative to their true dominance status or size/condition (Tibbetts & Dale, 2004), a social cost that may arise due to receiver recognition of mismatches between a signaller's behaviour and the signal itself (Tibbetts & Izzo, 2010). Interestingly, in addition to subordinates that signal high rank receiving increased aggression, dominants that signal low rank also had trouble establishing stable dominance relationships and were less likely to elicit submission from their opponents, indicating that female nestmates in this system are attentive to the match between signals and behavioural dominance.

Several aspects of the *P. dominulus* system may provide useful guides for future inquiries into systems where social costs may maintain signals. First, the signal used in *P. dominulus* is a seemingly inexpensive melanin signal (but see Tibbetts, 2010) that is displayed on the face of the wasp. Given that melanins can be endogenously synthesized by many animals, they are frequently assumed to be less expensive than carotenoids (McGraw & Hill, 2000), which need to be consumed before being modified or deposited (Hill, 2011). Additionally, the signal in this system was manipulated to determine the effect on the receivers, and the results show that individuals with facial patterns that do not represent their quality received increased aggression (Tibbetts & Izzo, 2010). Contests in this system also affect titres of juvenile hormone in individuals of both high and low quality (Tibbetts et al., 2016), with individuals manipulated to inaccurately signal high quality having reduced titres of juvenile hormone after social interactions. Thus, the effects of social interactions on hormone titres may link dishonest signalling to fitness.

CURRENT TRENDS IN LITERATURE ON SOCIAL COSTS

Although the three case studies we discuss above are informative regarding social costs and the maintenance of signals, a considerable number of studies have investigated questions about the use of signals in social contexts (Supplementary Table S1). We

summarize salient aspects of these studies in the context of predictions of the receiver-dependent cost hypotheses (Table 1). In total, we find indirect but suggestive evidence that social costs may be broadly important for the maintenance of honest signals. In this section we summarize some of this support and how it relates to the two receiver-dependent hypotheses.

Many studies have found that individuals signalling high quality or dominance often receive challenges and disproportionate aggression from other individuals, particularly from high-quality individuals (e.g. Murphy et al., 2009; Parker & Ligon, 2002; Santos, Maia, & Macedo, 2009; Studd & Robertson, 1985), whereas individuals that signal low quality receive less aggression (e.g. Karubian et al., 2008; Van Dongen & Mulder, 2007). In addition to showing that socially mediated (i.e. receiver-dependent) costs are plausible, these studies also provide some indirect support for the king-of-the-hill hypothesis. However, as with many studies of physiological costs (see above), most of these studies did not investigate whether there are differential social costs for low- and high-quality individuals. As discussed above, this is a key prediction and an important test for studies of social costs as well as physiological costs. We therefore advocate that future studies consider the costs to individuals of different quality when signalling at the same level (see Johnstone, 1997). Defining and measuring 'quality' is clearly relevant here, but also a notoriously difficult thing to do that is somewhat beyond the scope of this review; interested readers should consult the excellent discussions by Andersson (1982), Johnstone (1995b) and Hill (2011).

Other studies have found that social interactions affect the mechanisms that regulate signal production (Supplementary Table S1; see also Tibbetts, 2014; Tibbetts et al., 2016). For example, a large body of evidence shows that testosterone levels are responsive to social interactions in many, but not all, vertebrate systems (see reviews in Hirschenhauser & Oliveira, 2006; Oliveira, 2004), and testosterone in turn affects expression of many signalling traits (e.g. Gonzalez, Sorci, Smith, & Lope, 2001; Lindsay et al., 2011; Mougeot et al., 2004). Indeed, some studies have documented direct connections between social interactions and signal expression (e.g. Dey et al., 2014; Maia, Brasileiro, Lacava, & Macedo, 2012; McGraw, Dal, & Mackillop, 2003; Setchell, Smith, Wickings, & Knapp, 2008). Thus, in many systems ornamental signals affect social interactions, which in turn affect the mechanisms of ornament expression (Rubenstein & Hauber, 2008).

Another area for future research is the context and correlates of social aggression; that is, when does aggression happen, by whom, and towards whom. Numerous studies have found that individuals consistently challenge and behave aggressively towards others with similar signal levels (e.g. Johnson & Fuller, 2015; Martin et al., 2016; Møller, 1987; Pryke, 2007; Setchell & Wickings, 2005), and other studies have found that individuals with experimentally manipulated signals receive a disproportionate level of aggression (e.g. Dey et al., 2014). Although these results provide some support for the mismatch hypothesis, it is also plausible that this is dominance behaviour towards individuals signalling low quality, as would be predicted under the king-of-the-hill hypothesis. To date, the strongest evidence for punishment of signal mismatches comes from studies of *P. dominulus* (e.g. Tibbetts & Izzo, 2010), as discussed above.

In summary, considerable previous research demonstrates the feasibility of receiver-dependent (social) costs in maintaining honesty across diverse systems, and suggests that such costs could be central to the maintenance of honest signalling. However, few recent studies have addressed this topic directly (Fig. 1), and more research is needed into how and when social enforcement is mediated. In practice, it will be challenging to separate the two versions of receiver-dependent costs (incongruence versus king-of-

the-hill). Finally, social costs are not mutually exclusive from physiological costs when maintaining honest signals, as traits that are physiologically costly and used in intrasexual contests may also encumber an individual with social costs (Tibbets, 2014). Considering both physiological and social costs when studying potential mechanisms of signal honesty is therefore necessary to understanding the selective pressures acting on these signals.

CONCLUSIONS

The ideas presented in this essay are not new. Physiological cost hypotheses have been around for decades (e.g. Folstad & Karter, 1992; von Schantz et al., 1999) and have been refined in recent years (e.g. Hill, 2011) as better understanding of mechanisms have developed and more integrative approaches have become feasible. Similarly, the idea that social interactions and receiver-dependent costs may mediate honest signalling dates back to Rohwer (1975) or earlier. These ideas too have been refined in recent years, for example by integrating physiological and social costs (Tibbets, 2014). Nevertheless, most empirical research has focused on physiological costs (Fig. 1). The case studies summarized here, however, strongly implicate receiver-dependent mechanisms, and a survey of other work on social interactions and signals suggests that social mechanisms may be broadly important in maintaining honesty in signalling systems. We advocate that more attention be paid to receiver-dependent costs, in particular to better understand the conditions under which honesty is maintained by receiver-dependent costs, receiver-independent costs, or both.

Tibbets (2014) recently pointed out that social and physiological costs likely are not fully independent, because the consequences of social interactions on individuals often will be mediated by physiological processes (e.g. increases or decreases in hormone levels) that in turn affect signal production (e.g. see case studies above). One important consideration regarding the relative importance and prevalence of receiver-dependent versus receiver-independent costs is this: among signals used during aggressive interactions by contest participants (e.g. to gauge opponent quality or motivation), the honesty of even physiologically costly signals is likely enhanced by social costs. For example, a low-quality individual with a mutation that reroutes an enzymatic pathway that reduces physiological costs to enable greater signal expression (relative to true quality) will engage in more fights with higher-quality individuals, which, because of the low-quality of the mutant signaller, will inflict outsized costs. Hence, the signals used to mediate conflict will likely always be maintained, at least in part, by social costs.

Theory indicates that the absolute realized costs of signal production are not relevant to the maintenance of honest signalling, but that the potential costs are (see Higham, 2014, 2016), for example, the costs of aggression that are incurred only when a receiver attacks. Such potential costs are likely often imposed by conspecifics, particularly in social animals that forage or breed in groups (Dey et al., 2015; Tibbets & Safran, 2009; Whitfield, 1987). Accordingly, we advocate that social costs be tested in a larger diversity of systems. We also note the paucity of models that pertain to social costs relative to the number of models that analyse physiological costs and their ability to maintain honesty in signalling systems. Focused efforts on modelling social costs may elucidate whether one of the two receiver-dependent hypotheses is more likely than the other, and whether there are other receiver-dependent mechanisms that have not been considered as of yet.

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Supplementary material

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