

An integrative view of the signaling phenotype: Dynamic links between signals, physiology, behavior and social context

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Abstract Signal traits are often linked with the physiological state and behavior of their bearer. Direct examination of the causal links among these variables has provided substantial insight into the information content of signals, and into the costs and benefits of signal expression. Yet recent empirical work suggests that the social context in which signals are developed and displayed can play a major role not only in how signals are received, but also in coordinating and mediating the signaling phenotype itself. Here we review both well-established and emerging evidence for direct feedbacks among an individual's physiological state, behavior, and signal elaboration. We then describe an integrative view of signaling that takes into account the bidirectional relationships among components of phenotype and the social context in which signals are developed and displayed. Integrating dynamic feedback between context and phenotype within models of the evolution and maintenance of signals may yield insights into how signals evolve, how signaling phenotypes are coordinated and maintained on ecological and evolutionary time scales, and how static signals continue to convey relevant phenotypic information about their bearer through time [*Current Zoology* 60 (6): 739–754, 2014].

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Theory predicts that signal traits mediate social interactions by advertising information about their bearer to conspecifics (Grafen, 1990; Folstad and Karter, 1992; Andersson, 1994; Tazzyman et al., 2014). To be informative, signal traits should accurately indicate how an individual is likely to perform in a given social or environmental context (Zahavi, 1975; Schluter and Price, 1993; Miller and Svensson, 2014). Because performance (the ability to conduct an ecologically relevant task: Huey and Stevenson, 1979; Irschick et al., 2007) is intimately associated with physiological condition, signal traits that are linked with physiology (through condition-dependence or genetic linkage) may provide information about a variety of ecologically relevant aspects of an organism's phenotype (e.g., parasite load: Hamilton and Zuk 1982; Thompson et al. 1997; parental care: Siefferman and Hill 2003; resistance to oxidative damage: Perez-Rodriguez et al. 2010; the ability to maintain vital cellular processes: Hill 2011).

Studies of the dynamic links among physiological state, signal development and display, and behavior have yielded many important insights into the processes that generate variation in signaling phenotypes. Yet recent empirical work suggests that the social context in

which signals are developed and displayed can play a major role not only in how signals are received, but also in coordinating and mediating the signaling phenotype itself. In addition to influencing the relative cost and benefit of displaying a given signal, social context – defined here as the sum of social interactions with conspecifics experienced by an individual – can influence the behavioral and physiological state of an organism, as well as the degree to which they develop elaborate signals.

Here, we briefly review evidence for direct feedbacks among an individual's physiological state, behavior, and signal elaboration (Fig. 1A). Next, we describe an integrative view of the signaling phenotype in which signals and other aspects of phenotype are dynamically and bidirectionally linked with the social context in which they are developed and displayed (Fig. 1B). Explicitly including social context in models of signal function suggests that, in addition to the direct interactions among components of signal phenotype, indirect interactions may play an important role in maintaining the information content of signals. In this section, we discuss emerging evidence for multi-step feedbacks among elements of phenotype and social context. Fi-

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nally, we address some of the insight that could be gained by integrating social context into models of signal evolution and maintenance.

2 The Signaling Phenotype: A Review

2.1 Links between physiology and signal traits (A)

It has long been recognized that physiological state can play an important role in the development and expression of signal phenotypes (link A, Fig. 1A; Zahavi, 1975; Hamilton and Zuk, 1982; Andersson, 1994). Central to sexual selection theory is the prediction that exaggerated signal traits are often costly to produce or to display, and therefore serve as honest indicators of the quality of their bearer (Grafen, 1990; Folstad and Karter, 1992; von Schantz et al., 1999; Alonso-Alvarez et al., 2007; Tibbetts, 2014). Although not all signals are condition-dependent, experimental studies confirm that the development and/or display of many signals can be affected by changes in a variety of physiological parameters including nutritional state, endocrine levels, and dietary antioxidants (Evans et al., 2000; McGraw et al., 2002; Blount et al., 2003; Alonso-Alvarez et al., 2004; Weiss et al., 2013). Furthermore, within individuals, sig-

nal traits may be more strongly influenced by physiological state or ‘condition’ than similar traits that do not hold signal value (Cothran and Jeyasingh, 2010; Delcourt and Rundle, 2011; Emlen et al., 2012; San-Jose and Fitze, 2013). Thus, causal evidence exists for a role of physiological state on signal development and expression (link A, Fig. 1A).

Signal development can impose physiological costs (Zahavi, 1975; Evans et al., 2000; Alonso-Alvarez et al., 2007). While many signal types are also thought to be costly to display (e.g., elongated plumage or appendages, acoustic or behavioral signals), fewer empirical studies have quantified the physiological costs of signal expression. However, signal reduction has been found to decrease metabolic rate (Basolo and Alcaraz, 2003; Allen and Levinton, 2007, but see Cuervo et al., 1996) and mass loss (Pryke and Andersson, 2005), while signal enhancement can impair locomotion (Allen and Levinton, 2007; Kruesi and Alcaraz, 2007; Karino et al., 2011; but see Bro-Jørgensen et al., 2007; Baumgartner et al., 2011) and immune function (Saino and Møller, 1996; Saino et al., 1997a), and alter hematocrit levels (Saino et al., 1997b; Cuervo and de Ayala, 2005; Murphy, 2010). Additionally, for signals to reveal accurate information about their bearer they need not impose equivalent costs on all individuals; variable costs could result if individuals of higher condition are better able to absorb the cost imposed by signals without altering critical elements of physiological state, or if the costs themselves (and the resulting impact on physiological condition) are lower in individuals in good condition (e.g., Zahavi, 1975; von Schantz et al., 1999; Tibbetts, 2014).

2.2 Links between physiology and behavior (B)

From the hormonal mediation of the behavioral stress response to the context-dependent expression of behavioral signals, physiological state can have a substantial influence on the expression of behavior (link B, Fig. 1A). The myriad ways in which physiology influences behavior, and behavior influences physiological state, are beyond the scope of this review (see Adkins-Regan, 2005; Carlson, 2012). Here, we highlight several aspects of these relationships that are particularly relevant to the integrated signaling phenotype. First, the same physiological parameters that constrain signal development and display can also mediate the expression of social and sexual behaviors. For example, circulating levels of testosterone can both promote signal development and increase the expression of aggressive behaviors that may be crucial to securing or defending re-

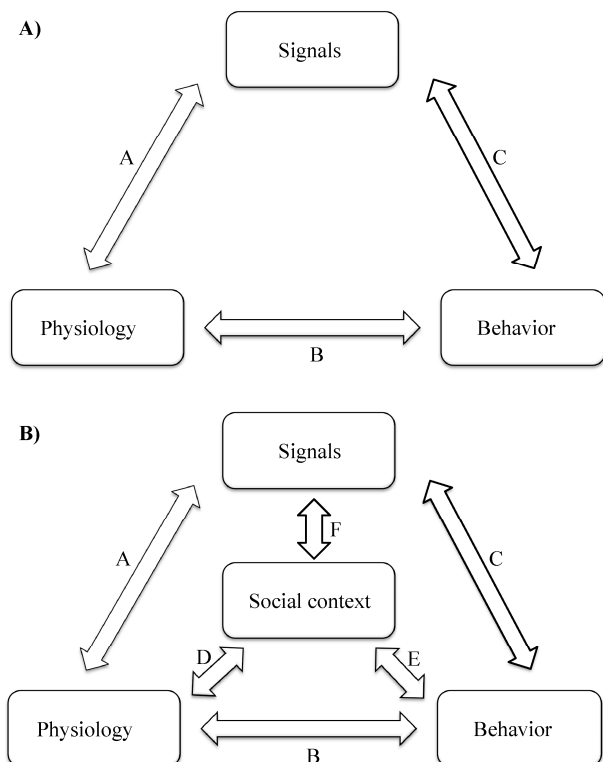


Fig. 1 The signaling phenotype

A) An individual-based model of the signaling phenotype in which signal expression is shaped by interactions with physiological state and behavior. **B)** An integrated model of the signaling phenotype in which social context influences, and is influenced by, the dynamic interactions among signals, physiology, and behavior.

sources or social dominance (Ardia et al., 2010; Vergara and Martínez-Padilla, 2012). Similarly, neural development, which is influenced by nutritional state during development, influences both the expression of acoustic signals and cognitive function in songbirds (Buchanan et al., 2013), and variation in immunocompetence can influence both sexual display and sickness behavior (Muehlenbein and Bribiescas, 2005). Second, the direct effect of behavior on physiological function can link signal elaboration with external context. For example, energetic and nutritional states are strongly dependent on both foraging behavior (e.g., the efficiency of energetic intake, the ingestion of exogenous antioxidants and other compounds that influence physiological state) and other potentially costly behaviors (e.g., vigilance and territorial defense, mate search, migration: Stephens et al., 2007). Individuals that behave in ways that increase critical aspects of physiological condition may therefore be more capable of developing exaggerated condition-dependent signals (Lailvaux and Irschick, 2006; Barnett and Briskie, 2007).

2.3 Links between signals and behavior (C)

The elaboration of signal traits can directly influence the behavior expressed by the signaler (link C, Fig. 1A), including display rate, aggressive behavior, and parental behavior. Direct effects of signal display on the expression of behavior could result from signal traits inflicting biomechanical or physiological limitations on an individual, thus constraining their ability to perform specific behaviors, such as foraging (Oufiero and Garland, 2007). Alternatively, exaggerated displays may impose trade-offs in time and resources with other behaviors (e.g., increased sexual signal display may force a trade-off with antipredator behavior: Mougeot and Bretagnolle, 2000; Cabido et al., 2009; Fowler-Finn and Hebets, 2011). Such direct links have been suggested by the manipulation of traits believed to influence the ability of an individual to perform specific behaviors. For example, in male barn swallows *Hirundo rustica* the experimental manipulation of tail length does not affect the total amount of food provided to offspring, but elongated males appear to differ in their foraging behavior, bringing more and smaller insects to their young. This difference could result from a direct effect of signal exaggeration on flight capacity and maneuverability (Møller et al., 1995). Engaging in non-signaling behaviors (e.g., foraging, parental care, aggression) could also impact the expression of behavioral displays or other dynamic signals through direct trade-offs in the time or resources necessary for signaling. While very

little is known about the potential for similar effects on static signals, it is conceivable that engaging in certain behaviors during the period of signal development could similarly influence the elaboration of static signals.

3 The Integrative Signaling Phenotype: Incorporating Social Context

The individual-based view of the signaling phenotype (Fig. 1A) has provided substantial insight into the direct feedbacks among physiology, behavior, and signal traits. Yet this perspective neglects a crucial component of the signaling environment: social context. The social interactions in which an individual engages – and the outcome of these interactions – are not only mediated by signals, but influence, and are influenced by, behavior and physiological state. Thus, to understand the ways in which signals are developed and maintained within the complex social contexts in which they operate, it is necessary to consider the bidirectional links between social interactions and each aspect of the signaling phenotype. This expanded perspective (Fig. 1B) will help to reveal how social interactions influence signal evolution and elaboration, and how signal-driven changes in social context can influence widespread aspects of behavior and physiological state.

3.1 Links among social interactions, physiology, and behavior (D and E)

The dynamic links among social interactions, behavior, and physiology are some of the best understood relationships among components of the integrated signaling phenotype described in Fig. 1B. Many of these relationships are mediated through hormone signal systems. Through their extraordinary context-sensitivity, hormones enable organisms to flexibly modulate the expression of many phenotypic traits in accordance with their current environment (Adkins-Regan, 2005). For example, in some vertebrates, social challenges, particularly during the breeding season, stimulate a rapid increase in circulating testosterone (link D, Fig. 1B; e.g., Wingfield et al., 1990). Elevated testosterone can alter the immediate expression of aggressive behaviors (link B, Fig. 1B), which may influence social interactions, and thereby the social context (link E, Fig. 1B). Hormone levels are also responsive to the outcome of social interactions (Bernhardt et al., 1998; Oyegbile and Marler, 2005; Oliveira et al., 2009). These socially mediated changes in hormonal phenotype can have wide-reaching effects on other hormone-mediated behaviors (e.g., parental care, extra-pair fertilization rates: Hegner

and Wingfield, 1987; Raouf et al., 1997).

Although the specific mediators of aggression and the hormones that are responsive to social challenges differ across species and sometimes between the sexes (Goymann et al., 2007; Rosvall, 2013; Rosvall and Peterson, 2014), dynamic and bidirectional relationships among an individual's behavior, circulating hormones, and the social interactions in which they engage are common across species. In insects, juvenile hormone appears to be both responsive to social interactions, and to function as a mediator of competitive behaviors during social challenges (Tibbetts and Huang, 2010; Tibbetts and Crocker, 2014). Glucocorticoid stress hormones – corticosterone and cortisol – are also central mediators of phenotypic expression. While some of the variation in these flexible traits is heritable (Jenkins et al., 2014), hormone levels are often highly sensitive to social interactions and outcomes (Creel et al., 2013; Leary and Knapp, 2014). In many species, glucocorticoids are rapidly altered following a change in social status. Shortly after the conclusion of dominance competitions, glucocorticoid levels and the activation of serotonergic and noradrenergic systems differ in dominant and subordinate rainbow trout, *Oncorhynchus mykiss* (Øverli et al., 2000). Furthermore, even when social context is relatively stable it can continue to influence hormonal state. In social groups with linear dominance hierarchies, glucocorticoid levels, as well as the range of social behaviors exhibited, are often strongly associated with social rank (Abbott et al., 2003; Sapolsky, 2005; Gesquiere et al., 2011). Glucocorticoid levels can be positively or negatively associated with social dominance; the directionality of this relationship depends in part on the ways in which social dominance is developed and maintained (Abbott et al., 2003; Creel et al., 2013).

3.2 The social context of signal display (F)

3.2.1 Signals influence social interactions

Signal traits commonly function as mediators of social behavior, including behaviors related to sexual, parental, aggressive and affiliative interactions. The degree to which signals are elaborated can therefore influence how individuals are responded to by conspecifics. In addition to altering social interactions, elaborated signals can alter the social context by influencing the outcomes of these interactions. This can occur directly (e.g., if manipulated individuals rise or fall in the social hierarchy as a direct result of conspecifics altering their behavior towards them; link F, Fig. 1B) or as a multi-component interaction (e.g., if signal-driven alter-

rations in the behavior of conspecifics influences an individual's aggressiveness, which then causes a change in social status; links F and E, described below). As few studies have explicitly differentiated among these alternatives, we describe these patterns here; however, signal-driven shifts in social context may commonly be mediated at least in part through changes in the social behavior of the signaler.

3.2.2 Sexual interactions

Unsurprisingly, the experimental enhancement of signals used in mate choice often increases the rate at which individuals are visited or displayed to by members of the opposite sex (Saetre et al., 1994; Hill et al., 1999; Torres and Velando, 2005), or their copulation success (Siitari et al., 2002). Conversely, when sexual signals are reduced, manipulated individuals may be visited less frequently by potential mates or engage in fewer copulations (Petrie and Halliday, 1994; Johnsen and Lifjeld, 1995; Vortman et al., 2013). In one of the classic examples of sexual selection, the experimental manipulation of tail length in male European barn swallows *H. r. rustica* reveals the role of this signal in mediating a diversity of social interactions. Males with elongated tails are accepted as social mates more quickly (Møller, 1988) and have higher paternity within their own nests (Saino et al., 1997c). Elongated males are also more likely to sire a second social brood within the same season (Møller, 1988), potentially altering a variety of reproductive behaviors and trade-offs. Similarly, male red-shouldered widowbirds *Euplectes ardens* with elongated tails have higher mating success (Pryke and Andersson, 2002), and red bishops *Euplectes orix* with experimentally enlarged tails are preferred as mates (Pryke and Andersson, 2008). Likewise, male swordtails (*Xiphophorus helleri* and *Priapella olmecae*) bearing surgically enhanced swords and male guppies *Poecilia reticulata* with elongated dorsal fins receive more attention from females than control or reduced males (Basolo, 1998; Karino et al., 2011).

These relationships are not limited to elongated morphological traits, or to a single signaling modality. In male house finches *Carpodacus mexicanus* both the frequency and temporal dynamics of reproduction are influenced by carotenoid-based plumage signals. Males with experimentally enhanced plumage pair earlier and are more likely to mate overall (Hill, 1991). In *Enchenopa* treehoppers, Hemipteran insects, the frequency of males' acoustic signals influences the likelihood that females will engage in a duetting display, an important precursor to copulation (Rodríguez et al., 2012). Simi-

larly, in harvest mice and house mice, which use olfactory cues in mate choice, males manipulated to increase the frequency of scent marking receive more visits from receptive females (*Micromys minutus*: Roberts and Gosling, 2004) and sire more offspring (*Mus musculus*: Thonhauser et al., 2013).

3.2.3 Parental interactions

Ornament quality can also alter social interactions by influencing the investment of reproductive partners (Noble, 1938; Qvarnstrom, 1997; Roulin, 1999; Dentressangle et al., 2008) or the begging intensity of young (Velando et al., 2013). In several species of birds, females paired to males with experimentally reduced ornaments lay smaller eggs (Velando et al., 2006; Osorno et al., 2006; McFarlane et al., 2010) that can also differ in the relative amount of yolk compounds (Dentressangle et al., 2008). Similarly, signal manipulations have revealed that ornament elaboration can increase the rate at which social mates provision offspring (Qvarnstrom, 1997; Limbourg et al., 2004; Morales et al., 2009; but see Sanz, 2001; Cuervo and Møller, 2006; Mahr et al., 2012). For example, female barn owls *Tyto alba* display melanin-based plumage spots as sexually selected ornaments (Roulin et al., 2001). When female plumage spottiness is experimentally reduced social mates feed offspring less; the resulting nestlings are smaller and less likely to survive to fledging than the nestlings of control females (Roulin, 1999).

3.2.4 Aggressive and affiliative interactions

Relationships between manipulated signal quality and aggressive or affiliative interactions have also been observed in a variety of species. Most commonly, individuals bearing more elaborate signals are responded to more aggressively by conspecifics (Møller, 1987; Huhta and Alatalo, 1993; Dale and Slagsvold, 1996; van Dongen and Mulder, 2007; Rick and Bakker, 2008; Tannure-Nascimento et al., 2008). Male stenogastrine wasps *Parischnogaster mellyi* manipulated to display more abdominal stripes – a sexually dimorphic signal used in intrasexual competition – are pursued and attacked more frequently than control or stripe-reduced males (Beani and Turillazzi, 1999), and territorial chiffchaffs *Phylloscopus collybita* are more likely to attack conspecifics in response to the playback of elongated songs than when exposed to control or shortened songs (Linhart et al., 2012). Consistent with these patterns, conspecifics often preferentially affiliate with individuals bearing less elaborate signals post-manipulation (Tibbetts and Lindsay, 2008; Tibbetts, 2008; Rémy et al., 2010; Crowhurst et al., 2012; Quesada et al., 2013). In

some studies, however, the opposite patterns are observed: individuals with enhanced signals receive less aggression (Pryke et al., 2002), or those with reduced signals receive more (Peek, 1972; Evans and Hatchwell, 1992; Rémy et al., 2010; Theis et al., 2012; Dey et al., 2013).

Despite the previously described patterns of increased aggression towards manipulated individuals, signal enhancement frequently results in an increase in social dominance or territory quality among enhanced individuals, and a decline in dominance among reduced individuals (Marler, 1955; Rohwer, 1985; Holberton et al., 1989; Thompson and Moore, 1991; Evans and Hatchwell, 1992; Qvarnstrom, 1997; Hagelin, 2002; Pryke et al., 2002; Pryke and Andersson, 2003a; Ferns and Hinsley, 2004; Stuart-Fox and Johnston, 2005; Benson and Basolo, 2006; Tringali and Bowman, 2012). Nevertheless, some studies have found that despite changes in the frequency or intensity of aggressive challenges, signal manipulations do not influence the outcome of competitive interactions (Møller, 1987; Pryke and Andersson, 2003b; Tibbetts and Dale, 2004; Järvisjö et al., 2013) and a few have even found that post-manipulation dominance is inversely related to signal elaboration (Rohwer, 1977; Yasukawa et al., 2009).

Differences among studies in the effect of signal manipulation on conspecific aggression could result from natural variation within and among species and social systems in the relative amount or form of aggression directed toward dominant and subordinate individuals (Reeve and Nonacs, 1997; Abbott et al., 2003; Thompson et al., 2014). Alternatively, these discrepancies could stem from differences in whether manipulated individuals are perceived as naturally stronger signalers, or are perceived as exhibiting unnatural or discordant signals worth “testing” with aggression. The presence and degree of aggression and resulting changes in social context may also depend on the signal quality of unmanipulated conspecifics (Midamegbe et al., 2011), the familiarity of competitors (Parsons and Baptista, 1980; Lemel and Wallin, 1993; Stuart-Fox and Johnston, 2005), or other phenotypic or life history characteristics of manipulated individuals and their social competitors (Peek, 1972; Fugle and Rothstein, 1987; Qvarnstrom, 1997; Vedder et al., 2007; Vedder et al., 2010). Finally, the influence of signals on social context may depend on the elapsed time since signal manipulation (Rohwer, 1985; Rohwer and Røskaft, 1989; Osorno et al., 2006) or on the social stability or frequency of information flow within the population (Ang and Manica, 2010).

3.2.5 Social context influences signal development and expression

A number of recent studies have also demonstrated the substantial role that social environment plays in the development of social and sexual signals. The competitive or mate choice environment during development is increasingly recognized as a driver of signal traits as well as other aspects of phenotype (Kasumovic and Brooks 2011; Kasumovic 2013). For instance, the social environment during rearing influences age-specific calling rate, a sexual signal, in black field crickets (*Teleogryllus comodus*: Kasumovic et al., 2012). Similarly, male blue-black grassquits *Volatinia jacarina* that are reared in more competitive environments molt into blue structural nuptial plumage more quickly, and remain more colorful than those raised in less sexually competitive environments (Maia et al., 2012).

Shifts in social environment and social structure during adulthood can also influence signal expression. In a population of swordtail fish *Xiphophorus hellerii* the color of the lateral sword stripe is plastically mediated based on an individual's position in the social hierarchy. Subordinate males display black stripes, which may reduce interspecific aggression or the risk of predation. However, when individuals become dominant the stripe quickly changes from black to the sexually preferred red (Rhodes and Schlupp, 2012). Male mandrills that gain rank rapidly redden the color of facial and genital skin, which function as social signals (Setchell and Dixson, 2001). Social standing also influences ornamentation in red-backed fairy wrens *Malarus melanocephalus*: following experimental removal of breeding males, subordinate helpers quickly assume breeding status, and concomitantly develop more colorful bills and produce redder plumage when feather growth is stimulated (Karubian et al., 2011). And in gray treefrogs *Hyla versicolor*, the spatial structure of displaying males influences the temporal dynamics of acoustic signaling (Reichert and Gerhardt, 2013). Social interactions may even have carry-over effects that persist across seasons: female blue tits *Parus caeruleus* stimulated to increase their reproductive effort via clutch removal develop blue cap plumage with lower ultraviolet reflectance in the following year than control birds (Doutrelant et al., 2012).

Learning has also gained increasing attention as a mechanism that is not only capable of influencing the development of mate choice preferences, but also the development of signal traits themselves (Verzijden et al., 2012). Passerine song is one of the most well-described

examples of learned signals (Catchpole and Slater, 2003; Beecher and Brenowitz, 2005), but the learning of sexual and social signals – which depends on the social environment – has also been shown to occur in other taxa and signaling modalities. Male fruit flies can learn to adaptively refine courtship displays following rejection or acceptance from both heterospecific and conspecific females (Dukas, 2004; Dukas and Dukas, 2012). Bottlenose dolphins *Tursiops truncatus* learn to copy the vocal whistles of closely associated individuals; these imitated signals are thought to play an important role in affiliative interactions within this species (King et al., 2013).

Ongoing feedback between relative signal quality and social context has been suggested by several recent studies that have manipulated signal quality to test its effects on the expression of true signals. House sparrows *Passer domesticus* housed in groups of males with uniform badge sizes – a situation predicted to promote more competitive interactions – develop more colorful bills than those housed in groups with mixed badge sizes (Laucht and Dale, 2012). The most comprehensive tests of this hypothesis to date have been conducted in pukeko *Porphyrio porphyria*. Birds whose frontal shields are manipulated to appear smaller receive more aggression from members of their social group, and decrease true shield size within ten days of treatment (Dey et al., 2013).

4 Implications of the Integrated Signaling Phenotype

In section three we discussed the bidirectional links between social context and specific components of the signaling phenotype. Adding insights from indirect and multi-step interactions among these components (e.g., signal-driven changes in social interactions that, in turn, influence the physiological state of the signaler; F to D in Fig. 1B) may help to demonstrate how components of the integrated signaling phenotype are coordinated and maintained in dynamic environments.

4.1 The role of social context in coordinating the integrated signaling phenotype

4.1.1 Signals, social interactions, and behavior (F to E)

The experimental elaboration of signal traits can influence many aspects of how the signaler behaves, including display rate, aggressive behavior, and parental behavior. As described above, most studies that have investigated the links between signal elaboration and an individual's subsequent behavior do not distinguish between the direct effects of signal manipulation on

behavior (link C) and effects mediated through changes in social context (F to E, Fig. 1B). However, as described below, concomitant changes in social interactions and behavior have been found in several species following signal manipulation – including species that display signals with no known direct cost – suggesting a potential role for social feedback in altering the behavior of manipulated individuals.

4.1.2 Sexual behavior

Feedback from signal manipulation on the sexual behavior of manipulated individuals has been widely described; these changes often occur in combination with changes in the behavior of conspecifics toward manipulated individuals. Individuals bearing manipulated signals typically increase the rate or intensity of behavioral displays when signals are elaborated, and decrease display behavior when signals are reduced (Johnsen and Lifjeld, 1995; Johnsen et al., 1998a; Johnsen et al., 1998b; Beani and Turillazzi, 1999; Saino et al., 2003; Royle and Pike, 2010). However, in some studies display behavior remains unchanged (Basolo and Alcaraz, 2003; Torres and Velando, 2003; Torres and Velando, 2005) or is even reduced following signal enhancement (Andersson, 1982; Pryke and Andersson, 2005; Stapley and Whiting, 2006; Karino and Kamada, 2009). These discrepancies could be due to differences in signal use or information content across species. Alternatively, if changes in display rate are driven by social feedback from conspecifics about relative signal quality, then we would predict temporal changes in the behavior of manipulated individuals. For example, soon after signal reduction, when manipulated individuals begin receiving signals that they are less attractive to conspecifics, they might temporarily increase behavioral displays (see Box 1). But if an increased display rate fails to elicit the desired response, or imposes an unsustainable cost, then display behavior may ultimately be reduced to match the relative quality of the manipulated signal.

4.1.3 Social dominance and aggression

Males whose signals are enhanced are subsequently more aggressive towards conspecifics in tree lizards *Urosaurus ornatus* (Thompson and Moore, 1991), house sparrows *Passer domesticus* (Møller, 1987), and red-winged blackbirds *Agelaius phoeniceus* (Yasukawa et al., 2009). A temporal component to behavioral changes following signal manipulation – which suggests that social feedback play a role in these changes – has also been found in pied flycatchers *Ficedula hypoleuca*. Shortly after manipulation, birds with enhanced plumage signals do not differ in their response to song play-

back; however, several days later enhanced individuals respond more aggressively to playback than control or signal-reduced conspecifics (Osorno et al., 2006).

4.1.4 Parental behavior

The parental behavior of individuals with manipulated signals often changes, a process that could be driven by several non-exclusive pathways. Because parental behavior frequently covaries among pair members, signal-induced shifts in the reproductive investment of social mates can feed back to influence the parental behavior of manipulated individuals (Houston et al., 2005; Hinde, 2005; Morales et al., 2009). Signal elaboration could also influence behavioral trade-offs in ways that influence parental care. For example, if enhanced signals increase the frequency or intensity of sexual interactions with potential mates then manipulated individuals might increase the time devoted to mate search or mating displays, which could impose a trade-off with parental behavior. Similarly, if signal elaboration influences the timing or total number of reproductive events (e.g., stronger signalers are accepted sooner as mates, and thus have more young or reproduce more often), then the frequency of parental behaviors will likely shift accordingly (Møller, 1988; Cuervo and Møller, 2006).

4.1.5 Signals, social interactions, and physiological state (F to D)

One of the most poorly understood multicomponent relationships within the integrated signaling phenotype is the influence of signal-induced changes in social context on physiological state (Rubenstein and Hauber, 2008). Because of the important role of hormones and other physiological parameters in coordinating many aspects of phenotypic expression, this pathway could provide a mechanism to adjust phenotypic expression in accordance with current signal quality and other aspects of the social environment. Although to date no definitive tests of these interactions have been conducted, the importance of social feedback for mediating these relationships is suggested by experimental manipulations of signal traits in songbirds. In North American barn swallows *H. r. erythrogaster*, melanin-based ventral plumage color, which imposes no known direct costs, functions as a social signal. Naturally darker males have higher circulating testosterone (Safran et al., 2008). Males manipulated to display darker ventral color increase circulating testosterone, lose body mass, and sire more offspring within their social nests (Safran et al., 2005; Safran et al., 2008). Intriguingly, in female barn swallows – which display the same plumage signals as males – darkened plumage has the opposite effect on

Box 1 Social feedback about signal quality: Punishment of cheaters or signal-driven phenotypic integration? Photo credits: Harris's sparrow by Julia Adamson, paper wasp by Joaquim Gaspar, barn swallow by Matthew Wilkins



The possibility of social feedback about signal quality imposing a cost on “cheaters” – individuals whose physiological or behavioral phenotype does not match the degree to which their signals are elaborated – was suggested by the pioneering studies of Sievert Rohwer. His early experiments revealed that juvenile Harris's sparrows *Zonotrichia querula* manipulated to display adult plumage receive more social aggression from conspecifics and, at least initially, decline in social status (Rohwer, 1977). Yet if birds are simultaneously made darker and implanted with testosterone, thereby making physiological state congruent with signaling phenotype, their social standing increases (Rohwer and Rohwer, 1978). These observations were instrumental in developing the theory of social enforcement of cheating. The social enforcement of cheating has more recently been detected in paper wasps (*Polistes dominula*). Female wasps manipulated to display facial patterns associated with social dominance receive more aggression from conspecifics; however, manipulated females that also receive exogenous juvenile hormone – potentially resulting in a congruent signaling phenotype – do not (Tibbetts and Izzo, 2010).

Although these experiments compellingly demonstrate the potential for social feedback to enforce signal honesty, other experiments in both of these systems have suggested that social enforcement is far from ubiquitous, and may instead depend on the context in which signals are expressed. The likelihood that the manipulated signals of paper wasps will be aggressively tested depends on the value of the resource in question: when manipulated individuals hold resources of high value they are more likely to be tested than when they hold resources of lower value (Tibbetts, 2008). Later experiments in Harris's sparrows indicated that not only do manipulated individuals sometimes escape social persecution, but that congruent signaling phenotypes may arise through social feedback. When juvenile sparrows are darkened and placed back into flocks in environments with distributed resources, they initially avoid aggressive interactions with conspecifics. But over time their behavior changes. After several hours of interacting with other birds, darkened individuals become more aggressive, actively displace conspecifics from feeders, and rise in the social hierarchy (Rohwer, 1985). Thus, over time – apparently in response to social feedback about manipulated signal quality – manipulated individuals begin to display the behavioral phenotype of naturally darker individuals (F to E).

Our work in barn swallows suggests that social feedback may also cause manipulated individuals to adopt the physiological phenotype of naturally stronger signalers (F to D). Male barn swallows with darker ventral plumage signals have higher circulating testosterone; free-living males manipulated to display darker ventral plumage increase their testosterone levels in the week following plumage manipulation (Safran et al., 2008). Similarly, naturally darker female barn swallows have lower levels of plasma oxidative damage; females manipulated to display darker signals decrease both oxidative damage and circulating testosterone following signal enhancement (Vitousek et al., 2013). Taken together, these studies on the behavioral and physiological effects of signal manipulation suggest that social feedback may provide a mechanism for adjusting dynamic aspects of signaling phenotype in accordance with the relative quality of static signals.

physiological state. Experimentally darkened females decrease both circulating testosterone levels and plasma oxidative damage (Vitousek et al., 2013). Feedback from signal manipulation on circulating hormones has also recently been shown in white-crowned sparrows *Zonotrichia leucophrys*, in which the size of white plu-

mage patches on the crown signal resource holding potential (Laubach et al., 2013). Males with experimentally enhanced crown white elevate baseline corticosterone levels and tend to decrease the corticosterone stress response compared with control and white-reduced males. Although the effects of signal manipulation on

social interactions have not been explicitly addressed, the observed changes in physiological state – and the apparently low to nonexistent direct cost of signal display in these systems – suggest that these changes are likely mediated through changes in the social context of manipulated individuals. A priority for future research is determining the extent to which the observed changes in physiology and behavior following signal manipulation are in fact manipulated through changes in social context.

4.2 Population-level effects: Social networks and signaling phenotype

Because signal expression influences not only the phenotype of the signaler but can have far-reaching effects on social context, signals have the potential to influence diverse aspects of the phenotype of other individuals within the social network. For example, connectivity within the social network – defined as the number of social groups with which an individual interacts – is lower in male house finches with more elaborate plumage (Oh and Badyaev, 2010). The nature of the interactions within social groups can also be influenced by signal elaboration: rock sparrows *Petronia petronia* with more colorful ornaments exert more influence within foraging groups, and are followed by more conspecifics (Tóth and Griggio, 2011). Although the causality of these relationships has not been tested, these findings raise the possibility that individuals could adjust their interactions with conspecifics based on signal elaboration in order to maximize perceived quality or information transfer. If this process occurs, then alterations in the quality of a single individual's signal could potentially alter the social context and connectivity of entire groups.

Through altering the social context, signals may also influence diverse aspects of the phenotype of the individuals with which they interact. For example, male red grouse *Lagopus lagopus* implanted with testosterone increase the size of their combs, a sexually selected trait (Mougeot et al., 2005). At the same time, comb size decreases in their unmanipulated neighbors (Vergara and Martínez-Padilla, 2012). In Galápagos marine iguanas *Amblyrhynchus cristatus* the largest males compete for display territories during the breeding season, from which they court visiting females with a testosterone-mediated head bob display (Wikelski et al., 2001; Vitousek et al., 2007; Vitousek et al., 2008). When testosterone levels are blocked, territorial males decrease display rate and territory size, and receive fewer visits from females (Wikelski et al., 2005). But at the same

time, the behavioral and physiological state of unmanipulated conspecifics changes: males whose territories are located adjacent to testosterone-blocked males elevate testosterone and baseline corticosterone, head-bob at higher rates, increase territory size, and are visited by more females during mate choice (Wikelski et al., 2005).

4.3 Coordinated signaling

Despite the demonstrated importance of individual signal traits for mediating social interactions (Andersson, 1982; Hill, 1991; Tibbetts and Dale, 2004; Safran et al., 2005) signals are not evaluated in isolation, but rather in conjunction with other aspects of phenotype, and often with other signal traits (Møller and Pomiankowski, 1993; Candolin, 2003; Hebets, 2011). The coordination of signaling phenotype has emerged as a central factor in predicting mating success in several systems, including in the European subspecies of barn swallows, *H. r. rustica* (Møller et al., 1998; Saino et al., 2003; Candolin, 2003). Yet the mechanisms that coordinate dynamic links among multicomponent signals, and the role of social feedback in mediating signal expression, are poorly understood.

Substantial evidence indicates that behavioral displays are often flexibly modulated following the experimental manipulation of morphological signal traits (described above). Acoustic signals may also be dynamically altered based on the relative quality of other signal traits. Male European barn swallows with experimentally increased tail lengths produce songs with longer terminal 'rattles' (Saino et al., 2003), which are used in intersexual competition and are associated with high circulating testosterone (Galeotti et al., 1997). Similarly, bluethroats *Luscinia svecica* with experimentally reduced signals sing at lower rates than controls (Johnsen and Lifjeld, 1995); a similar trend has been observed in red-winged blackbirds (Yasukawa et al., 2010). Signal-mediated changes in song characteristics may also occur in blue tits, which bear ultraviolet-reflectant crown ornaments that function as sexual signals (Sheldon et al., 1999; Alonso-Alvarez et al., 2004). Following experimental manipulation of crown ornaments, the song of ultraviolet-enhanced males elicits a stronger response from neighbors than the song of experimentally reduced males (Poesel et al., 2007); however, it is not known whether the song itself differs following manipulation.

While dynamic signal traits, such as behavioral and acoustic displays, can be flexibly altered based on social context (Laucht and Dale, 2012; Dey et al., 2013), static signals (e.g., plumage color, horns, antlers) do not

change appreciably following development. Nevertheless, the relative quality of a static signal can change over time, sometimes dramatically (e.g., as the composition of social groups shifts across life history stages, following migration, or during territory and pair bond establishment). The ability to shift physiological and behavioral phenotype in accordance with the relative quality of signal traits could enable coordinated signaling in species that display static signals as well as those that exhibit dynamic signals.

Taken together, these studies suggest that dynamic linkages among multicomponent signals may be driven by social feedback about relative signal quality influencing physiological state. In this way the honesty and information content of multicomponent signals could be regulated to reflect both signal quality and physiological state, enabling individuals to present a coordinated and integrated signaling phenotype that conveys current physiological information to conspecifics.

5 Conclusions and Future Directions

Signals are complex aspects of phenotype that are selected to transmit information to their receivers. While empirical studies have uncovered fascinating patterns in the causes and consequences of signal variation, we emphasize that signaling phenotype is influenced not only by dynamic, bidirectional interactions among an individual's signals, physiology, and behavior (Fig. 1A), but by the ways in which these aspects of phenotype influence social interactions and social context (through more complex interactions mediated by social context, as portrayed in Fig. 1B). Thus, a broader view of the social environment in which signals are

being developed and expressed may fill some important gaps in our understanding of signal evolution and use (Table 1). With a few exceptions (e.g., causal links between signal quality and behavior: C in Fig. 1B) the direct interactions among components of phenotype, and between phenotype and social context (links D, E, and F in Fig. 1B) are fairly well-described. However, much less is known about how multi-step interactions that involve feedback between social context and different components of phenotype affect the integrated signaling phenotype. Puzzles also remain about how static signal traits that are developed anew each year, often in a non-reproductive context, remain informative over time and across social contexts. Yet evidence for causal links between static signals, physiology, and behavior provide important and we believe fairly intuitive clues as to how organisms could match the expression of an integrated signaling phenotype with their social context. Despite the fixed nature of static traits, their relative quality is potentially quite dynamic. The same individual bearing the same signal trait could be considered a relatively high-quality or low-quality signaler depending on the signal quality of other members of the social group. The ability to adjust other aspects of the integrated signaling phenotype based on feedback about the relative quality of static signals may be adaptive in changing social environments. For example, individuals that possess a signal of higher quality than most members of their social group may be particularly likely to benefit from exhibiting aggressive or dominant behavior. In contrast, if the same individual moves to a social group in which its static signal quality is lower than average, mechanisms that downregulate aggression and

Table 1 Gaps in our understanding of the integrated signaling phenotype, and potential opportunities for elucidating these relationships

Relationship	Potential research questions	Potential ways to address
Signals and behavior (link C; Fig. 1B)	How does the expression of signals influence an individual's behavior?	Manipulate signal traits, and when possible similar non-signal traits, to test effects on behavior. Alter social context to test for direct vs. indirect (multi-step) relationships.
Social context and signals (F)	How do social interactions influence the development and expression of signal traits?	Manipulate aspects of social group (size, familiarity, network connectivity, relative dominance, stability) to test effects on signal development and expression.
Signals-context-behavior (F to E)	Multistep interactions: when and how do signal-driven changes in social interactions influence the expression of behavior?	Simultaneously manipulate signals and social context; test the effect of signal manipulations on social context and behavior.
Signals-context-physiology (F to D)	Multistep interactions: when and how do signal-driven changes in social interactions influence physiological state?	Simultaneously manipulate signals and social context; test the effect of signal manipulations on social context and physiology.
Population-level effects	How do signal-driven changes in social context influence the phenotype of conspecifics, social networks, or the evolution and maintenance of signal traits?	Manipulate signal elaboration/relative signal quality, assess effects on social networks, conspecific phenotypes, and the strength of selection on signal traits.

dominance accordingly are likely to be adaptive. Signal-driven changes in widespread elements of the phenotype may have tremendous implications, not only for the reproductive performance of a particular individual, but for evolutionary dynamics related to trait variation within the population at large. For example, if signals mediate many aspects of phenotypic expression then population-level divergence in signal-preference may increase the likelihood or rate of reproductive isolation (Safran et al., 2013).

In Table 1 we highlight gaps in our understanding of the interactions among components of the integrated phenotype. While in this review we have focused on ecological time-scales, elucidating the ways in which integrated signaling phenotypes evolve is a critical next step for exploration. For example, the dynamic links among components of the integrated signaling phenotype likely vary within and across populations. If this aspect of phenotypic flexibility is heritable (Nussey et al., 2005; Husby et al., 2011; Dingemanse et al., 2012) then selection could favor the ability to rapidly or effectively alter the integrated signaling phenotype in accordance with changes in social context. Integrating feedback between social context and phenotype within models of the evolution and maintenance of signals may yield insights into how signals evolve, how coordinated signaling phenotypes are maintained, and how static signals continue to convey relevant phenotypic information about their bearer in dynamic social contexts.

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