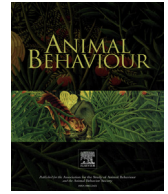


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Social costs are an underappreciated force for honest signalling in animal aggregations

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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 & Hohlft, 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

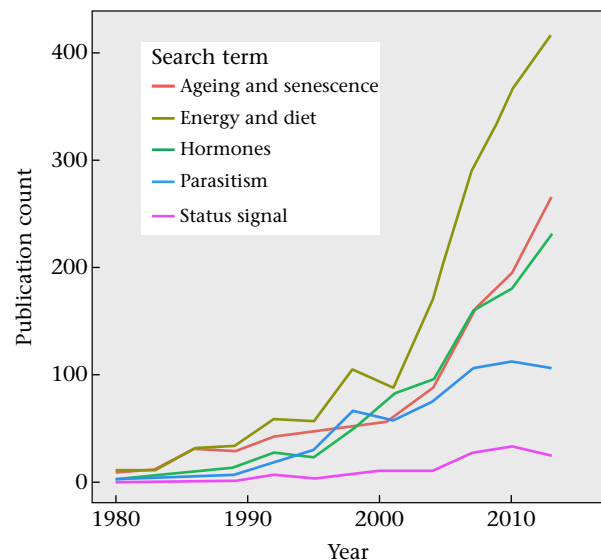


Figure 1. Publications on costs of signalling over time. Plotted are the number of publications in each of the categories from 1979 to 2016 from a select subset of animal behaviour, evolutionary biology and physiological journals. We used a subset of journals as some of the search terms (specified below) 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 enforce*', '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*').

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