Animal Signaling and Function

An Integrative Approach

Edited by

Duncan J. Irschick, Mark Briffa and Jeffrey Podos

WILEY Blackwell

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1

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.

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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