

INTRODUCTION

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Animal signals are among nature's most compelling and diverse phenomena. Human cultures have long celebrated the expression of elaborate signals and displays, such as colors, songs, and dances of birds, which impress with their exuberance. Yet equally impressive are subtle modes of communication that had until recently eluded our detection. Some examples include the low-voltage electrical signals emitted and detected by some fishes as they orient, navigate, and communicate (Lissmann, 1958); the emission of pheromone plumes leading moths on a path upwind toward mates (David *et al.*, 1983); the inaudible, ultrasonic echolocation cries of bats (Griffin, 1958); the ultraviolet reflectance structures of many birds, butterflies, and flowers (Sheldon *et al.*, 1999); and the subtle substrate-borne signals that insects like lacewings use to communicate species identity (Wells and Henry, 1992). In many animal groups, signals express structures that are species-specific (e.g., Sueur, 2002) and that are partitioned over time and space (e.g., Luther, 2009). And many animal displays involve the coordination of multiple modalities, perhaps as a way to signal simultaneously to multiple audiences, or alternatively to enhance detectability, discriminability, and memorability. Documenting the diversity and intricacies of natural signaling modes, structures, and strategies is of itself a highly worthwhile endeavor.

Signals also demand our attention because they hold additional conceptual relevance in the fields of animal behavior and evolutionary biology (Andersson, 1994; Berglund *et al.*, 1996; Maynard-Smith and Harper, 2003). Signals and communication behavior turn out to be central to understanding varied processes of fundamental interest such as how animals optimize their social interactions, how animals choose mates, and how new species arise. We define signals as traits that are produced by senders, which transmit information through the environment, and which help receivers decide if and how to respond. Typically, but not always, both sender and receiver benefit via this transfer of information. This definition encompasses the presentation of morphological structures specialized for transmitting information to other individuals (e.g., a colorful anoline lizard dewlap) as well as elaborate displays that require high levels of skill, such as bird song (e.g., Podos and Nowicki, 2004; Byers *et al.*, 2010). The majority of communication occurs within species, and signals thus evolve primarily in the context of social selection (West-Eberhard, 1983). When signals of co-occurring species overlap in structure, they tend to diverge through a process of reproductive character displacement, thus emphasizing interspecific distinctions (e.g., Grant and Grant, 2010). Within species, much communication occurs between the sexes as each vies to maximize reproductive success, typically in circumstances in which the interests of signalers and receivers conflict with one another (Searcy and Nowicki, 2005). The signals that mediate these interactions, and other conflicts of interest, have been the focus of a large body of work in recent decades, with contributions from both modeling and empirical perspectives (e.g., Andersson, 1994; Johnstone 1995; Briffa and Hardy, 2013).

Yet despite years of research, our state of knowledge concerning sexual signals and their evolutionary basis has remained surprisingly unsettled. Some of this can be explained by a lack of certainty about which sexual selection models are most broadly applicable, whether it is possible to identify relevant null models, and the degree to which we should assume that signals convey information that is reliable (e.g., Hunt *et al.*, 2004a, 2004b). Most well-known is the difficulty in reconciling classic Fisherian (runaway) models of sexual selection with those requiring that signals provide reliable indicators of sender attributes (e.g., Maynard-Smith and Harper, 2003; Prum, 2010). From an empirical standpoint, Fisherian models of sexual selection require a genetic association of signal and preference traits, the demonstration of which still remains mostly beyond reach (Prum, 2010). Indicator models, by contrast, require that “high-quality” senders possess “good genes” (Møller and Alatalo, 1999) and are thus desirable as mates (the “sexy son” hypothesis, Zeh, 2004). Yet in practice it is daunting to determine whether a signaler possesses high genetic quality, and therefore most studies attempt to find a more pragmatic proxy. For example, some models of sexual signal evolution assume costs and benefits to the possession of a signal, such as a diminished flight performance as a result of unusually elongated tail feathers (Balmford *et al.*, 1993), or increased energetic or developmental costs (e.g., drumming in wolf-spiders, Kotiaho *et al.*, 1998; vocalization in frogs, Wells and Tiagen, 1989; see Kotiaho, 2001). This integration of physiological and mechanistic methods

with more traditional sexual selection theory has been formalized as the functional approach to sexual selection (Lailvaux and Irschick, 2006; Mowles *et al.*, 2010). This approach has gained significant traction over the past decade, with many studies emerging to test theories of sexual selection across a range of behavioral contexts. Our goal in this volume is to bring together a wide variety of papers applying diverse approaches to this topic, ranging across empirical, experimental, and theoretical perspectives. As a result, this work should hold special interest for researchers in three fields: sexual selection, physiological ecology, and functional morphology.

Functional approaches hold the promise of providing insight into several key aspects of sexual selection theory, especially in regard to signal honesty and the handicap hypothesis. The handicap hypothesis is predicated on the notion that we should be able to define individual male quality and relate it to measurements of sexual signal elaboration (e.g., size, color, and shape) as well as to reproductive effort and output. Researchers have devoted much effort toward this end, focusing on quality traits such as condition (Kodric-Brown and Nicoletto, 1993; Jakob *et al.*, 1996; Kotiaho, 1999; Peig and Green, 2010) and levels of parasitism. Yet such measures can be intrinsically problematic (e.g., Jakob *et al.*, 1996; Green, 2000; Peig and Green, 2010). For example, while values of condition may shed some light on an animal's overall health and vigor, simple observations of human or animal sporting events shows that one cannot easily predict human athletic performance based on external appearance (consider the case of the legendary thoroughbred horse Seabiscuit, which outperformed many other larger and more imposing horses in the 1930s and 1940s). On this point, it is important to recognize that no one trait will likely represent a valid measure of quality for all species. But we can ask whether certain kinds of traits offer a more general and satisfying link to our underlying model of individual quality. Over the last decade, and especially within the last few years, functional research has emphasized the utility of measurements of either whole-organism performance capacity (e.g., maximum sprint speed, bite force, locomotor endurance) or physiological variables such as metabolic rate and lactic acid level (e.g., Garland *et al.*, 1990; Briffa *et al.*, 2003; Huyghe *et al.*, 2005; Lappin and Husak, 2005; Wilson *et al.*, 2007; reviewed in Lailvaux and Irschick, 2006; Mowles *et al.*, 2010).

Although the first applications of a functional approach in the study of communication focused on sexual signals, it has now been applied to signals of individual quality that occur in an array of contexts, for example, during agonistic behavior that can occur over resources other than mates (e.g., Briffa *et al.*, 2003; Mowles *et al.*, 2010). Furthermore, the case for a useful interplay between the domains of sexual and non-sexual signals seems increasingly clear from a conceptual viewpoint as well as from a methodological one. As discussed above, the handicap hypothesis is often assumed to be most relevant to the context of sexual signaling, but it also pertains to the question of signal honesty during agonistic encounters as well as signals between prey and predators. Similarly, models of repeated signals are most often assumed to be relevant to animal contests even though it was first suggested in 1997 (Payne and Pagel, 1997) that these models could explain signals

in other contexts as well (Mowles and Ord 2012). Thus, the functional approach to the analysis of animal signals is relevant to a wide range of contexts, which are reflected in the chapters of this volume.

The logic of using performance or physiology traits as metrics of individual quality is straightforward. Whereas the role of variables such as condition or parasite levels for dictating the outcome of male fights is unclear, divergence among signalers in performance and physiology seems often far more obvious to us, and perhaps for females choosing mates as well (for female choice, which variables form the basis for it remain far less clear, Wong and Candolin, 2005). For example, for animals that fight by biting one another, the measurement of bite force is likely to be particularly important for determining who will win or lose the fight. Similarly, for animals that fight each other for relatively long time periods, measurements of locomotor endurance or perhaps physiological measurements of lactic acid buildup over time (Schuett and Grober, 2000; Briffa and Elwood, 2001) can inform us which males are well-suited to fight for periods, and which are likely to become exhausted (and why). A second reason for why a functional approach is useful is that performance or physiological traits may offer more holistic overall metrics of male “vigor” because they emerge as a result of many lower-level processes (Arnold, 1983; Bennett and Huey, 1990; Garland and Losos, 1994; Irschick and Garland, 2001). A very fast animal, to illustrate, is one that is likely to be generally healthy across the board, because of running’s intense demand on its muscular and skeletal systems, which in turn rely on cellular and metabolic efficiency and capacity. Finally, apart from studies of sexual selection, there is a long and vital tradition of measuring performance and physiological traits in a wide variety of animals and relating variation in them to variation in habitat use, behavior, and morphology (see above references).

In practice, the integration of functional traits into studies of sexual selection can take several forms. First, we can ask whether there is any linkage between performance or physiological traits and the shape, design, or size of sexual signals, a methodology that ultimately tests whether sexual signals are honest. Second, we can ask whether male reproductive success or its correlates, such as dominance, is enhanced by improved performance and physiology, especially in the context of the use of signaling during such encounters. Finally, we can generally examine the evolutionary relationships between sexual signals and functional traits to understand how and why their linkage has arisen.

The chapters in this book showcase the wide variety and utility of functional approaches for enhancing our understanding of signaling evolution, across a range of such contexts. In the second chapter, Royle *et al.* focus their discussion on oxidative stress, and outline how it may serve a causal link between life-history tradeoffs and signal evolution, particularly in taxa under strong sexual selection. Oxidative stress is a price animals pay for using oxygen in its typical reactive form, which in sufficient concentration can as a byproduct cause cells to degrade in structure and function. Selection should thus favor antioxidant defenses, which in turn can compete in life-history development and evolution with investment in elaborate secondary sexual traits. This hypothesis is being supported by multiple emerging

lines of evidence. A particularly interesting point emphasized in this chapter is the diversity of ways in which oxidative stress and responses to it can interface with proximate mechanisms that underlie signal expression.

In Chapter 3, Husak *et al.* review a rapidly expanding literature on interrelationships among costs (e.g., energetic, reproductive costs), performance traits, and sexually selected traits. The authors divide their attention between receiver-dependent and receiver-independent costs, and emphasize the interface between these types of capacities and organisms' overall performance capacities. One point of this chapter is that evidence is accumulating for significant function costs in signal evolution. Moreover, in parallel to the discussion of life-history tradeoffs in Chapter 2, Husak *et al.* focus on the idea that animals may evolve "compensatory traits" in response to the negative effects of sexually selected traits.

Chapter 4, by Borgia and Keagy, focuses specifically on the evolution of complex songs, which is an emerging area in which a functional approach is yielding some answers where prior approaches had stalled. The neuroanatomy of bird song has been well-studied, yet the links between the anatomy of the brain and song behavior, as well as these links with social behavior and learning, remain poorly understood. Keagy and Borgia examine how their own work on bowerbirds, a fascinating species in which males construct colorful nests that are designed to attract females, sheds light on the link between social behavior, song, and color signals.

In Chapter 5, Kemp and Grether show how a totally different kind of signal, namely color, offers exciting opportunities to characterize linkages between sexual selection theory and animal function. A main point emphasized by these authors is that colors come in many different forms and vary widely in degrees of phenotypic plasticity, ranging from those that are largely invariant from birth (and thus cannot really be changed) to those that are under considerable environmental influence. It is this latter set of colors, of which the most common form are carotenoid pigments, that have been of particular interest in the realm of sexual selection. Accumulating evidence indicates that such pigments, which are acquired through the consumption of food such as fruit, are limited in nature, and thus the acquisition of them, and their expression in brilliant colors, may be a strong indicator of male quality. Understanding the functional and mechanistic underpinnings of color production, and how animals vary in this trait thus allows us to more clearly understand why different colors have evolved.

Chapter 6, Briffa, evaluates the way in which signals are important for understanding how animals resolve conflicts. His historical approach shows that there has been a steady succession of models aiming to understand how animals resolve fights, especially through the use of signals, which in many cases, are designed to resolve fights without males resorting to violence that could injure either participant. The fact that sexual signals are so strongly linked with functional traits that play a key role during male fights indicates that the resolution of fights may often occur with the use of agonistic signals as advertisements of male quality, and particularly male ability to either persist in the contest or hurt the other opponent. Such examples suggest another key feature of signals that advertise individual quality.

While recent work on communication has perhaps been dominated by sexual signals, signals that advertise quality may also occur in non-reproductive contexts, such as during fights over resources other than mates (see Chapter 1 in Bradbury and Vehrencamp, 2012 for a discussion).

In Chapter 7, Podos and Patek return to acoustic signals, presenting a broad framework for asking how proximate mechanisms of acoustic production can shape signal evolution and divergence. They focus on three interrelated facets of acoustic production: biomechanics, size, and performance, and consider how each constrains and provides opportunities for signal divergence. A proximate focus on acoustic signal production, the authors argue, provides a useful complement to more traditional analyses of signal evolution that adopt optimality-based approaches.

In Chapter 8, Wilson and Angilletta continue the theme of animal contests, this time focusing on the question of the honesty of agonistic signals. The ability to convey false information is characteristic of humans and may even have contributed to the evolution of large brain size. It is therefore a fascinating topic and “bluffing” or exaggerating could clearly be of benefit to any animal involved in a conflict-of-interest situation. After reviewing the underlying theory of honest signals, they focus on how crustaceans have been used as model species to test these ideas. Moreover, they demonstrate the application of functional performance techniques, such as analysis of claw strength, to the analysis of signal honesty. This approach has given many new insights into the question of signal honesty, potentially providing alternative explanations for apparent bluffing during a fight.

Finally, in Chapter 9, Wilgers and Hebets turn to the condition-dependency of animal signals. Although the term *condition* is intuitive and widely used, it is a somewhat difficult concept to define. Nevertheless, signals are often influenced by an individual’s health and vigor and may thus be indicative of viability. Many studies have relied on body condition as a proxy for available energy reserves. In this chapter, the authors discuss the advantages of measuring energy reserves directly and explore the potential for genetic correlates of condition to yield new insights about the links between resource allocation and signals. Thus they promote the idea of moving beyond “black box” proxies for condition, such as body size measurements. Such metrics may mean different things for different individuals, species, and taxa. Therefore, the authors explain, we would do better to focus on analyzing the actual proximate mechanisms that may underlie condition and the signals that advertise this state.

This collection thus assembles some of the premier researchers in behavioral ecology and functional morphology, discussing some of the newest ideas to emerge at these fields’ interface. It is our hope that this book will generate new ways of thinking about sexual signals, animal function, and performance, and thereby open new avenues for collaborative research and new ways of testing theories both classic and emerging.

REFERENCES

- Andersson, M. (1994) *Sexual Selection*, Princeton University Press, Princeton, New Jersey.
- Arnold, S.J. (1983) Morphology, performance, and fitness. *American Zoologist*, **23**, 347–361.
- Balmford, A., Thomas, A.L., and Jones, I.L. (1993) Aerodynamics and the evolution of long tails in birds. *Nature*, **631**, 628–631.
- Bennett, A.F. and Huey, R.B. (1990) Studying the evolution of physiological performance. *Oxford Surveys in Evolutionary Biology*, **7**, 251–284.
- Berglund, A., Bisazza, A., and Pilastro, A. (1996) Armaments and ornaments: an evolutionary explanation of traits of dual utility. *Biological Journal of the Linnean Society*, **58**, 385–399.
- Bradbury, J.W. and Vehrencamp, S.L. (2012) *Principles of Animal Communication*, 2nd edn, Sinauer, Sunderland, MA.
- Briffa, M. and Elwood, R.W. (2001) Decision rules, energy metabolism and vigour of hermit-crab fights. *Proceedings of the Royal Society of London, Series B: Biological Sciences*, **268**, 1841–1848.
- Briffa, M., Elwood, R.W., and Russ, J.M. (2003) Analysis of multiple aspects of repeated signal: Power and rate of rapping during shell fights in hermit crabs. *Behavioral Ecology*, **14**, 60–65.
- Briffa, M. and Hardy, I.C.W. (2013) Preface, in *Animal Contests* (eds I.C.W. Hardy and M. Briffa), Cambridge University Press, Cambridge, pp. xxi–xxiv.
- Byers, J., Hebets, E., and Podos, J. (2010) Female mate choice based upon male motor performance. *Animal Behaviour*, **79**, 771–778.
- David, C.T., Kennedy, J.S., and Ludlow, A.R. (1983) Finding of a sex-pheromone source by gypsy moths released in the field. *Nature*, **303**, 804–806.
- Garland, T. Jr., Hankins, E., and Huey, R.B. (1990) Locomotor capacity and social dominance in male lizards. *Functional Ecology*, **4**, 243–250.
- Garland, T. Jr. and Losos, J.B. (1994) Ecological morphology of locomotor performance in squamate reptiles, in *Ecological Morphology: Integrative Organismal Biology* (eds P.C. Wainwright and S.M. Reilly), University of Chicago Press, Chicago, pp. 240–302.
- Grant, B.R. and Grant, P.R. (2010) Songs of Darwin's finches diverge when a new species enters the community. *Proceedings of the National Academy of Sciences of the United States of America*, **107**, 20156–20163.
- Green, A.J. (2000) Mass/length residuals: measurements of body condition, or generators of spurious results? *Ecology*, **82**, 1473–1483.
- Griffin, D.R. (1958) *Listening in the Dark*, Yale University Press, New Haven, CT.
- Hunt, J., Bussiere, L.C., Jennions, M.D., and Brooks, R. (2004a) What is genetic quality? *Trends in Ecology and Evolution*, **19**, 329–333.
- Hunt, J., Brooks, R., Jennions, M.D., Smith, M.J., Bentsen, C.L., and Bussiere, L.C. (2004b) High quality male field crickets invest heavily in sexual display but die young. *Nature*, **432**, 1024–1027.

- Huyghe, K., Vanhooydonck, B., Scheers, H., Molina-Borja, M., and Van Damme, R. (2005) Morphology, performance and fighting capacity in male lizards, *Gallotia galloti*. *Functional Ecology*, **19**, 800–807.
- Irschick, D.J. and Garland, T. Jr. (2001) Integrating function and ecology in studies of adaptation: studies of locomotor capacity as a model system. *Annual Reviews of Ecology and Systematics*, **32**, 367–396.
- Jakob, E.M., Marshall, S.D., and Uetz, G.W. (1996) Estimating fitness components: a comparison of body condition indices. *Oikos*, **77**, 61–67.
- Johnstone, R.A. (1995) Sexual selection, honest advertisement and the handicap principle: reviewing the evidence. *Biological Review*, **70**, 1–65.
- Kodric-Brown, A. and Nicoletto, P. (1993) The relationship between physical condition and social status in pupfish *Cyprinodon pecosensis*. *Animal Behaviour*, **46**, 1234–1236.
- Kotiaho, J.S. (1999) Estimating fitness: comparison of body condition indices revisited. *Oikos*, **87**, 399–400.
- Kotiaho, J. (2001) Costs of sexual traits: a mismatch between theoretical considerations and empirical evidence. *Biological Reviews*, **76**, 365–376.
- Kotiaho, J., Alatalo, R.V., Mappes, J., Nielson, M.G., Parri, S., and Rivero, A. (1998) Energetic costs of size and sexual signaling in a wolf spider. *Proceedings of the Royal Society of London, Series B: Biological Sciences*, **265**, 2203–2209.
- Lailvaux, S. and Irschick, D.J. (2006) A functional perspective on sexual selection: insights and future prospects. *Animal Behaviour*, **72**, 263–273.
- Lappin, A.K. and Husak, J. (2005) Weapon performance, not size, determines mating success and potential reproductive output in the collared lizard (*Crotaphytus collaris*). *American Naturalist*, **166**, 426–436.
- Lissmann, H.W. (1958) On the function and evolution of electric organs in fish. *Journal of Experimental Biology*, **35**, 156–191.
- Luther, D. (2009) The influence of the acoustic community on songs of birds in a neotropical rain forest. *Behavioral Ecology*, **20**, 864–871.
- Maynard-Smith, J. and Harper, D. (2003) *Animal Signals*, Oxford University Press, Oxford.
- Møller, A.P. and Alatalo, R.V. (1999) Good-genes effects in sexual selection. *Proceedings of the Royal Society of London, Series B: Biological Sciences*, **266**, 85–91.
- Mowles, S.L., Cotton, P.A., and Briffa, M. (2010) Whole-organism performance capacity predicts resource holding potential in the hermit crab *Pagurus bernhardus*. *Animal Behaviour*, **80**, 277–282.
- Mowles, S.L. and Ord, T.J. (2012) Repetitive signals and mate choice: insights from contest theory. *Animal Behaviour*, **84**, 295–304.
- Payne, R.J.H. and Pagel, M. (1997) Why do animals repeat costly signals? *Animal Behavior*, **54**, 109–119.
- Peig, J. and Green, A.J. (2010) The paradigm of body condition: a critical reappraisal of current methods based on mass and length. *Functional Ecology*, **6**, 1323–1332.
- Podos, J. and Nowicki, S. (2004) Performance limits on birdsong, in *Nature's Music: The Vocal Life of Birds* (eds P. Marler and H. Slabbekoorn), Elsevier Academic Press, San Diego, pp. 318–342.

- Prum, R.O. (2010) The Lande–Kirkpatrick mechanism is the null model of evolution by intersexual selection: implications for meaning, honesty, and design in intersexual signals. *Evolution*, **64**, 3085–3100.
- Schuett, G.W. and Grober, M.S. (2000) Post-fight levels of plasma lactate and corticosterone in male copperheads, *Agkistrodon contortrix* (Serpentes, Viperidae): differences between winners and losers. *Physiology & Behavior*, **71**, 335–341.
- Searcy, W.A. and Nowicki, S. (2005) *The Evolution of Animal Communication: Reliability and Deception in Signaling Systems*, Princeton University Press, Princeton, NJ.
- Sheldon, B.C., Andersson, S., Griffith, S.C., Ornborg, J., and Sendecka, J. (1999) Ultraviolet colour variation influences blue tit sex ratios. *Nature*, **402**, 874–877.
- Sueur, J. (2002) Cicada acoustic communication: potential sound partitioning in a multi-species community from Mexico (Hemiptera : Cicadomorpha : Cicadidae). *Biological Journal of the Linnean Society*, **75**, 379–394.
- Wells, M.M. and Henry, C.S. (1992) The role of courtship songs in reproductive isolation among populations of green lacewings of the genus *Chrysoperla* (Neuroptera, Chrysopidae). *Evolution*, **46**, 31–32.
- Wells, K.D. and Tiagen, T.L. (1989) Calling Energetics of Neotropical Treefrog, *Hyla microcephala*. *Behavioral Ecology and Sociobiology*, **25**, 13–22.
- West-Eberhard, M.J. (1983) Sexual selection, social competition and speciation. *Quarterly Review of Biology*, **58**, 155–183.
- Wilson, R.S., Angilletta, M.J., James, R.S., Navas, C., and Seebacher, F. (2007) Dishonest signals of strength in male slender crayfish (*Cherax dispar*) during agonistic encounters. *The American Naturalist*, **170**, 284–291.
- Wong, B.B.W. and Candolin, U. (2005) How is female mate choice affected by male competition? *Biological Reviews*, **80**, 559–571.
- Zeh, J.A. (2004) Sexy sons: a dead end for cytoplasmic genes. *Proceedings of the Royal Society of London, Series B: Biological Sciences*, **271**, S306–S309.

