




SYMPOSIUM

How Signaling Geometry Shapes the Efficacy and Evolution of Animal Communication Systems

Sebastian A. Echeverri ^{*,1} Audrey E. Miller,[†] Jason Chen,^{*,‡} Eden W. McQueen,^{*} Melissa Plakke,^{*,§} Michelle Spicer,^{*,||} Kim L. Hoke,^{||} Mary Caswell Stoddard[†] and Nathan I. Morehouse^{*,|||}

^{*}Department of Biological Sciences, University of Pittsburgh, 4249 Fifth Avenue, Pittsburgh, PA 15260, USA;

[†]Department of Ecology and Evolutionary Biology, Princeton University, 106A Guyot Hall Princeton University

Princeton, NJ 08544-2016, USA; [‡]Department of Biology, Emory University, 1510 Clifton Road NE, Room 2006, Atlanta,

GA 30322, USA; [§]Department of Ecology and Evolutionary Biology, University of Kansas, 2045 Haworth Hall 1200

Sunnyside Ave. Lawrence, KS 66045, USA; [¶]Department of Biology, University of Puget Sound, 1500 N. Warner St.

Tacoma, WA 98416, USA; ^{||}Department of Biology, Colorado State University, 251 W Pitkin St, Fort Collins, CO 80521,

USA; ^{|||}Department of Biological Sciences, University of Cincinnati, PO Box 210006 Cincinnati, OH 45221-0006, USA

From the Symposium “Spatiotemporal dynamics of animal communication” presented at the virtual annual meeting of the Society for Integrative and Comparative Biology, January 3–7, 2021.

¹E-mail: spiderdaynightlive@gmail.com

Synopsis Animal communication is inherently spatial. Both signal transmission and signal reception have spatial biases—involving direction, distance, and position—that interact to determine signaling efficacy. Signals, be they visual, acoustic, or chemical, are often highly directional. Likewise, receivers may only be able to detect signals if they arrive from certain directions. Alignment between these directional biases is therefore critical for effective communication, with even slight misalignments disrupting perception of signaled information. In addition, signals often degrade as they travel from signaler to receiver, and environmental conditions that impact transmission can vary over even small spatiotemporal scales. Thus, how animals position themselves during communication is likely to be under strong selection. Despite this, our knowledge regarding the spatial arrangements of signalers and receivers during communication remains surprisingly coarse for most systems. We know even less about how signaler and receiver behaviors contribute to effective signaling alignment over time, or how signals themselves may have evolved to influence and/or respond to these aspects of animal communication. Here, we first describe why researchers should adopt a more explicitly geometric view of animal signaling, including issues of location, direction, and distance. We then describe how environmental and social influences introduce further complexities to the geometry of signaling. We discuss how multimodality offers new challenges and opportunities for signalers and receivers. We conclude with recommendations and future directions made visible by attention to the geometry of signaling.

Introduction

When animals communicate, their relative spatial position in the environment impacts the efficacy, and often the outcome, of their interactions. In the first instance, this is the result of directional biases in both signal propagation and reception, which impact the angles in space from which signals can be perceived (e.g., Fig. 1; Rosenthal 2007; Bradbury and Vehrencamp 2011; Hutton et al. 2015). Signals also

attenuate as they move through environments, making the distance between signaler and receiver a key consideration for communicating animals (Rosenthal 2007; Johnsen 2012; Cronin et al. 2014). Thus, to optimize signal transmission and reception, both senders and receivers must actively manage their location and orientation, a feature of animal communication which we call the geometry of signaling. However, behavioral ecologists rarely quantify the

geometry of signaling interactions, relying instead on assumptions about “typical” spatial positioning, sometimes based on informal field observations. In the best case, these assumptions stand up to more careful scrutiny. At worst, they mislead us to emphasize traits that have minor significance or no role at all in the communicatory behaviors of the focal animals. Either way, we argue that greater attention to the geometry of signaling promises to reveal new insights into the complexity and evolution of animal signaling systems, whether by uncovering overlooked behavioral and cognitive adaptations or by overturning conventional yet unfounded understandings.

The explicitly geometric view of animal communication that we develop in this review has number of broad implications worth highlighting at the start. For example, signalers are not only under selection to produce the best signal, but they must also coordinate their posture and spatial position in relation to intended receivers to ensure that their signal is available for reception (Rosenthal 2007; Echeverri et al. 2017). The nature and strength of selection on signaler positioning will itself depend on the directionality of the signal, a property for which we often lack rigorous quantification. Likewise, receivers are not only under selection to make optimal decisions based on signaled information, but must also attend to their posture and location in space so as to maximize their ability to evaluate signals of interest (Land 1999; Rosenthal 2007; Hutton et al. 2015). Again, selection on receiver positioning will also depend on the directional biases of relevant perceptual systems for which we often lack specific knowledge in focal systems. Taken together, these observations imply that animals must often work in concert to optimize signaling geometry (Fig. 1). Many of us know this from personal experience. If someone is having a hard time hearing us, we turn to face them, perhaps even moving closer to make our auditory communication easier to perceive. If we are the listener, we might turn one ear toward the speaker, lean closer, or even cup our hand around the ear to improve sound reception.

Such behavioral responses are, for many, an intuitive part of how we as humans communicate effectively. But what about animals? Do nonhuman communicators actively adjust their positions so as to address challenges facing effective signaling? How are these dynamics influenced by constraints imposed by signaling modalities? How are they accommodated by animal cognition, including perceptions of space and time? In this review, we discuss what is known about how animals have evolved to meet the demands imposed by the geometry of signaling, from

the directionality of signaling and sensing to the requirements of particular modalities and signaling contexts. Our overarching goal is to reveal how essential this aspect of signaling is for a holistic understanding of animal communication, and yet how much there remains to be explored by researchers in the field.

To illustrate how and why the geometry of signaling is important across modalities and social contexts, we begin with a few case studies. Take male Costa’s hummingbirds (*Calypte costae*), for example. These showy birds perform highly coordinated aerial courtship displays to prospective female mates (Simpson and McGraw 2018a). The male “shuttle” display involves rapid flights back and forth in front of a perched female during which the male erects his colorful throat and crown feathers. If such aerial acrobatics were not enough, he must also position himself such that the colors on his iridescent (i.e., highly directional) throat and crown feathers are as bright as possible from the female vantage point. Maximizing the brilliance of this iridescent display for his prospective mate involves not only managing his location, but also the position of his plumage with respect to the sun and the position of the female, all in three dimensions (Simpson and McGraw 2018a). Impressively, male Costa’s hummingbirds appear to engage in such complicated positional management (Simpson and McGraw 2018a), a feat that they share with related hummingbirds, such as Anna’s hummingbird (*Calypte anna*; Hamilton 1965) despite major differences in the aerial maneuvers exhibited by these two species. Intriguingly, Simpson and McGraw (2018a) also found that variation in male location and body positioning was more predictive of male appearance from the female vantage than variation in the intrinsic properties of male plumage coloration (e.g., maximal brightness, chroma, etc.), indicating that male display behavior is at least as important as male color quality in determining how a female perceives his coloration. In contrast, male broad-tailed hummingbirds (*Selasphorus platycercus*) appear not to constrain their shuttles or U-shaped display dives in relation to solar position, despite the fact that the gorgets of these animals are similarly iridescent (Hogan and Stoddard 2018; Simpson and McGraw 2018b). Understanding how and why these species have evolved different display strategies requires attention to the positional determinants and limitations of effective courtship: we must consider the geometry of their signaling dynamics. Further, we know nothing about how females position and orient themselves during assessment of these displays, a critical detail

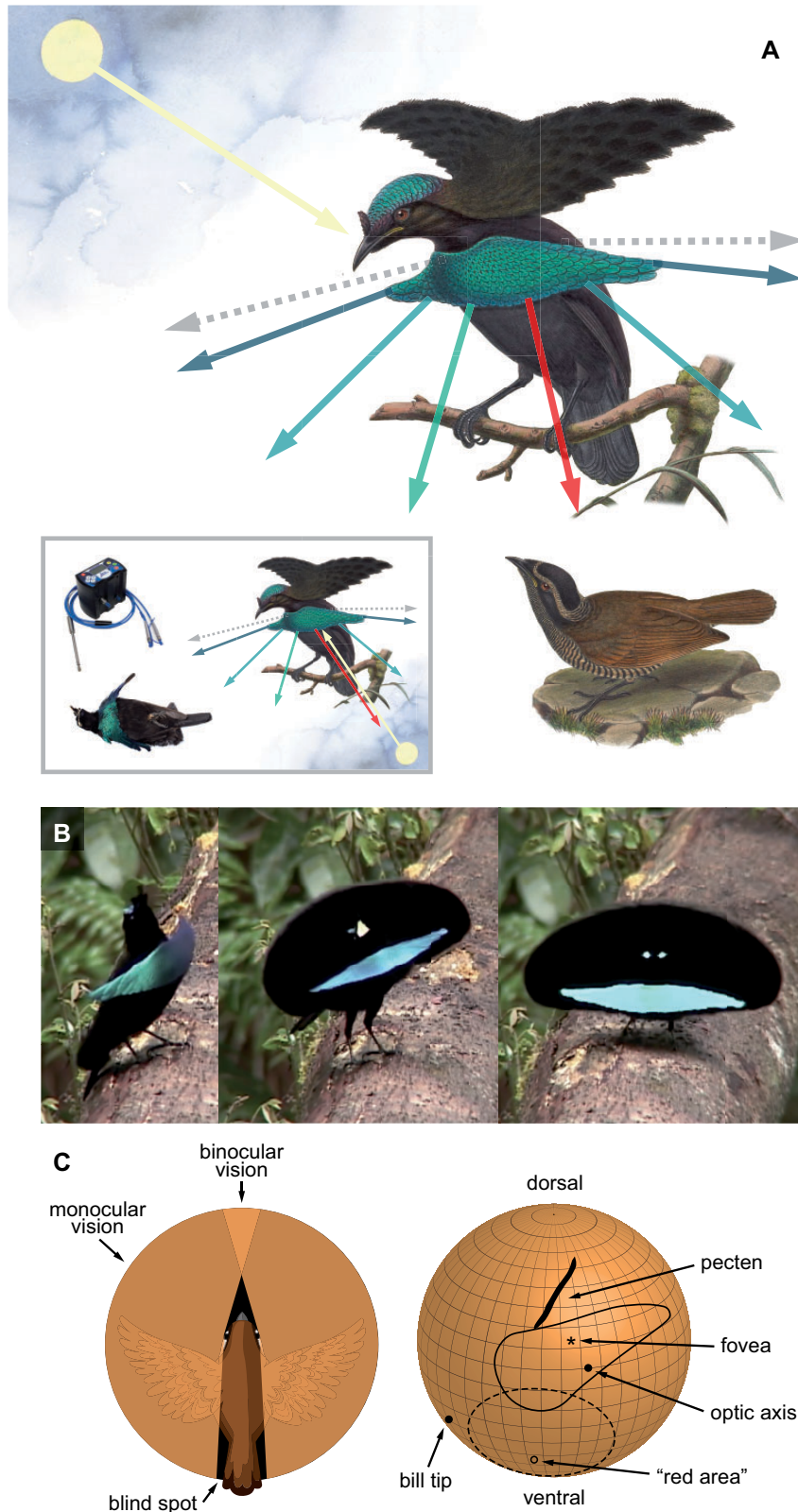


Fig. 1. Illustration of key concepts in the geometry of signaling using courtship in the Superb Bird of Paradise (*L. superba*) as an example. **(A)** Because elements of the male visual display are iridescent, their appearance is dependent on the position of illumination (the sun), the plumage patch, and the viewer. Some viewing positions may not be able to see the color patch (dashed grey arrows), whereas others will differ in the perceived color. Researchers often measure a single angle of reflection (red arrow) when characterizing such traits, thereby implicitly adopting a specific signaling geometry that places both the sun and the receiver at fixed locations

that determines whether the male's signal is fully perceived by the female regardless of his valiant attempts to optimize his own signaling.

Beyond the visual realm, communication in other sensory modalities is also often influenced by spatial considerations. For example, sound propagation is frequency dependent. Higher frequency sounds are both more directional and experience higher rates of distance-dependent attenuation than lower frequency sounds (Richards and Wiley 1980; Bradbury and Vehrencamp 2011). Based on these inherent properties of sound, researchers have argued that rodent ultrasonic communication may have evolved in part because these high-frequency vocalizations can be deployed more discreetly and in a more directed way during intraspecific communication (Arch and Narins 2008). These properties also play a role in context-dependent use of ultrasonic alarm calls in Richardson's ground squirrels (*Spermophilus richardsonii*), which are more likely to use ultrasonic rather than nonultrasonic alarm calls the farther away the threatening stimulus is, thereby taking advantage of the privacy benefits of higher ultrasonic sound attenuation (Wilson and Hare 2006). These observations reveal a central role for spatial relationships, including distance and directionality, in the evolution of vertebrate ultrasonic communication.

Finally, in many modalities, features of the environment can heavily impact effective signaling geometries. For instance, chemical communication often (but not always) relies on environmental fluid flows that move signaling molecules through space. For example, many insects communicate via wind-borne pheromones, and transit of these pheromones through the environment is often complicated by objects within a habitat (e.g., trees in forests; Fares et al. 1980) and/or turbulence in air flow (Crimaldi and Koseff 2001). This suggests that in complex environments, signaler's spatial positioning during pheromone release may be an essential consideration, a result supported by observations from spatial arrays of pheromone-based insect traps (e.g., in

trapping efforts focused on the oriental fruit moth, *Grapholitha molesta*; Kong et al. 2014, and the mosquito *Aedes aegypti*; Melo et al. 2020).

While the examples described above may lead the reader to believe that the geometry of signaling is often well characterized, our review of the literature indicates that such considerations remain overlooked or unreported in most systems. Thus, we call for increased attention to this essential aspect of animal communication. In the sections below, we first discuss how intrinsic factors (related to signal and reception properties alone) play a role in determining optimal signaling geometries and associated behavioral dynamics in animal communication. Then, we explore the additional interactions brought on by extrinsic factors of communication interactions: environmental context (related to structure and physical properties of the signaling environment), and social complexity (related to the number and identity of signaler(s) and receiver(s), and whether their locations are known). We have endeavored to illustrate how these various factors play a role across a range of signaling modalities, focusing our survey on visual, acoustic, and chemical communication. Perhaps, most interestingly, signaling modalities differ from each other in the ways that the geometry of signaling impacts them the most. This suggests that multimodal communication may often evolve as a set of interconnected compromises between these various geometric advantages and constraints, a topic that we approach at the end of the review. We conclude by pointing to open questions and new directions revealed by a more explicit focus on the geometry of signaling.

Intrinsic factors of signaling geometry

Even in "laboratory conditions" where environmental effects are removed or minimized, some relative positionings of signaler and receivers are better than others for signaling efficacy as a result of directional biases in signal propagation and reception. These

in the environment. However, some approaches involving commonly used equipment (e.g., a bifurcated probe applied to a study skin, inset) force unrealistic geometries (e.g., situating the sun and the receiver at the same location in space). (B) By adopting a single measurement geometry, researchers collapse the vibrant dynamism of real displays, thereby implicitly assuming that they have either identified the most important moment (and geometry) of a male's display, or at least one that is representative of the display as a whole. Such assumptions are rarely if ever verified. (C) In addition to the complexities of displays, the sensory fields of receivers are likewise spatially complex. For example, although bird visual fields often provide access to a nearly complete visual surround, the quality of visual information varies dramatically across these visual fields thanks to retinal specializations (e.g., the fovea, foveal region, "red area" in ground foraging birds, etc.) and blind spots (e.g., from the pecten). This retinal variation impacts the perception of color, pattern, and motion in the world, yet researchers rarely account for this when considering what receivers see during signaling interactions, opting instead to implicitly assume optimal reception (i.e., maximal color vision, acuity, and motion detection) when applying receiver visual abilities to analysis of focal visual signals. Illustrations in (A) are modified from the drawings of William Matthew Hart (1891), available in the public domain; the still images in (B) are from the video footage of Edwin Scholes, used with permission, and archived at the Macaulay Library at the Cornell Lab of Ornithology (ML458003).

intrinsic factors form the initial basis for expectations of signaling geometry in animal systems (e.g., Fig. 1). In some instances, directionality and distance-dependence of signaling or reception are unavoidable. For example, it is virtually impossible to produce an omnidirectional vocalization, given that the animal mouths open in a particular location on the head, and heads are prone to blocking or absorbing sounds, thereby creating sound shadows (Hunter et al. 1986). Similar issues arise for hearing organs. However, animals often mitigate (e.g., rotating during vocalization to sweep a wide area) or exaggerate (e.g., via the use of limbs or facial structures to increase sound beaming, or external ears for sound reception) the inherent directionality of their signals and sensors. Thus, in the animal kingdom, evolutionary responses to these intrinsic factors range from tactics to overcome directional constraints to adaptive strategies that harness this aspect of animal communication. Below, we describe the theory and evidence behind how directionality and distance influence signaling efficacy for both signalers and receivers, and further, how animals compensate for, or exploit, these geometric features of animal communication.

Directionality

The directionality of signals—the set of angles at which they are effectively transmitted and received—is a crucial aspect of signaling geometry. For directional signals, selection for efficient transmission can influence signaler behavior, which can act to beam the signal toward intended receivers. Receivers in turn can be under selection to orient their body and relevant sensory organs in a way that optimizes signal reception (Rosenthal 2007; Bradbury and Vehrencamp 2011; Hutton et al. 2015; Echeverri et al. 2017). Some animals have even evolved exploitative strategies that force signals to be perceived from specific directions. In this section, we explore how animals respond and adapt to the inherent directionality of signaling.

Causes of directionality in signaling

Even ignoring environmental influences, animal communication is always directional to some degree because: (1) most animals do not produce signals that propagate uniformly in all directions, with natural signals ranging from weakly to strongly directional and (2) most animals do not receive signals uniformly from all directions. Here we explore these intrinsic causes of directionality in visual, acoustic, and chemical communication.

Many visual signals are highly dependent on viewing angle (Fig. 1A and B). For example, some structural colors, such as iridescent colors, are highly directional, changing in hue and brightness as a function of viewing and/or illumination angle. Many pigment-based colors are also somewhat directional, despite often being treated by researchers as Lambertian reflectors (i.e., scattering light equally in all directions, Oren and Nayar 1995; Santos et al. 2007). To add to this intrinsic directionality, visual signals are often displayed on flattened body surfaces (e.g., a peacock's feather train) or are highly asymmetric (e.g., the dewlap of *Anolis lineatus*, which is more orange on one side and more yellow on the other; Gartner et al. 2013; Losos et al. 2017), introducing further constraints on the angle from which a signal is best viewed.

The courtship signals of the Common Eggfly (*Hypolimnna bolina*) provide a good illustration of how these sources of directionality combine within a display: male butterflies of this species have flat wings featuring both an asymmetric appearance (i.e., the colorful dorsal wing patterns contrast with the more cryptic ventral wing patterns, as in most butterfly species) and vibrant UV-reflecting iridescent markings on the dorsal wing surfaces. Have male eggflies evolved to strategically enhance the appearance of their iridescent UV markings to females? In a detailed study of signal design and courtship behavior, White et al. (2015) demonstrated that males position themselves just beneath females when performing a “fluttering” mating display. This orientation ensures that females will see a maximally bright UV signal from the dorsal surface of the male's wings at the bottom of each wingbeat downstroke—a result consistent with similar observations from the iridescent UV color displays of male orange sulfur butterflies (*Colias eurytheme*; Rutowski et al. 2007). Additionally, the male eggfly's position (relative to the female) allows the female to perceive a series of flashes as he flaps his wings. Outside of this precise arrangement, other observers—such as avian predators—would be less likely to see the male's flashy UV signal. These results are consistent with the growing literature on iridescent signals, their directionality (reviewed in Doucet and Meadows 2009; Meadows et al. 2009), and their use in dynamic color communication (reviewed in Hutton et al. 2015). However, for many less obviously “flashy” visual signals, information about spatial biases in their visibility remains uncharacterized, despite the potential for such biases, even minor, to influence how they are used during communication (Hutton et al. 2015).

The visual systems used to assess these visual signals also have directional biases. Animal eyes differ in their visual fields, and further directional biases are introduced by retinal specializations that lead to regional differences in the perception of color, pattern, and motion (Fig. 1C; Temple 2011; Land and Nilsson 2012). For example, although bird visual fields often encompass most of the visual surround (except a small rear-facing blind spot), the highest visual acuity and color sensitivity is typically restricted to a small central fovea, sometimes accompanied by other specialized areas of the visual field such as the ventrally-facing “red area” in ground foraging species (Letelier et al. 2004; Querubin et al. 2009). An even more extreme example can be found in the modular visual systems of jumping spiders, where achromatic, low-resolution vision is provided by a set of six “secondary” eyes with a combined field-of-view of nearly 360° (Harland et al. 2012). A pair of forward-facing “principal” eyes augment this field-of-view with high acuity and color vision (Morehouse et al. 2017). The latter, however, have extremely limited fields of view, narrowing to only 2° visual angle in the horizontal plane (Land 1969a). Thus, colors and fine details must be placed within the fields of view of these “principal” eyes to be perceived. These spatial biases in vision are further complicated by dynamic control of receiver gaze through movements of the eyes (e.g., bird gaze; Chow and Frye 2009; Yorzinski et al. 2013; Fernández-Juricic et al. 2019), or in the case of jumping spiders, the retinas themselves (Land 1969b). Thus, receivers must often manage their location in the environment, as well as the position of their heads and their visual organs, when assessing a visual signal of interest (Rosenthal 2007). Properly understanding these “active vision” behaviors, however, must be built on foundational knowledge regarding the spatial distribution of visual functions (e.g., color vision, motion sensitivity, and acuity). We are only just beginning to understand this rigorously even in model organisms (e.g., zebrafish; Zimmermann et al. 2018), and for many classic models in animal communication, such information remains to be collected.

Given these spatial biases in vision, how do receivers dynamically control their position and posture during visual assessment? It is still relatively uncommon for researchers to report the direction of receiver gaze or field-of-view in studies of signal directionality, despite this being a critical determinant of signaling efficacy. However, the rare studies that have assessed receiver gaze have held some surprises. A study in which female peacocks were outfitted

with tiny telemetric gaze-trackers revealed that females do not fixate their foveas on a displaying male’s bright and colorful eyespots but rather focus on the lower part of the male’s train (Yorzinski et al. 2013). Moreover, females spent 63% looking away from the male during a display bout, such that the male display was either not visible at all or was viewed entirely by the female’s peripheral vision. Similarly, in *Habronattus pyrrithrix* jumping spiders, females faced away from males for over 73% of the courtship interaction (Echeverri et al. 2017), meaning that they spent the vast majority of the time without being able to assess the color and detail of the complex displays that these males perform. Future work on the geometry of visual signaling should capitalize on breakthroughs in gaze-tracking technologies combined with our growing understanding of eye placement and visual fields (Stevens 2007; Land and Nilsson 2012), eye specialization (e.g., Foelix 2011; Harland et al. 2012), intraretinal variability (Temple 2011; Zimmermann et al. 2018), and eye lateralization (Salva et al. 2012; Templeton et al. 2012), all of which can influence how eyes detect and process visual information coming from particular directions.

Acoustic signals also tend to be directional because they are typically produced by body parts with a precise location in or on the signaler’s body. Sound waves originating from these body parts will propagate through the transmission medium in certain directions (e.g., out of the mouth of a singing bird (Patricelli et al. 2007), off the wings of a chirping cricket (Forrest 1991)), while being blocked or dampened by the signaler’s body in other directions (Fig. 2B and C). External and internal structures can further channel sounds in certain directions: the external bell-shaped horns around the mouths and nostrils of some bats (Zhuang and Müller 2006; Bradbury and Vehrencamp 2011; Müller 2015) and the internal melon (a ball of fatty tissue near the forehead) of toothed whales (Au et al. 2006) help achieve this. In birds, vocalization directionality is the result of interactions between the frequency content of the call, beak morphology, and body posture (Larsen and Dabelsteen 1990; Nelson et al. 2005; Patricelli et al. 2007; Bradbury and Vehrencamp 2011). The directionality of sound signals has been quantified in diverse taxa, with sounds ranging from weakly directional—as in human speech (Marshall and Meyer 1985)—to strongly directional—as in elephant seal calls (Holt et al. 2010), where high-frequency components of calls can be up to 30 dB louder in the direction pointing away from the seal’s mouth than directly behind the animal.

The directionality of sound communication is also affected by the position and posture of receivers: sound reception has directional biases that arise from the structure and location of sound-sensing body parts. For example, the mammalian pinna (external ear) can amplify and direct incoming sounds: its shape, structure, and movability influence the ear's sensitivity to sounds coming from different directions (Phillips et al. 1982; Jen and Chen 1988; Muller and Bovet 1999). In dolphins and other cetaceans, which have lost their external ears, sound sensitivity depends in part on which materials and tissues sounds pass through from their point of incidence on the skull toward the internal ear (Aroyan 2001; Branstetter and Mercado 2006). Birds likewise lack a pinna but some owls have something similar: a feathery ruff covering the outer ear that acts as a highly direction-sensitive sound collector, aiding in sound localization (Von Campenhausen and Wagner 2006). Internally coupled ears of lizards and insects are intrinsically directional, with up to 30 dB difference in amplitude depending on receiver angle (reviewed in Römer and Schmidt 2016; Christensen-Dalsgaard and Manley 2019). However, despite these clear indications of directionality in sound production and hearing, little work has focused on how receivers manage the location and orientation of sound receiving organs. Even less has characterized the dynamic spatial interactions between signalers and receivers during acoustic communication, leaving this an area ripe for study.

The factors influencing the directionality of chemical communication have some marked differences from those of other modalities. As in visual and sound communication, the locations of chemical-producing glands and chemical-sensing receptors on the body introduce some directional biases. However, chemical signal molecules (i.e., semiochemicals), once released from the signaler, must physically travel the distance between the signaler and receiver. At very short distances and/or in highly viscous fluids, semiochemicals will travel primarily by simple diffusion, with only weak directionality (Atema 1995; Bradbury and Vehrencamp 2011). However, many chemical signals rely on fluid flow (e.g., the currents of wind and water; Alberts et al. 1992; Atema 1995; Muller-Schwarze 2006; Webster and Weissburg 2009) for transmission. Such fluid flow can be environmental (see section Environmental context given below) and/or generated by the signaler (e.g., wing-based vortices in sac-winged bats, Voigt and von Helversen 1999; and the butterfly *Pieris napi*, Andersson et al. 2007; currents generated via gill movement in crayfish and

lobsters, Atema 1995; Bergman et al. 2005). Likewise, the directionality of chemoreception depends on the patterns of fluid flow immediately adjacent to the sensory organ, which is influenced by the morphology of the sensor and surrounding body, as well as any receiver behaviors (e.g., respiration and non-respiratory sniffing) that direct fluid toward the receptor (Atema 1995; Settles et al. 2003; Riffell et al. 2008; Bradbury and Vehrencamp 2011). Such “olfactory aerodynamics” have been well described for canines (Settles et al. 2003; Craven et al. 2010), and some aquatic arthropods (reviewed in Koehl 2006) but rarely in other systems (but see Jaffar-Bandjee et al. 2020 for a review of challenges and advances for this research in terrestrial insects). Previous work has also described how some receivers orient their chemoreceptors, but specifically in the context of extracting spatial information from odor gradients (e.g., in lobsters; Goldman and Koehl 2001; Koehl et al. 2001). More work to understand how receivers manage the positioning of chemical sensors during dynamic signaling interactions would be a welcome advance.

Compensation for directionality

To compensate for the limited active space of directional signals, signalers are often under strong selection to ensure efficient delivery of a signal by directing their signals at the intended receiver. Animals have evolved a number of strategies to address this challenge. For example, on a lek, where males typically compete for the attention of multiple females, the challenges of directional signaling are drawn in sharp relief. Tantalizingly, male sage grouse—despite rarely facing females head-on during their charismatic strut displays—may nevertheless adopt an orientation that allows them to effectively beam the loudest part of their whistle calls in the direction of attentive females (Dantzker et al. 1999). In contrast, when receiver position is unknown, and therefore signal directionality is something of a liability, signalers often rotate their bodies during signal production, a strategy that animals share with revolving sirens and lighthouse beacons. This behavior has been observed in nightingales and sedge warblers (Brumm and Todt 2003; Brumm et al. 2011), northern mockingbirds (Breitwisch and Whitesides 1987), and red-winged blackbirds (Brenowitz 1982; Patricelli et al. 2007). In the chemical realm, signalers may evolve methods to impart a fluid flow to emitted semiochemicals and propel them toward a receiver. For example, female mara (a large rodent) sprays urine at other females, the scent of which serves to reduce harassment from males (Ottway et

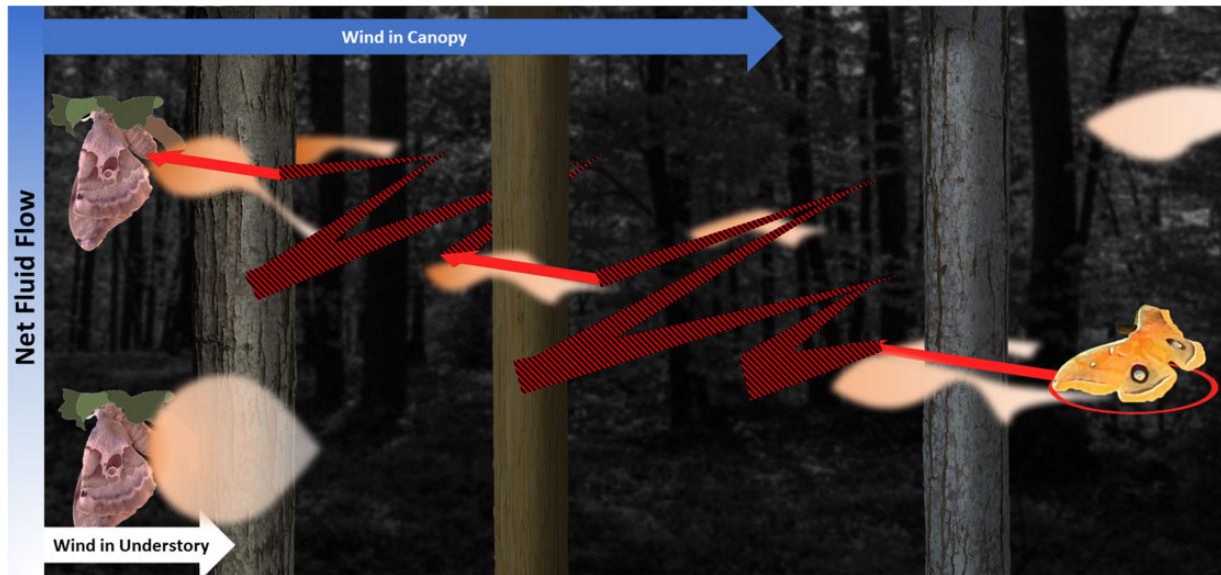


Fig. 2. A signaler's location in the environment, and how their signal interacts with environmental features, can determine signal efficacy. A female moth (upper left) located in a forest canopy produces multiple volatile pheromones from her scent gland, which diffuse and blow downwind to create an odor plume. Because of stochastic turbulence in the air, changes in wind direction, and environmental obstacles, the odor plume has a complex, discontinuous 3D structure. A male (lower right) accounts for this signal complexity by alternating between anemotaxis (following a single plume upwind, solid lines) and lateral casting (moving perpendicular to the direction of the current, dashed lines) in search of the odor plume, to finally reach the canopy female, sensing the directionality of the plumes with his well-developed pectinate antennae. However, another female located in the understory (lower left) experiences slower fluid flow, and her pheromone plume travels far less, making it unlikely to reach a male. Moth illustrations are by J. Chen.

al. 2005). Likewise, crayfish use gill movement to generate their own flow currents and use these to direct urine toward receivers (Bergman et al. 2005). Similar behaviors are seen in lobsters, newts, and bats (Atema 1995), and above the water in the wing-based vortices of sac-winged bats (Voigt and von Helversen 1999) and the butterfly *P. napi* (Andersson et al. 2007). Given the diversity and inherent directionality of animal signals, similar—or, indeed, novel—compensatory strategies may be both common and critical to efficient communication.

Exploitation of directionality

Do animals with highly directional signals exploit this feature to their benefit? As noted above, many animals, from butterflies to hummingbirds, actively manage their body position in space over time to ensure that their highly directional signals are viewed by intended receivers. This has the related advantage of preventing other unintended receivers from seeing such directional signals. There is even evidence that the flashiness of iridescent signals may be under selection itself (e.g., in sexual signaling in pierid butterflies, Kemp and Rutowski 2007; Kemp 2008; aposematism in the Pipevine Swallowtail, *Battus philenor*, Pegram et al. 2013; Pegram and Rutowski 2014), suggesting that the flashiness of these signals may in-and-of-itself be beneficial. One possibility is

that flashing signals may be more memorable or more detectable than similar, but static signals, a possibility that has received some support from both iridescent aposematic signals (Pegram and Rutowski 2014) and iridescent floral signals learned by pollinators (Whitney et al. 2016).

Alternatively, what if the goal is to be visible (or invisible) from all angles? To appear conspicuous or camouflaged from a variety of angles—for example, to broadcast territorial or social information or to evade predators—animals may have evolved weakly directional signals. However, camouflage signals need not always be weakly directional. Intriguingly, strongly directional iridescent signals may provide insects with excellent camouflage against birds, perhaps because it produces inconsistent shape and color cues that make an insect's body outline difficult to detect (Kjernsmo et al. 2020). Moreover, some highly asymmetric signals—such as the dorsoventral countershading on a wide variety of animals—appear to provide effective camouflage if viewed from specific directions (Johnsen 2002; Donohue et al. 2020).

In the acoustic realm, signalers can control—to some extent—the degree to which directional sounds reach intended receivers through changes to frequency usage (and associated frequency-dependent

directionality), posture, and body orientation. For example, red-winged blackbirds (*Agelaius phoeniceus*) use strongly directional calls for courtship but weakly directional calls (radiating in many directions) for alerting conspecifics to a threat (Patricelli et al. 2007). Remarkably, some birds even adjust the directionality of their antipredator calls, preferentially beaming sounds toward the predator—perhaps to signal to the predator that it has been detected (Yorzinski and Patricelli 2010). Finally, some male hummingbirds may have evolved to conceal information about their speed from females—a trick achieved by changing the angle at which females will receive the acoustic signal (Clark and Mistick 2018). During their courtship dives, male Costa's hummingbirds (*C. costae*) produce acoustic tones using their tail feathers: the tone's pitch can increase by up to 28% (from 7 to 9 kHz) due to Doppler shift. Males, however, minimize the frequency shift experienced by females by diving not at the female directly but off to her side, thereby obscuring acoustic information that could otherwise convey dive speed. This auditory illusion may alter the female's perception of this dive component while she evaluates a male's performance during courtship.

Finally, we note that while many chemical signalers certainly use the directionality of their signals to their advantage, the mechanisms and behaviors by which they do so often rely on interactions with extrinsic, environmental conditions. As such, we discuss these in detail in the section Extrinsic factors of signaling geometry given below.

Distance

In addition to the directional challenges described above, all signals degrade in some manner as they travel the distance from signaler to receiver (Rosenthal 2007; Bradbury and Vehrencamp 2011). Some causes of degradation are due to, or accelerated by, environmental conditions (e.g., degradation of semiochemicals in transmitting media, discussed in “Environmental structure impacts signal transmission and processing” section given below), but many are intrinsic to the mechanisms of signal propagation. Signal efficacy tends to decrease with increasing distance between signaler and receiver, usually due to shrinking image size (Caves et al. 2018), sound attenuation (Wiley and Richards 1978), or diffusion of semiochemicals. Beyond a certain distance, the signal is no longer detectable. As a result, the perception and even function of signals can change dramatically with the distance between signal and receiver (termed here and in the literature as “receiver

distance” or “communication distance”). Because of these distance-dependent effects on signal propagation, signalers are likely under selection to assess receiver distance, compensate for distant-dependent degradation, and/or exploit this effect to control information. Receivers should likewise be under selection to adjust their position in relation to signalers to better receive signals of interest.

Causes of signal degradation

For visual signals, distance-dependent degradation occurs due to the optics of vision. As viewing distance increases, the resulting smaller images are detected by fewer photoreceptors (Bradbury and Vehrencamp 2011; Land and Nilsson 2012; Cronin et al. 2014; Caves et al. 2018). Details mix together, and contrast between the signal and its surroundings can also decrease (Land and Nilsson 2012; Caves et al. 2018). The perceived image of an object can also become blurry if the distance between signaler and receiver is outside of the range within which the receiver's eye can focus on objects (Land and Nilsson 2012). In addition, signals seen at an extremely close range may not “fit” within the receiver's field-of-view and therefore may not be visible in their entirety. These observations indicate that the distance between signaler and receiver plays a critical role in the efficacy of visual communication, and is therefore a property likely to be actively managed by signalers and receivers alike.

Sound signals also attenuate as they travel (Wiley and Richards 1978). As a wave spreads from the point of origin, the initial kinetic energy is spread out over more and more molecules, resulting in the so-called spreading loss. In addition, at each collision of molecules that propagates the sound wave, additional energy is lost in the form of heat to entropy, called attenuation via heat loss. As a result of these two forms of loss, amplitude (“loudness”) decreases, and sound information becomes harder for receivers to detect and interpret. Sound attenuation is also frequency-dependent, with higher frequency sounds experiencing higher heat loss. In addition, temporal information in acoustic signals can be affected by reverberation, a phenomenon which we discuss further in “Extrinsic factors of signaling geometry” section, given its environmental dependence. Taken together, these sources of attenuation and degradation mean that different components of a sound signal will be more or less affected by communication distance.

Released semiochemicals also diffuse from the point of emission into the surrounding medium, a phenomenon analogous to spreading loss (Atema

1995; Webster and Weissburg 2009; Bradbury and Vehrencamp 2011). As this volume of diffusing molecules grows, the concentration of semiochemicals will decrease, reducing the number of molecules that can be detected by a receiver. The rate of diffusion depends on the chemical properties of the signal molecule and of the medium it is diffusing into, including the thermal environment (see Environmental context section given below; reviewing in Riffell et al. 2008; Webster and Weissburg 2009; Bradbury and Vehrencamp 2011). At a certain distance from the location of emission—or after enough time has passed—the concentration will decrease below the receiver's threshold for detection.

Compensation for signal degradation

Communicators can improve signal efficacy by assessing communication distance and adjusting their behavior. Several sensory mechanisms exist that allow animals to estimate distance from a stimulus and respond appropriately (e.g., attention to signal loudness in acoustic orientation, Naguib and Wiley 2001; Mhatre and Balakrishnan 2008; depth perception in visual signaling, Land and Nilsson 2012; Cronin et al. 2014). Based on such distance cues, signalers often actively change their signals to improve saliency at different distances. For example, distance-dependent signal modification is well established for some acoustic signals (e.g., zebra finches calls, Brumm and Slater 2006; human speech, Marshall and Meyer 1985) and movement-based visual signals (e.g., head-bob displays in *Anolis gundlachi* lizards, Steinberg and Leal 2013). In these systems, signalers increase signal intensity for more distant receivers, and this modulation increases saliency relative to unmodified signaling behavior.

Signalers may also qualitatively change their signal in response to communication distance. For example, male *A. gundlachi* anoles append an additional signal component to their display when signaling at a farther distance (Steinberg and Leal 2013). Such facultative signal modifications provide another option for signalers to compensate for distance, especially if modulation of the primary signal may alter its information content. Distant-dependent signal modification may also allow signalers to conserve energy by signaling at reduced intensity until receivers are nearby (e.g., distance-dependent modifications of male greater sage grouse display calls, Patricelli and Krakauer 2010). Signalers capable of rapid color and pattern change (e.g., paradise whiptail fish, chameleons, cuttlefish, and other cephalopods; reviewed in Hutton et al. 2015) might also use this ability for signal modulation if certain colors are

better able to reach a distant receiver, as in the case in marine environments, but this possibility remains to be more carefully explored.

The taxonomic breadth of distance-dependent signal modification strongly suggests that this ability has evolved repeatedly, and may be more common than current evidence suggests. Much of the work we review above comes from vertebrates (e.g., birds and lizards), but evidence from invertebrates is beginning to appear. For example, males of the jumping spider *H. pyrithrix* increase the amplitude of waving displays when they perform them farther away from prospective female mates (Echeverri 2020). Anecdotal observations suggest that humans also engage in distance-dependent signal modification of a movement-based signal: when waving arms to get others' attention, signaling humans often increase the speed and amplitude of their waves with increasing distance from intended receivers. However, the extent of this human behavior, and its impact on signal effectiveness, awaits formal investigation.

Chemical signalers may combat the effects of signal degradation by changing the rate or initial concentration of semiochemical emission, and/or manipulating the chemical properties of their emissions to change their rate of travel through the air or water. For example, sea hares have chemical defenses in the form of both ink and opaline secretions that they use to escape predation by spiny lobsters (Kicklighter et al. 2005). In an anti-predatory defense, sea hares release both their ink and opaline at the same time. The ink binds to the highly viscous opaline, which limits the diffusion of the stimulus to an area near the attacker. We note little evidence of signalers adjusting emission rate or initial concentration in response to communication distance in particular, despite demonstrated ability to do in other contexts (e.g., based on mating history Umbers et al. 2015). This lack of evidence may be a result of an existing literature bias toward the study of long-range chemical signaling (e.g., scent plumes of insects). At such ranges “up-to-date” distance information may rarely be available to signalers due to the relatively slow speed of signal travel and the resulting asynchronous nature of the communication interaction. However, at close range, chemical signalers may use information from other modalities to assess distance and adjust their chemical signals appropriately.

Exploitation of signal degradation

Attenuation with distance may at times be a part of an intended signal function, rather than a limitation. For signals that provide receivers with relative

location information (termed “ranging” or “localization” in the literature; Naguib and Wiley 2001), selection for reliable methods to locate conspecifics may result in signals with properties that enhance the perception of attenuation. This is seen in the acoustic signals of pygmy marmosets and several forest birds, where wide frequency sweeps (“trills”) allow receivers to better estimate distance via the extent of frequency-specific attenuation (Snowdon and Hodun 1981; Naguib and Wiley 2001). More simply, because diffusing semiochemicals often form a gradient of increasing concentration toward the signaler, many species’ chemical signals function at least in part to guide receivers toward the signaler (reviewed in Vickers 2000; Webster and Weissburg 2001; Moore and Crimaldi 2004; Koehl 2006; Fig. 2).

Signalers may also use distance-dependent signaling strategies to exclude unintended receivers (e.g., eavesdroppers such as predators) from accessing distance or location information. For visual signals, species disparities in visual acuity may allow for semi-private communication channels—at certain viewing distances, one species may be able to clearly perceive a signal, while another species may perceive the image differently, or not be able to detect it at all (reviewed in Caves et al. 2018). Acoustic signalers may selectively use high- versus low-frequency calls to control how far a signal will travel. High-frequency sounds will degrade more quickly, thereby excluding more distant receivers (e.g., predators, in the alarm calls of Richardson’s ground squirrels, Wilson and Hare 2006, see above).

Signals may also evolve to serve dual functions by exploiting distant-dependent degradation. This may be particularly true for visual signals whose appearance depends on viewing distance. For example, at greater viewing distances, coarser-scale features will dominate the perceived image, while at closer distances, fine-scale features become more noticeable. As a result, visual displays can have distance-dependent appearances and, thus, induce distance-dependent responses (Kelley and Kelley 2014). For example, the striped aposomatic patterns of many lepidopteran larvae (Tullberg et al. 2005; Bohlin et al. 2008; Barnett and Cuthill 2014; Barnett et al. 2018a), skunks (Caro 2013), and frogs (Barnett et al. 2018b) have been shown to function as aposomatic markings up close, and as camouflage at a greater distance (e.g., “distance-dependent defensive coloration” *sensu* Barnett and Cuthill 2014). Likewise, the pointillist patterns of reef fish allow for species discrimination at close range but also

provide camouflage from more distant predators (Marshall 2000; reviewed in Stevens 2007).

Signalers may even produce deceptive distance information by mimicking the effects of degradation themselves (Naguib and Wiley 2001). Mantled howler monkeys (*Alouatta palliata*), for example, produce both a normal grunt call and a grunt with additional reverberation that may be perceived as deceptively distant (Whitehead 1987). These deceptive signals may allow the signalers to avoid confrontation with other groups of conspecifics.

Extrinsic factors of signaling geometry

The saying “location, location, location” holds true not only for real estate and advertising, but also for communication in the animal kingdom. Extrinsic environmental complexities like obstructions, noise, or dynamic fluid flows, modulate the effects of the intrinsic factors described above. Similarly, the location and number of intended receivers can shape the strategies of signalers and vice versa. Thus, where signaler and receiver(s) are located within their environment impose new challenges and opportunities to improving efficacy. In this section, we review what is known about how such extrinsic factors have shaped animal signaling, including environmental and social factors, while highlighting areas where future work should focus.

Environmental context

The physical environment within which signaler and receiver communicate modifies how distance and directionality alter signal effectiveness across all modalities (Rosenthal 2007; Cole 2013; Ryan and Cummings 2013). Illumination, physical obstructions, and the environmental background against which signalers display can all affect signal efficacy. Natural environments are often heterogeneous in the distribution of these properties, a phenomenon most well characterized for visual signaling (Endler 1992; Rosenthal 2007). However, such environmental variables are also critical determinants of communication in other modalities as well. Physical properties of the environment alter sound transmission and signal-to-noise ratio in acoustic communication (Wiley and Richards 1978; Padgham 2004), and fluid flow dynamics shape the spread of chemical cues and hence olfactory communication (Riffell et al. 2008; Webster and Weissburg 2009). Selection may thus act on behaviors that tune geometries of signaler and receiver to either their immediate or most common environmental contexts, something observed

for thermal gradients and bird song (Henwood and Fabrick 1979).

Multiple constraints may limit individuals' abilities to respond to environmental variation to improve signaling efficacy. First, dynamic positioning may require the signaler to evaluate details of the environment and infer likely receiver perspectives. Assuming signalers (and receivers) can assess different positions in the environment, they may face trade-offs between optimizing for signaling distance versus signal directionality. Furthermore, the positions of signalers and receivers may be constrained because of other factors, such as exposure to predation risk, forfeiture of foraging opportunities, competition from conspecifics, or the simple inability to access an optimal position in the environment. These factors may impede optimal positioning during communication, resulting in signaling behaviors that are expressed seemingly at random in time and space.

Environmental structure impacts signal transmission and processing

Effective signaling geometries for visual communication are often influenced by environmental conditions. For example, the location of the source of illumination (e.g., the sun) and the amount and quality of incident light can impact visual signal contrast and luminosity for a given signaler–receiver geometry (Long and Rosenqvist 1998). Visual signals dependent on incident light degrade more quickly with viewing distance in dim light than in bright light (Johnsen 2012; Cronin et al. 2014). The transmission medium may also interact with certain wavelengths of light such that some colors attenuate more quickly than others. For example, red light attenuates more rapidly in water than blue light, leading to strong gradients in the spectral quality of available light at different depths in aquatic environments (Cronin et al. 2014) as well as the transmission distance of certain color signals. The quality and density of particles in the transmission medium (e.g., in air or in water) also determine how light is scattered and/or absorbed per unit distance (Johnsen 2012; Cronin et al. 2014). Because aquatic environments often have greater amounts of suspended particulate matter, visual signals tend to degrade more quickly with distance when underwater than in air (Johnsen 2012; Cronin et al. 2014). However, weather conditions (e.g., fog, rain, and dust storms) may transiently produce similar effects on land. Finally, signals may appear more or less conspicuous to a receiver based on the background against which they are viewed (Johnsen 2012; Cronin et al. 2014), and objects that interfere with the “line-of-sight”

between signaler and receiver can further frustrate visual signaling. More physically complex environments are therefore more challenging for visual communicators.

Similarly, refraction of sound waves within different layers of a medium can affect the distance a sound signal can travel. Transitions between warm and cold layers of a transmission medium bend sound waves toward the colder layer, as a result of the difference in speed of sound between the two (Henwood and Fabrick 1979). For example, in an open habitat, sound signals produced near the ground on a hot day will bend upward, and thus away from a distant receiver located at the same height as the signaler. This temperature-gradient refraction creates a space where the sound waves bend too far upward for a receiver at ground level to hear them clearly, termed as “shadow zone.” The distance at which the shadow zone begins increases as a function of the height within the thermal gradient at which the sound was produced (Wiley and Richards 1982). Thus, terrestrial signalers may be under selection to call from higher above the ground, either by adjusting their posture and/or position during communication, such that a nearby receiver would be close enough to avoid the shadow zone effect (Henwood and Fabrick 1979). Similar phenomena occur in aquatic systems, most famously in the sound fixing and ranging zone of the world's oceans, a deep horizontal layer that acts as a waveguide for sound and may be used by whales for extremely long-distance signaling (Payne and Webb 1971). In addition, mismatches between an animal's current sound transmission medium, and that within which its hearing evolved can disrupt the underlying mechanisms of sensor directionality. For example, while terrestrial vertebrates typically localize sound sources by comparing intensity and arrival time between paired ears, when underwater, sound waves travel through the skull, not around it, due to the similarity in transmissivity between the two materials. As a result, directional information is much harder to extract (Hollien 1973; Bovet et al. 1998), selecting for modified hearing systems in secondarily marine lineages (e.g., cetaceans; Branstetter and Mercado 2006).

For chemical signaling, fluid flow dominates the effects of simple diffusion on semiochemical spreading in most natural conditions and hence defines the signal's directionality and active space (Fig. 2; Alberts et al. 1992; Atema 1995; Muller-Schwarze 2006; Riffell et al. 2008). Chemical signals arriving at a receiver, particularly in turbulent fluids, are intermittent, and receivers compare the patchy odor signals

sensed by receptors across the body with mechanosensory measures of fluid flow to localize sources of odors (Vickers 2000; Weissburg 2000). Physical characteristics such as environmental structure (e.g., trees in a forest; Fares et al. 1980) and surface roughness affect fluid dynamics and therefore receiver ability to detect and localize odor sources (Riffell et al. 2008; Webster and Weissburg 2009). These environmental complexities for localizing odor sources are likely to often constrain the function of olfactory cues and behavioral strategies used during olfactory-guided search. Semiochemicals can also degrade due to properties of the transmitting media (e.g., pH and temperature) and/or chemical interactions with solutes, environmental objects, or suspended particles.

Animals fine-tune communication to current environmental context

Signalers and receivers position themselves to improve signal transmission within heterogeneous environments based on current environmental information. Many terrestrial insects that produce mate-attractant pheromones advertise their location from elevated locations that allow access faster and/or more consistent fluid flows (Fig. 2; Moore and Crimaldi 2004; Bradbury and Vehrencamp 2011), and some also align themselves with the direction of fluid flow to increase signal transmission (e.g., in orchid bees; Pokorný et al. 2017). Receivers may likewise improve signal detection by resting on the upwind or upstream side of objects. While this hypothesis has not been widely tested, evidence from the resting orientation of wood cockroaches on trees (genus *Parcoblatta*) suggests that, in this system, air flows are not sufficiently blocked by trees to affect behavior (Miller et al. 2007).

Similarly, manakins may choose lek locations based on whether their color patterns will have high contrast in the local light environment, a phenomenon which seems to be widespread for lekking birds in tropical forests (Endler and Thery 1996). Male poison frogs (*Allobates femoralis*) sing at lower amplitudes when on higher perches, such that their overall signal propagation is similar from all perch heights (Rodríguez et al. 2020). To compensate for low illumination levels, male guppies (*Poecilia reticulata*) move closer to females when courting in dimmer lighting (Long and Rosenqvist 1998). In addition, when traffic noise impacts communication, male great tits sing closer to female nest boxes, and adjust their positions based on feedback from females (Halfwerk et al. 2012). However, in general, the extent to which animals' positional adjustments is based on social feedback or directly sensing their

environments is largely unknown (but see Patricelli et al. 2002).

Because some signals, particularly visual signals, are acutely dependent on orientation within a specific lighting environment, signalers often reposition themselves relative to receivers depending on the position of dominant illumination (often the sun). This adjustment is regularly observed in displays that involve iridescent colors. Male peacocks, for example, shake their tail feathers at females while positioning themselves about 45° to the right of the sun azimuth, an orientation that might minimize specular reflectance or produce desirable iridescent hues (Dakin and Montgomerie 2009)—including the blue-green eyespot color that females evaluate during courtship (Dakin and Montgomerie 2013). Similar evidence in some hummingbirds (Hamilton 1965; Simpson and McGraw 2018b, 2018a see above) and butterfly species (Rutowski et al. 2007; White et al. 2015) suggests that strategic orientation to the sun may be a common feature of iridescent courtship displays. However, in some contexts—for example, broad-tailed hummingbird courtship dives (Hogan and Stoddard 2018) and peacock wing-shaking displays (different from the tail-shaking displays referenced above, Dakin and Montgomerie 2009)—signaler positional management in relation to the sun appears to be inconsistent or absent. Non-iridescent signalers also orient their display toward the sun. Great bustards (*Otis tarda*) orient their bright white tail displays toward the sun, particularly when the sun is low in the sky and thus best positioned to shine upon the male's vertically-held tail feathers (Olea et al. 2010). Likewise, snowy owls (*Bubo scandiacus*) orient their white breast feathers toward the sun, which may increase apparent brightness (Bortolotti et al. 2011, but see Wiebe and Chang 2018).

Signalers and receivers may also position themselves to adjust signal detectability against the sensory background. In some systems signalers may modify their visual environment prior to communication (e.g., clearing debris from a display court in manakins; Uy and Endler 2004). Signalers also reposition themselves dynamically based on the background to tune how conspicuous their patterns and displays are. The geometrid moth (*Jankowskia fuscaria*) has a bark-like pattern on its wings and experiences high predation on nonpattern-matching trees; these moths orient their bodies so their markings match the directionality of the tree bark (Webster et al. 2009), potentially using touch to detect the orientation of bark patterning (Kang et al. 2013, 2015). Male jumping spiders (*H. pyrrithrix*) move closer to females when courting against more

spatially and temporally complex backgrounds (Echeverri 2020), perhaps leveraging their wide field-of-view to assess their background without turning away from the receiver. Receivers may also position themselves within the environment to modify their ability to best detect signals against the background. For example, territorial insects select portions of the habitat that provides them with a clear view of the area in front of them by perching on the edges of woods, along corridors, or at hilltops (Alcock 1987).

The concept of sensory background is slightly different in nonvisual modalities, in part because perception in these modalities has much coarser spatial resolution. However, avian songs are thought to evolve in response to habitat structure, a phenomenon called the acoustic adaptation hypothesis (for in-depth reviews, see Boncoraglio and Saino 2007; Ey and Fischer 2009). In addition, acoustic signalers often respond to persistent background noise by moving to frequency ranges where there is less interference, a phenomenon now well established for urban bird populations (Slabbekoorn and den Boer-Visser 2006). Whether this shapes the geometric relationships between signaler and receiver is less well known, although one might expect that increases in song frequency, which result in increased directionality and attenuation, might impact effective spatial positioning in urban environments. Reverberation caused by sound reflections from habitat objects can also muddy temporal information in acoustic signals, an issue that inhabitants of structurally complex environments must contend with (Richards and Wiley 1980; Padgham 2004).

Animals may also use physical objects in the signaling environment to influence what receivers perceive. For visual signaling, one of the most striking suggestions of using objects to force a particular receiver perspective comes from great bowerbirds (*Chlamydera nuchalis*; Endler 2010; Endler et al. 2012; Kelley and Endler 2012). Male great bowerbirds decorate their courts with stones in a positive size-distant gradient, with the largest objects the furthest from the bower—a carefully constructed visual signal that females typically evaluate from inside the bower. Male great bowerbirds build an “avenue” of reeds that function to block females from viewing the male’s bower from all but head-on. From the female’s highly angle-specific viewpoint in the bower, the stones will appear uniform in size—an illusion only visible from this forced perspective (Endler et al. 2012; Kelley and Endler 2012). Whether males that create the best illusions enjoy the most mating success remains an

intriguing yet unanswered question (Kelley and Kelley 2014). In a similar vein, some male birds-of-paradise (genus *Parotia*) prepare courtship stages underneath low-hanging tree branches. These branches serve as perches from which females can watch the male’s courtship dance unfold from above, including the males’ highly iridescent plumage patches (Scholes 2008a, 2008b). By constraining the female’s viewing angle, males help to ensure optimal viewing. In contrast, structures built for other functions may impose signaling challenges by limiting the visibility of a nearby signaler. In *Uca mustica* fiddler crabs, males build sand hoods near their burrows, which attract females by exploiting a sensory preference for objects that provide cover from predators. However, these hoods also block males’ field-of-view from certain directions, reducing the number of females he can potentially see and court, and thus limiting the fitness benefits of the structure (Christy et al. 2003).

Signalers may also use obstructions for “peek-a-boo” displays, repeatedly presenting and hiding the signal from behind cover, as seen in some jumping spiders (genera *Saitis* and *Jotus*; Hill 2009; Otto and Hill 2016). Such interactions have been studied in the context of human development (e.g., Greenfield 1972), but not in communication of other animals. These peek-a-boo displays may allow signalers to avoid visual desensitization and/or exploit biases for novel stimuli. However, they require signalers to track the receiver’s position without a clear line of sight, as the peek-a-boo only functions if the obscuring object remains between signaler and receiver (and therefore obstructs the signaler’s view of receiver location).

Although the phenomena of forced perspective and peek-a-boo displays do not have ready alternatives in other sensory modalities, auditory signalers do at times make use of objects in their environments to change the properties of their signals. For example, tree crickets (*Oecanthus* sp.) use leaves as acoustic baffles that increase the effective loudness of their calls through sound reflection, fine-tuning the properties of these acoustic tools through leaf selection (larger leaves are better baffles) and body positioning when singing (leaf centers are more effective than margins, Mhatre et al. 2017). For chemical communication, animals depositing scent marks often make use of strategically selected environmental objects (e.g., felids selecting trees in objects with properties that reduce the rate of signal degradation; Allen et al. 2017; Mohorović and Krofel 2020).

Evolution tailors signaling strategies to environmental contexts

Signals can evolve to compensate or exploit effects of distance and directionality when signaler and receiver positions within the environment tend to be consistent, even if absolute location is unknown. For example, counterillumination, countershading, and reverse countershading are widespread in marine environments and occur even in terrestrial, arboreal, and aerial systems (Johnsen 2002; Kamilar and Bradley 2011; Cuthill et al. 2016; Donohue et al. 2020). While functionally distinct from many conspecific signals, these camouflage markings still involve transmitting visual information (albeit deceptive information) to elicit a behavior (e.g., avoidance), and are similarly shaped by the geometric constraints of communication. The effectiveness of these visual patterns lies in the ecological consistency of the animal's position relative to predators or prey, whose perspective may be looking up or down, as well as the approximate position of the sun. Another example is the convergent evolution of eyespots on pupal Lepidoptera (butterflies and moths) on different parts of the body for deterring avian predators (Janzen et al. 2010); because the pupae are sessile and concealed, these eyespots are typically positioned on the area of the body most likely to be exposed to view by a foraging bird. Many species tend to signal from relatively standard heights in fairly consistent vegetation types, such that natural selection can tailor signal properties and receiver sensory systems to tune transmission properties to the likely habitats (e.g., Persons et al. 1999; Witte et al. 2005). Similarly, chemical signaling strategies may evolve to meet consistent ecological conditions; for example, xeric and mesic lizard species use different types of molecules for chemical signaling that allow scent marking or long-distance chemical signaling within the environment (Baeckens et al. 2018). Comparative studies that integrate these environmental drivers alongside variation in intrinsic spatial biases in signaling hold great promise for explaining extant diversity in signaling strategies across taxa (e.g., the differences in display behaviors described between hummingbird species).

Social complexity

Thus far, we have discussed signaling geometry largely in the context of directed dyadic interactions (i.e., between one signaler and one receiver, at mutually known locations, Fig. 3A). However, communication can and often does occur between multiple signalers and/or receivers (e.g., at leks, or in resource

defense situations, Fig. 3B), with unknown receivers (e.g., broadcast signals, Fig. 3B), and/or with hetero-specific participants (e.g., predator alert calls and eavesdropping). Each of these complex social structures will influence optimal responses to the challenges of distance, directionality, and position, thereby producing new, and largely understudied, selection pressures on communicators. For instance, many of the adaptive signaling behaviors discussed above rely on the signaler locating a communication partner and responding to the relative spatial arrangements between itself and its communication target. Signalers attempting to communicate with receiver(s) at ambiguous or unknown locations will thus be limited in their ability to compensate for spatial biases in communication.

Social structures impact signaling behaviors

As the number of participants in a communication interaction increases, so do potential spatial conflicts of interest. Adopting a spatial arrangement that improves signal transmission to one receiver may reduce or block transmission to another individual. Consider a signaler displaying for multiple receivers (whose locations are known; e.g., in a lek); signalers are likely constrained in their ability to orient their signals toward more than one receiver especially if using a strongly directional signal and/or if receiver positions are dispersed in space (Fig. 3B). How do signalers manage to communicate effectively with their entire audience? Do lekking males select one female to aim their display at, or orient themselves such that the greatest number of receivers have an adequate, if sub-optimal, viewing angle? And what influences these decisions? While lekking great bustards do occasionally orient their signals toward a female, the consistency of this signaler behavior (i.e., only ~20% of the time; Olea et al. 2010) is far less than what is seen in dyadic interactions between peafowl (~60% of the time; Dakin and Montgomerie 2009) and jumping spiders (~99% of the time, Echeverri et al. 2017). This suggests that courting multiple females may indeed challenge signalers' abilities to orient their displays appropriately.

Receivers attempting to simultaneously assess the signals from multiple signalers face a similar challenge, particularly in the case of sound and chemical signals, which can more readily interfere with each other than visual displays. While adjacent displays may affect contrast-based perception or assessment (Rosenthal 2007; Bradbury and Vehrencamp 2011), visual signals can at least be clearly identified as the product of an individual signaler based on line of sight, sound, and chemical signals may be harder

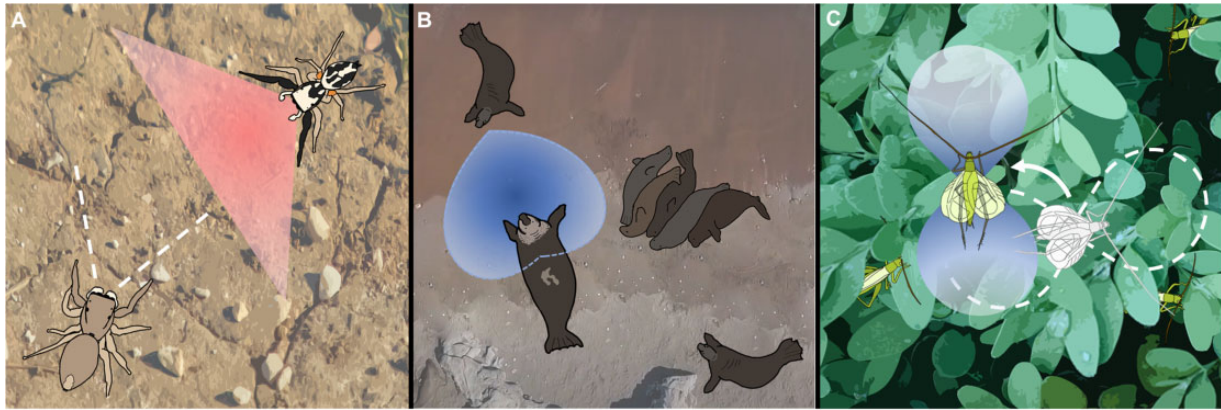


Fig. 3. The social complexity of a communication interaction modulates the effects of signaling geometry. In a dyadic interaction, such as the courtship of paradise spiders (genus *Habronattus*) (A), signalers and receivers can most easily respond to spatial biases to improve signaling alignment. Here, a male (top right) aims his colorful forward-facing visual display toward the female's (bottom left) field of color vision (delimited by dashed lines). In a multiple-receiver interaction (B), signalers are likely constrained in their ability to effectively orient their signals toward each receiver simultaneously. Here, a northern elephant seal (*Mirounga angustirostris*) bull (center left) guards several females (center right) and barks a threat call at a nearby subordinate male (top left), but due to the strong directionality of the high frequency component of the call and the bull's orientation, a second approaching male (bottom right) is undeterred. In a broadcast interaction (C), signalers lack information on both the number and position of (potential) receivers, and are thus unable to effectively aim their signals. Instead, signalers may compensate with their behavior, such as tree cricket (*Oecanthus quadripunctatus*; center) increasing the active space of its bilobate call by rotating. Signal directionality in (B) and (C) redrawn from (Holt et al. 2010) and (Forrest 1991), respectively. Illustrations are by S.A. Echeverri.

to differentiate (Mcgregor et al. 2013; Baumann-Pickering et al. 2015). How do receivers process multiple incoming signals and prioritize which signalers to attend to? Unfortunately, most studies on receiver orientation during communication have focused on dyadic or single-signaler interactions. Exceptions to this come mostly from work on acoustic orientation in chorusing species, where female receivers often adopt simple heuristics, such as orienting toward the loudest calls (Mhatre and Balakrishnan 2008). Such simple behavioral rules conflate information about proximity with individual differences between male calling effort/amplitude. Whether females modify their behavior once male location becomes clearer (i.e., to reject quieter but closer males) remains to be studied. However, work on the cricket *Gryllus integer* suggests the lack of such finer-scaled discriminations on the part of females (Cade 1975, 1979). In this species, some males forgo acoustic mate signaling entirely, choosing instead to wait silently next to calling male conspecifics. These “satellite” males then intercept and mate with females as they approach calling males. Given that this “satellite” male strategy persists in natural populations, this suggests that females are at least prone to errors in identifying the precise location of calling males.

Finally, in cases of heterospecific communication, signaler and/or receiver must contend with species-specific variation in sensory systems. Visual acuity, for example, can vary by three orders of magnitude

between species, such that a community of heterospecific receivers may have drastically different perceptions of a signal from the same distance (reviewed in Caves et al. 2018). Species disparities in visual acuity may also allow for semi-private communication channels—at certain viewing distances, one species may be able to clearly perceive a signal, while another may perceive the image differently, or not be able to detect it at all. Restricted sensitivity to specific sound frequencies and/or restricted ability to detect particular semiochemicals can result in similar variation in effective communication among a diverse community of prospective receivers. However, such disparities may allow for private communication channels for conspecifics. Otherwise, signalers and (intended) receivers may also be under selection to attend to potential heterospecific eavesdroppers (e.g., predators), and manage their spatial behavior to constrain the signal active space.

Adaptive signaling responses to changing social conditions

Evidence is growing that signalers and receivers are able to assess their social context and respond to changing spatial constraints. When the position of the intended receiver is unknown (or a signal must reach multiple receivers), signalers may compensate by producing their signal in multiple directions to increase the chances of facing a receiver (Fig. 3C). Sedge warblers rotate on their perch during calling

when receiver position is unclear, much like a rotating siren (Brumm et al. 2011). Similar patterns of spatial positioning have been observed in northern mockingbirds (Breitwisch and Whitesides 1987), red-winged blackbirds (Brenowitz 1982; Patricelli et al. 2007), and crickets (Fig. 3C; Forrest 1991). This suggests that aiming a strongly directional sound at a known receiver, and rotating while signaling to unknown receivers may be a frequently evolved solution to the constraints of directional sound. In addition, experimental tracking of a signaler's orientation movements can help to identify intended receivers, and thus be a particularly useful tool for determining signal function (Brumm et al. 2011).

When communicating with multiple receivers, signalers may also adjust the directionality of their signals to increase the range of habitat positions where the signal can be received. For example, red-winged blackbirds (*A. phoeniceus*) produce at least five different call types, with weakly directional calls used to communicate with receivers located in potentially many different directions (alarming conspecifics to danger, Patricelli et al. 2007). Likewise, the antipredator calls of nine other songbird species are also less directional than their courtship calls (Yorzinski and Patricelli 2010). In addition, signalers may modulate the directionality of a specific sound signal in response to the spatial arrangement of receivers. Dark-eyed juncos, and yellow-rumped warblers all increase the directionality of their weakly directional alarm calls such that the sound is louder toward the location of a one focal receiver (e.g., a predator), but without excluding nearby conspecifics (Yorzinski and Patricelli 2010). This may improve the efficacy of a signaled message to the predator (e.g., that the predator has been detected and the hunt will not be successful), indicating that alarm calls in these species might serve dual functions. Signalers might also weaken the directionality of a strongly directional sound signal if the number of receivers increases. This, however, has yet to be observed. Nevertheless, modulation of directionality may be an important mechanism—potentially unique to sound signaling—for compromise between signal functions with conflicting spatial constraints.

Depending on the message, multiple simultaneous signalers may be under selection to position themselves to minimize or maximize overlap in their signals. In situations where individuals seek to draw receiver attention to themselves specifically, signalers may monitor other signalers to distance themselves from others in space or time. For example, work on orchid bees suggests that signalers may avoid chemical “noise” from other signalers by partitioning

signaling heights (Pokorny et al. 2017), and some sympatric moths instead emit their pheromones at different times of night (reviewed in Nehring et al. 2013). Male frogs use the amplitude of neighbors' calls to maintain spacing (e.g., Wilczynski and Brenowitz 1988; Brenowitz 1989). However, where supernormal signal intensity is beneficial, signalers may instead cluster together, although this behavior remains to be tested for.

As communication interactions progress, signalers may actively update their behavior as their social context changes. An interaction may begin with a signal broadcasting to unknown receivers, then advance to a multiple-receiver context, and end in a dyadic interaction. For example, many jumping spider courtship sequences move from motifs that are arguably designed to capture receiver attention, wherever the receiver might be, followed by elements much more focused on displaying to a known observer (Elias et al. 2012; Echeverri et al. 2017). How effectively animals adjust their spatial behavior in response to changing social contexts may be another mechanism for selection for spatio-social skill (*sensu* Sih et al. 2014, 2019; Echeverri et al. 2017). Evaluation of complex communicatory sequences with an eye toward these geometric considerations may reveal how animals use different signals, with different spatial biases, to navigate through sequential social arrangements.

Spatial and temporal integration across modalities

Much of our review has discussed the geometric considerations relevant to modalities in isolation. However, many communicatory displays are multimodal, involving the coordination of visual, acoustic, chemical, and even tactile signals. How might our explicitly geometric perspective aid in deepening understandings of these complex forms of communication? The first thing to note is that although nearly all signals have directional biases in both propagation and reception, these biases differ in severity, directionality, and distance-dependence across modalities. For example, jumping spiders often pair highly directional visual signals with more omnidirectional (at least in idealized transmission conditions) vibratory signals (Elias et al. 2012). Quantifying these differences offers new inroads into classic hypotheses about multimodal communication. For instance, one longstanding hypothesis for the evolution of multimodality focuses on the adaptive value of signal redundancy (called signal degeneracy in Hebets et al. 2016), particularly in noisy

environments (Hebets and Papaj 2005). Similarly, if environmental noise impedes the propagation and/or reception of signals in a particular modality, signalers may benefit from sending the same information in another less affected modality, something that Hebets and Papaj (2005) referred to as the “efficacy tradeoff” hypothesis. By adding geometric considerations to this hypothesis, we might observe that signal redundancy offsets ineffective signal transmission of highly directional signals. Further, even signals that lack intrinsic directionality under ideal conditions may become directional in natural situations (e.g., high fluid flow for chemical plumes, directional propagation of substrate-borne vibrations based on substrate properties). Again, by attending to these geometric issues, new motivations for the evolution of signal redundancy and/or the evolution of multimodality due to efficacy tradeoffs emerge. Finally, differences in distance-dependent attenuation may mean that redundant signals function to ensure that the same information is conveyed at a range of distances.

Another common hypothesis for the evolution of multimodal communication is that different modalities communicate different messages (the so-called “multiple messages” hypothesis, Hebets and Papaj 2005). The geometry of signaling has much to offer here as well, because it may help to illuminate how, and when, different messages are typically received. Although it is true that for some multimodal displays, viewers receive multiple messages simultaneously, the directionality and distance-dependence of many signals offer opportunities to modify the order in which messages are relayed and received. For example, directed, long-distance signals may function to transmit species- and/or sexual-identity first, later giving way to signals at closer range that provide information upon which to base evaluative mate-choice decisions. Receivers may also employ selective attention and body positioning to separately evaluate different aspects of multimodal signals, thereby reducing cognitive load during decision-making. Careful attention to the geometry of signaling across both space and time is thus likely to uncover the sequence and/or coincidence of information flow during signaling of multiple messages.

Yet, another hypothesis for the evolution of multimodality, that of multimodality as an adaptive response to multiple sensory environments (Hebets and Papaj 2005), takes on new meaning when viewed from the standpoint of signaling geometry. Many animals signal in heterogeneous environments, and this heterogeneity is often evident even on small spatial scales. In other words, even during a single signaling bout, individuals may move through a variety

of micro-environments that impact the directionality, attenuation, and therefore efficacy of different signaling modalities. By attending to these geometric impacts on signaling across space and time, we may find that signalers and receivers dynamically adjust their position and effort in order to specifically optimize signal transmission and/or receipt, with these behavioral adjustments predicated on the severity of biases in particular signaling modalities.

Finally, one topic in multimodal signaling (and indeed signaling in general) that would benefit from additional study is the issue of signal synchronization and temporal coordination. Many complex, multimodal signals are highly synchronized, from the extraordinary synchrony of visual and vibratory signals in *Habronattus* jumping spiders (Elias et al, 2012) to the split-second coordination of auditory and iridescent visual signals of male Broad-Tailed Hummingbirds (Hogan and Stoddard 2018; Fig. 4). How common is such synchronization in animal displays, and to what extent does such synchronization not only deliver signals at the same time, but also to the same vantage point in space? We are only beginning to find out. Similar to the “sensory explosion” male Broad-tailed Hummingbirds deliver at the base of their dives, male Montezuma Oropendolas (*Psarocolius montezuma*) time dramatic choreography (a swing and wing spread) to coincide precisely with key parts of their songs, creating a very dynamic moment in their elaborate courtship displays (Miles and Fuxjager 2019). Few studies have explored the adaptive benefit of such tight coordination in multimodal signals, yet it requires remarkable control across modalities on the part of the signaler. One might ask whether this temporal coordination holds benefits for the signaler, the receiver, or both. For example, is temporal coordination easier for signalers to adopt, rather than syncopated delivery of signals in different modalities? Is temporal coordination the result of tethering display elements to particular behavioral landmarks (e.g., all signals are deployed at the nadir of an aerial dive)? Or is temporal coordination selected for because it “jams” the evaluative sensory and cognitive systems of the receiver in a way that benefits the signaler, either through reduced scrutiny of each individual element and/or through the creation of a hyper-stimulus? Do receivers benefit from the coordinated delivery of information as a way of surmounting the geometric constraints on signal receipt, and if so, does such synchronization focus the spatial optima for all signals at the locus of the receiver? Or is it motivated by the cognitive benefits of perceptual binding of dissimilar stimuli? A geometric perspective not only

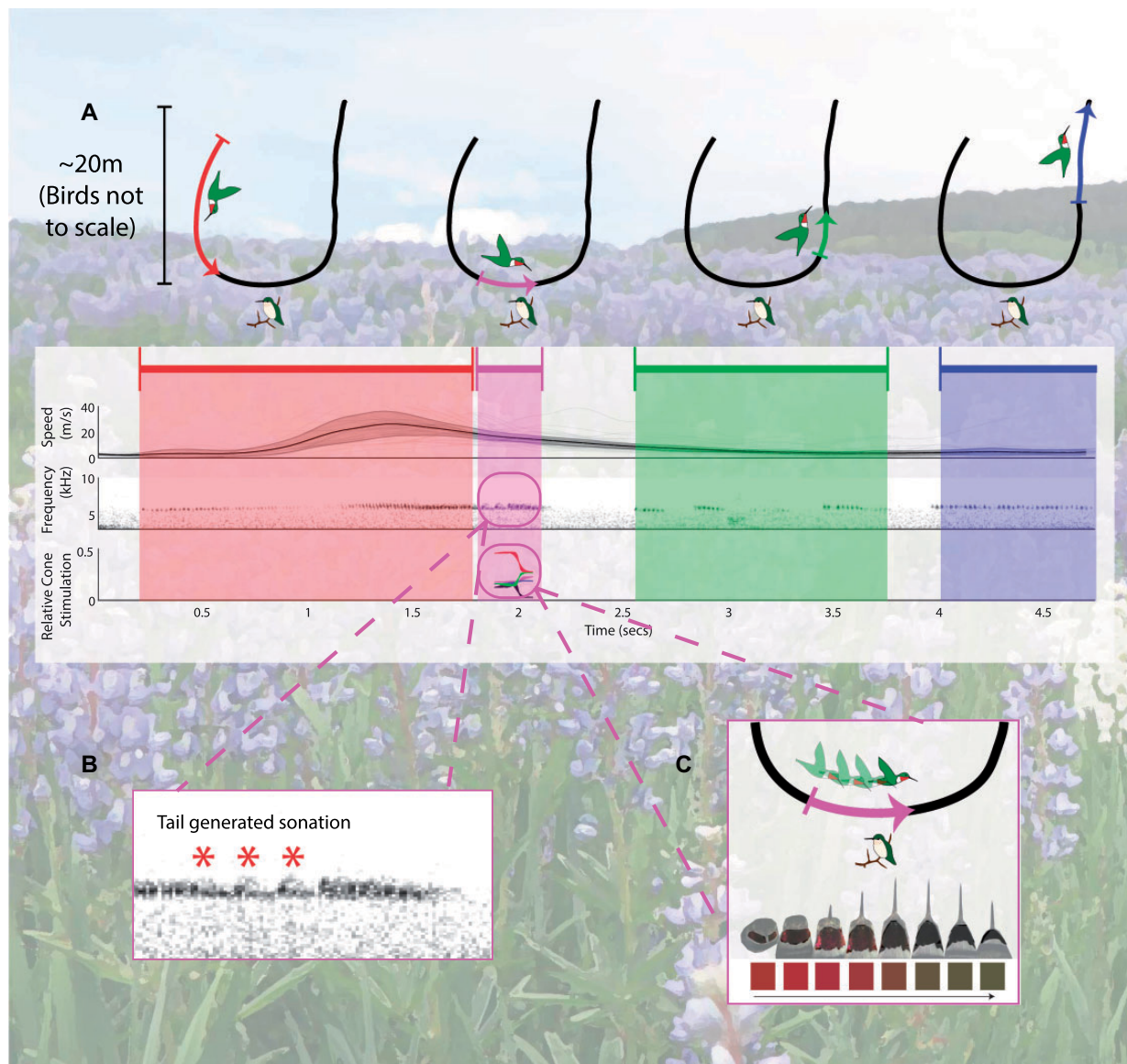


Fig. 4. Signalers can synchronize signals in space and time to increase their efficacy. Male broad-tailed hummingbirds perform highly synchronized U-shaped dives during their courtship displays. A single dive trajectory is illustrated here (A) in four discrete segments: the approach (red), the “sensory explosion” (magenta), the ascent (green), and the climb (blue). The graphs below the dives show the changes in maximum speed, sound, and gorget color over time for the duration of the dive. Shaded boxes indicate the area of the graph that corresponds to each of the four segments. Shortly after the male reaches his maximum speed in his approach (red), the male reaches the base of his dive and a highly synchronized “sensory explosion” occurs directly over the female (magenta). This segment of the dive is characterized by a short sonation generated from the male’s tail. As the male reaches his maximum horizontal velocity (not shown here), his tail feathers vibrate to produce a “buzz” as he approaches the female. The tail buzz sound, indicated by the three asterisks, is visible in the sonogram (B). Immediately after the tail buzz, the male’s gorget becomes visible to the female and quickly flashes from bright red to a dull greenish-black (also shown as RGB color composite in C). The tail buzz and color change occur within ~300ms, a very short section of the overall dive. The approach (red), ascent (green), and climb (blue) also have stereotyped sonations produced by the male’s wings, but these sections of the dive lack the high synchrony between visual and auditory modalities of the “sensory explosion” (magenta) at the base of the dive. $N = 17$ (17 dive events comprising 48 total dives) for the average maximum speed. The sonogram is from one representative male to more clearly illustrate the sections of the sonogram that correspond to different segments of the dive. The change in gorget color is depicted in (A) as four colored lines representing estimated changes in the four color cone types in the female’s eye. Using photographs of 10 male museum specimens, we estimated how a female’s long (red line), medium (green line), short (blue line), and ultraviolet (magenta line) wavelength-sensitive cone types would be stimulated (see Hogan and Stoddard 2018 for details). Shown also is the estimated change in double cone stimulation (black line). The gorget color change is also illustrated in (C), which shows photos of the male’s gorget as seen from the base of the dive (broadly replicating female perspective), along with color estimates based on the long, medium, and short wavelength-sensitive cone responses. Data are adapted from Hogan and Stoddard (2018).

inspires these questions, but it also makes answering them more tractable.

Synthesis and future directions

Our survey of animal communication systems makes it clear that animals must often attend to their location in space over time when signaling or evaluating the signals of others. These geometric considerations emerge from the directionality and distance-dependence of nearly all signals and receptors, but are further exacerbated by environmental and social complexities. Without taking this geometry of signaling into account, researchers often implicitly assume optimal geometries when investigating the evolution of animal communication strategies. Although such simplifying assumptions run the risk of misrepresenting the true state of communication between animals, they also forego the opportunity to discover the many ways in which animals respond to the geometric challenges they face when communicating. Herein lies the more significant shortcoming: for most species, we have little knowledge about how animals tailor their displays and/or evaluatory behaviors to maximize adaptive information flow. Yet, anyone who studies animal behavior knows that signalers and receivers are constantly adjusting their positions during communication. We, therefore, call for renewed efforts to understand this critically understudied aspect of animal communication.

As researchers actively working in this space, we are acutely aware that tracking animal position and posture in space across time can be laborious. Thankfully, new tools for automated tracking are now readily at hand. These include standalone programs such as DeepLabCut (Nath et al. 2019), R-based packages like “TrajR” (McLean and Skowron Volponi 2018), MATLAB-based packages such as DLTdv5 (Hedrick 2008), and/or general image analysis programs such as ImageJ (Schindelin et al. 2012; Schneider et al. 2012). With these tools, researchers can now more easily film and track signalers as they display to freely moving receiver(s) or to experimenter-controlled model receivers (e.g., Patricelli et al. 2002; Olea et al. 2010; Echeverri et al. 2017).

Such positional information should then be combined with careful quantification of the directionality of signals (e.g., by photographing a visual signal from a range of viewing angles and illumination angles, a technique refined by many studies on iridescent colors; Rutowski et al. 2007; Santos et al. 2007; Stevens et al. 2007; White et al. 2015; Gruson et al. 2019). For some species, presenting

each of these incrementally rotated views to receivers in a video-playback experiment allows for measurement of signal effectiveness based on the extent or likelihood of receiver responses (Nelson and Fijn 2013). Software packages such as AcuityView (Caves and Johnsen 2018; Caves et al. 2018) can also estimate the effects of acuity and viewing distance on signal appearances. Even virtual reality systems for animals, especially those with closed-loop designs that allow individuals to “move” within a virtual space, have the potential to allow for realistic control over the visual environment experienced by an individual (Peckmezian and Taylor 2015; Stowers et al. 2017). Taken together, these techniques permit quantitative estimation of how signal appearance changes moment-to-moment in response to the dynamic positioning of signaler and receiver.

We note, however, that many of the techniques and approaches described above are focused on visual signaling, and similar tools are often not yet available for other modalities. An exception to this is in the realm of auditory communication, where researchers have been using spatially calibrated microphone arrays to excellent effect for quite some time (Patricelli et al. 2008; Yorzinski and Patricelli 2010; Blumstein et al. 2011; Brumm et al. 2011). Paired with video footage of signaler and receiver location, such microphone arrays promise to unveil new insights into how acoustic communication unfolds across space and time. Advances in real time odorant quantification (e.g., SP_MESH paired with DART-MS, Rafson et al. 2019) promise to bring spatial and temporal quantification into the realm of chemical signaling. Novel tools for quantifying fluid flow are also being developed (e.g., a 3D anemometer; Girling et al. 2013). As these technologies mature and become more widely available, we expect that researchers will have greater ability to measure spatial and temporal properties of animal signals across modalities. This opens up the exciting possibility of comparing such properties between trait types in multimodal displays, even in natural environments. Although perhaps something of a “hopeful monster,” we can at least imagine a day when playback paradigms include not only spatially realistic visual playbacks, but also auditory, vibratory, and even chemical playbacks that allow us to probe the various geometric tradeoffs that signalers face when signaling across modalities.

As we make progress characterizing the spatio-temporal properties of signals, it will be equally crucial to describe the spatial and temporal biases of relevant sensory systems. In the same way that behavioral ecologists studying animal coloration have

increasingly integrated information about the spectral sensitivities of their focal animals into their analyses, we hope that researchers will begin to include the role of spatial biases in sensory systems when studying animal responses to signals. At the moment, information about such sensory biases (e.g., retinal specializations across visual fields) is taxonomically sparse, much in the same way that measurements of spectral sensitivity were once available only for token species within key animal groups. However, as demand for such information increases, so (we hope) will supply. One area where information about spatial biases is critically limited is in the study of chemical senses. Work on fluid dynamics has shown that the shape of chemical sensors and the properties of their morphological surroundings (e.g., location on body, presence of other nonsensory body parts) affect how fluid flows in and through the sensor, loosely defining a volume of surrounding space that feeds into the sensory cells (Settles et al. 2003; Craven et al. 2010; Jaffar-Bandjee et al. 2020). Discovering how such fluid flows and sensor properties interact to produce spatial biases in chemical sensing is an area ripe for future work.

Finally, studies of the geometry of signaling must account for how animals adaptively change the posture of their bodies and sensory systems. This is a multifaceted challenge involving investigation not only of active control of signals and sensors but also mechanisms involved in navigation, self-referential spatial awareness, and tracking of other interactors within a communicatory bout. Many of these capacities are interlinked, from the use of gaze in guidance of spatial navigation, to feedback loops between display intensity and receiver responses. Such work necessitates moving from peripheral sensory systems and motor controls to deeper cognitive integration. We see this work as both daunting and extremely exciting, with the potential to open up new directions even in well-established fields. For example, decades of careful work have revealed how animals navigate to different geographic locations and around physical obstacles (reviewed in Collett and Graham 2004; Berdahl et al. 2018). However, we know almost nothing about how individuals handle navigation with respect to an active, close-range, communication partner (but see research on long-range navigation via odor plumes toward an unknown signaler for potential inspiration; reviewed in Vickers 2000; Vasey et al. 2015; Fig. 2). Unlike in geographic navigation, the sensory cues and “landmarks” associated with signal and sensor orientation are not fixed in space due to the movement of both signaler and receiver. This may

preclude simple navigational strategies such as path integration or tracking of fixed landmarks. Instead, communicators may require new strategies or heuristics focused on signaling-relevant cues. Such strategies may make use of navigational centers in the brain or may require the recruitment of entirely different neural pathways. Individual variation in the ability to adaptively deploy these mechanisms, either to optimize signal production and/or signal reception, may itself be fodder for selection in the form of “social skill” (Sih et al. 2014, 2019; Echeverri et al. 2017).

In conclusion, the geometry of signaling is an essential, and oft-overlooked, aspect of animal communication. Yet, attention to it motivates new and exciting work at a variety of levels of biological organization, from the physics of signal propagation and reception to the evolutionary ecology of habitat-specific adaptations, and from the neurobiology of referential spatial navigation to the evolution of social skill. We hope that by highlighting the many ways in which the geometry of signaling is important, we will have inspired at least some of our readers to join us in exploring these issues which—while they may seem new to us—our study animals have been contending with for millions of years.

Funding

The authors’ participation in the “Spatio-Temporal Dynamics in Animal Communication” workshop and symposium, which took place at the 2020 and 2021 annual meetings of the Society for Integrative and Comparative Biology (SICB) respectively, was supported by the National Science Foundation (NSF) [grant IOS-2010768 to N.I.M.] as well as the SICB Divisions of Ecology and Evolution (DEE), Comparative Biomechanics (DCB), Invertebrate Zoology (DIZ), Animal Behavior (DAB), and Neurobiology, Neuroethology, and Sensory Biology (DNNSB). The efforts of S.A.E. and N.I.M. were also supported by the National Science Foundation [grants IOS-1557549/IOS-1734291/IOS-1933714/IOS-1831767], the University of Pittsburgh, and the University of Cincinnati. The effort of K.L.H. was supported by NSF DEB-1911619 and IOS-1350346. The efforts of A.E.M. and M.C.S. were supported by Princeton University. M.C.S. was also supported by NSF IOS-2029538.

Conflicts of interest

We declare that we have no conflicts of interest.

Acknowledgments

The authors thank “Spatio-Temporal Dynamics in Animal Communication” workshop and symposium co-organizers Sara Wasserman, Nicholai Hensley, and Jess Kanwal (alongside N.I.M. and K.L.H.) for providing the opportunity to discuss, mature, and communicate our ideas. Sara Wasserman and Emma Coddington provided critical insights during manuscript preparation. We are also thankful to the Society for Integrative and Comparative Biology for providing a rich intellectual environment within which to develop and discuss these and other related scientific topics. The idea for, and early work on this manuscript began in a graduate level seminar at the University of Pittsburgh, and we are grateful to Nikki Forrester, Paul Crawford, and James L. Loving-Lichtenstein for their early contributions to our ideas. We also thank the Macaulay Library at the Cornell Lab of Ornithology and Edwin Scholes for the use of still images from his video of *Lophorina superba* (ML458003) in Fig. 1. Finally, we thank three anonymous reviewers, whose feedback improved the quality of the manuscript.

References

- Alberts AC, Winkler DW, Hall C. 1992. Constraints on the design of chemical communication systems in terrestrial vertebrates. *Am Nat* 139:526–43.
- Alcock J. 1987. Leks and hilltopping in insects. *J Nat Hist* 21:319–28.
- Allen ML, Hočevár L, de Groot M, Krofel M. 2017. Where to leave a message? The selection and adaptive significance of scent-marking sites for Eurasian lynx. *Behav Ecol Sociobiol* 71:136.
- Andersson J, Borg-Karlson AK, Vongvanich N, Wiklund C. 2007. Male sex pheromone release and female mate choice in a butterfly. *J Exp Biol* 210:964–70.
- Arch VS, Narins PM. 2008. “Silent” signals: selective forces acting on ultrasonic communication systems in terrestrial vertebrates. *Anim Behav* 76:1423–8.
- Aroyan JL. 2001. Three-dimensional modeling of hearing in *Delphinus delphis*. *J Acoust Soc Am* 110:3305–18.
- Atema J. 1995. Chemical signals in the marine environment: dispersal, detection, and temporal signal analysis. *Proc Natl Acad Sci U S A* 92:62–6.
- Au WWL, Kastelein RA, Benoit-Bird KJ, Cranford TW, McKenna MF. 2006. Acoustic radiation from the head of echolocating harbor porpoises (*Phocoena phocoena*). *J Exp Biol* 209:2726–33.
- Baeckens S, Martín J, García-Roa R, Pafilis P, Huyghe K, Van Damme R. 2018. Environmental conditions shape the chemical signal design of lizards. *Funct Ecol* 32:566–80.
- Barnett JB, Cuthill IC. 2014. Distance-dependent defensive coloration. *Curr Biol* 24:R1157–58.
- Barnett JB, Cuthill IC, Scott-Samuel NE. 2018a. Distance-dependent aposematism and camouflage in the cinnabar moth caterpillar (*Tyria jacobaeae*, Erebididae). *R Soc Open Sci* 5:171396.
- Barnett JB, Michalis C, Scott-Samuel NE, Cuthill IC. 2018b. Distance-dependent defensive coloration in the poison frog *Dendrobates tinctorius*, Dendrobatidae. *Proc Natl Acad Sci U S A* 115:6416–6421.
- Baumann-Pickering S, Roch MA, Wiggins SM, Schnitzler HU, Hildebrand JA. 2015. Acoustic behavior of melon-headed whales varies on a diel cycle. *Behav Ecol Sociobiol* 69:1553–63.
- Berdahl AM, Kao AB, Flack A, Westley PAH, Codling EA, Couzin ID, Dell AI, Biro D. 2018. Collective animal navigation and migratory culture: from theoretical models to empirical evidence. *Philos Trans R Soc B Biol Sci* 373:20170009.
- Bergman DA, Martin AL, Moore PA. 2005. Control of information flow through the influence of mechanical and chemical signals during agonistic encounters by the crayfish, *Orconectes rusticus*. *Anim Behav* 70:485–96.
- Blumstein DT, Mennill DJ, Clemens P, Girod L, Yao K, Patricelli G, Deppe JL, Krakauer AH, Clark C, Cortopassi KA, Hanser SF, et al. 2011. Acoustic monitoring in terrestrial environments using microphone arrays: applications, technological considerations and prospectus. *J Appl Ecol* 48:758–67.
- Bohlin T, Tullberg BS, Merilaita S. 2008. The effect of signal appearance and distance on detection risk in an aposematic butterfly larva (*Parnassius apollo*). *Anim Behav* 76:577–84.
- Boncoraglio G, Saino N. 2007. Habitat structure and the evolution of bird song: a meta-analysis of the evidence for the acoustic adaptation hypothesis. *Funct Ecol* 21:134–42.
- Bortolotti GR, Stoffel MJ, Galván I. 2011. Wintering Snowy Owls *Bubo scandiacus* integrate plumage colour, behaviour and their environment to maximize efficacy of visual displays. *Ibis (Lond 1859)* 153:134–42.
- Bovet P, Drake C, Bernaschina F, Savel S. 1998. Underwater sound localization: role of interaural time and intensity differences. *J Acoust Soc Am* 103:2844.
- Bradbury JW, Vehrencamp SL. 2011. Principles of animal communication. 2nd ed. Sunderland (MA): Sinauer.
- Branstetter BK, Mercado EI. 2006. Sound localization by cetaceans. *Int J Comp Psychol* 19:26–61.
- Breitwisch R, Whitesides GH. 1987. Directionality of singing and non-singing behaviour of mated and unmated northern mockingbirds, *Mimus polyglottos*. *Anim Behav* 35:331–9.
- Brenowitz EA. 1982. The active space of red-winged blackbird song. *J Comp Physiol A* 147:511–22.
- Brenowitz EA. 1989. Neighbor call amplitude influences aggressive behavior and intermale spacing in choruses of the pacific treefrog (*Hyla regilla*). *Ethology* 83:69–79.
- Brumm H, Robertson KA, Nemeth E. 2011. Singing direction as a tool to investigate the function of birdsong: an experiment on sedge warblers. *Anim Behav* 81:653–9.
- Brumm H, Slater PJB. 2006. Animals can vary signal amplitude with receiver distance: evidence from zebra finch song. *Anim Behav* 72:699–705.
- Brumm H, Todt D. 2003. Facing the rival: directional singing behaviour in nightingales. *Behaviour* 140:43–53.
- Cade W. 1975. Acoustically orienting parasitoids: fly phonotaxis to cricket song. *Science* 190:1312–4.

- Cade W. 1979. The evolution of alternative male reproductive strategies in field crickets. In: Blum MS, Mlum NA, editors. Sexual selection and reproductive competition in insects. New York (NY): Academic Press. p. 343–79.
- Caro T. 2013. Are spotted skunks conspicuous or cryptic? *Ethol Ecol Evol* 25:144–60.
- Caves E, Johnsen S. 2018. AcuityView: an r package for portraying the effects of visual acuity on scenes observed by an animal. *Methods Ecol Evol* 9:793–97.
- Caves E, Brandley NC, Johnsen S. 2018. Visual acuity and the evolution of signals. *Trends Ecol Evol* 33:358–72.
- Chow DM, Frye MA. 2009. The neuro-ecology of resource localization in *Drosophila*: behavioral components of perception and search. *Fly (Austin)* 3:50–61.
- Christensen-Dalsgaard J, Manley GA. 2019. Sound localization by the internally coupled ears of lizards: from biophysics to biorobotics. *J Acoust Soc Am* 146:4718–26.
- Christy JH, Backwell PRY, Schober U. 2003. Interspecific attractiveness of structures built by courting male fiddler crabs: experimental evidence of a sensory trap. *Behav Ecol Sociobiol* 53:84–91.
- Clark CJ, Mistick EA. 2018. Strategic acoustic control of a hummingbird courtship dive. *Curr Biol* 28:1257–1264. e6.
- Cole GL. 2013. Lost in Translation: adaptation of mating signals in changing environments. *Springer Sci Rev* 1:25–40.
- Collett TS, Graham P. 2004. Animal navigation: path integration, visual landmarks and cognitive maps. *Curr Biol* 14:475–7.
- Craven BA, Paterson EG, Settles GS. 2010. The fluid dynamics of canine olfaction: unique nasal airflow patterns as an explanation of macrosmia. *J R Soc Interface* 7:933–43.
- Criminaldi JP, Koseff JR. 2001. High-resolution measurements of the spatial and temporal scalar structure of a turbulent plume. *Exp Fluids* 31:90–102.
- Cronin TW, Johnsen S, Marshall NJ, Warrant EJ. 2014. Visual ecology. Princeton (NJ): Princeton University Press.
- Cuthill IC, Sanghera NS, Penacchio O, Lovell PG, Ruxton GD, Harris JM. 2016. Optimizing countershading camouflage. *Proc Natl Acad Sci U S A* 113:13093–7.
- Dakin R, Montgomerie R. 2009. Peacocks orient their courtship displays towards the sun. *Behav Ecol Sociobiol* 63:825–34.
- Dakin R, Montgomerie R. 2013. Eye for an eyespot: how iridescent plumage ocelli influence peacock mating success. *Behav Ecol* 24:1048–57.
- Dantzker MS, Deane GB, Bradbury JW. 1999. Directional acoustic radiation in the strut display of male sage grouse *Centrocercus urophasianus*. *J Exp Biol* 202:2893–909.
- Donohue CG, Hemmi JM, Kelley JL. 2020. Countershading enhances camouflage by reducing prey contrast. *Proc R Soc B* 287:20200477.
- Doucet SM, Meadows MG. 2009. Iridescence: a functional perspective. *J R Soc Interface* 6 (Suppl 2):S115–32.
- Echeverri SA. 2020. How spatial constraints on efficacy and dynamic signaling alignment shape animal communication. Pittsburgh (PA): University of Pittsburgh.
- Echeverri SA, Morehouse NI, Zurek DB. 2017. Control of signal alignment during the dynamic courtship display of a jumping spider. *Behav Ecol* 28:1445–53.
- Elias DO, Maddison WP, Peckmezian C, Girard MB, Mason AC. 2012. Orchestrating the score: complex multimodal courtship in the *Habronattus coecatus* group of *Habronattus* jumping spiders (Araneae: Salticidae). *Biol J Linn Soc* 105:522–47.
- Endler JA. 2010. Natural selection on color patterns in *Poecilia reticulata*. Author (s): John A. Endler Published by: society for the study of evolution stable Soc Study Evol 34:76–91.
- Endler JA. 1992. Signals, signal conditions, and the direction of evolution. *Am Nat* 139:S125–S153.
- Endler JA, Mielke PW, Kelley LA. 2012. Illusions promote mating success in great bowerbirds. *Science* 337:292.
- Endler JA, Thery M. 1996. Interacting effects of lek placement, display behavior, ambient light, and color patterns in three Neotropical forest-dwelling birds. *Am Nat* 148:421–52.
- Ey E, Fischer J. 2009. The “acoustic adaptation hypothesis”—a review of the evidence from birds, anurans and mammals. *Bioacoustics* 19:21–48.
- Fares Y, Sharpe PJH, Magnuson CE. 1980. Pheromone dispersion in forests. *J Theor Biol* 84:335–59.
- Fernández-Juricic E, Baumhardt PE, Tyrrell LP, Elmore A, Deliberto ST, Werner SJ. 2019. Vision in an abundant North American bird: the Red-winged Blackbird. *Auk* 136:1–27.
- Foelix RF. 2011. Biology of spiders, insect systematics & evolution. New York (NY): OUP USA.
- Forrest TG. 1991. Power output and efficiency of sound production by crickets. *Behav Ecol* 2:327–38.
- Gartner GEA, Gamble T, Jaffe AL, Harrison A, Losos JB. 2013. Left-right dewlap asymmetry and phylogeography of *Anolis lineatus* on Aruba and Curaçao. *Biol J Linn Soc* 110:409–26.
- Girling RD, Higbee BS, Cardé RT. 2013. The plume also rises: trajectories of pheromone plumes issuing from point sources in an orchard canopy at night. *J Chem Ecol* 39:1150–60.
- Goldman JA, Koehl MAR. 2001. Fluid dynamic design of lobster olfactory organs: high speed kinematic analysis of antennule flicking by *panulirus argus*. *Chem Senses* 26:385–98.
- Greenfield PM. 1972. Playing peekaboo with a four-month-old: a study of the role of speech and nonspeech sounds in the formation of a visual schema. *J Psychol* 82:287–98.
- Gruson H, Andraud C, De Marcillac WD, Berthier S, Elias M, Gomez D. 2019. Quantitative characterization of iridescent colours in biological studies: a novel method using optical theory. *Interface Focus* 9:20180049.
- Halfwerk W, Bot S, Slabbekoorn H. 2012. Male great tit song perch selection in response to noise-dependent female feedback. *Funct Ecol* 26:1339–47.
- Hamilton WJ. 1965. Sun-oriented display of the Anna’s Hummingbird. *Wilson Ornithol Soc* 77:38–44.
- Harland DP, Li D, Jackson RR. 2012. How jumping spiders see the world. In: Lazareva O Shimizu T, editors. How animals see the world: comparative behavior, biology, and evolution of vision. New York (NY): Oxford University Press. p. 133–63.
- Hebets EA, Barron AB, Balakrishnan CN, Hauber ME, Mason PH, Hoke KL. 2016. A systems approach to animal communication. *Proc R Soc B Biol Sci* 283:20152889.

- Hebets EA, Papaj DR. 2005. Complex signal function: developing a framework of testable hypotheses. *Behav Ecol Sociobiol* 57:197–214.
- Hedrick TL. 2008. Software techniques for two- and three-dimensional kinematic measurements of biological and biomimetic systems. *Bioinspir Biomim* 3:034001.
- Henwood K, Fabrick A. 1979. A quantitative analysis of the dawn chorus: temporal selection for communicatory optimization. *Am Nat* 114:260–74.
- Hill DE. 2009. Euophryine jumping spiders that extend their third legs during courtship (Araneae: Salticidae: Euophryinae: Maratus, Saitis). *Peckhamia* 74:1–27.
- Hogan BG, Stoddard MC. 2018. Synchronization of speed, sound and iridescent color in a hummingbird aerial courtship dive. *Nat Commun* 9:5260.
- Hollien H. 1973. Underwater sound localization in humans. *J Acoust Soc Am* 53:1288–95.
- Holt MM, Southall BL, Insley SJ, Schusterman RJ. 2010. Call directionality and its behavioural significance in male northern elephant seals, *Mirounga angustirostris*. *Anim Behav* 80:351–61.
- Hunter ML, Kacelnik A, Roberts J, Vuillermoz M. 1986. Directionality of avian vocalizations: a laboratory study. *Condor* 88:371–75.
- Hutton P, Ligon RA, McGraw KJ, Seymoure BM, Simpson RK. 2015. Dynamic color communication. *Curr Opin Behav* 6:41–49.
- Jaffar-Bandjee M, Krijnen G, Casas J. 2020. Symposium article: challenges in modeling pheromone capture by pectinate antennae. *Integr Comp Biol* 60:876–885.
- Janzen DH, Hallwachs W, Burns JM. 2010. A tropical horde of counterfeit predator eyes. *Proc Natl Acad Sci U S A* 107:11659–65.
- Jen PHS, Chen D. 1988. Directionality of sound pressure transformation at the pinna of echolocating bats. *Hear Res* 34:101–17.
- Johnsen S. 2002. Cryptic and conspicuous coloration in the pelagic environment. *Proc Biol Sci* 269:243–56.
- Johnsen S. 2012. *Optics of life*. Princeton (NJ): Princeton University Press.
- Kamilar JM, Bradley BJ. 2011. Countershading is related to positional behavior in primates. *J Zool* 283:227–33.
- Kang CK, Moon JY, Lee SI, Jablonski PG. 2013. Cryptically patterned moths perceive bark structure when choosing body orientations that match wing color pattern to the bark pattern. *PLoS One* 8:e78117.
- Kang C, Stevens M, Moon JY, Lee SI, Jablonski PG. 2015. Camouflage through behavior in moths: the role of background matching and disruptive coloration. *Behav Ecol* 26:45–54.
- Kelley LA, Endler JA. 2012. Male great bowerbirds create forced perspective illusions with consistently different individual quality. *Proc Natl Acad Sci USA* 109:20980–85.
- Kelley LA, Kelley JL. 2014. Animal visual illusion and confusion: the importance of a perceptual perspective. *Behav Ecol* 25:450–63.
- Kemp DJ. 2008. Female mating biases for bright ultraviolet iridescence in the butterfly *Eurema hecabe* (Pieridae). *Behav Ecol* 19:1–8.
- Kemp DJ, Rutowski RL. 2007. Condition dependence, quantitative genetics, and the potential signal content of iridescent ultraviolet butterfly coloration. *Evolution* 61:168–83.
- Kicklighter CE, Shabani S, Johnson PM, Derby CD. 2005. Sea hares use novel antipredatory chemical defenses. *Curr Biol* 15:549–54.
- Kjernsmo K, Whitney HM, Scott-Samuel NE, Hall JR, Knowles H, Talas L, Cuthill IC. 2020. Iridescence as Camouflage. *Curr Biol* 30:551–555.e3.
- Koehl MAR. 2006. The fluid mechanics of arthropod sniffing in turbulent odor plumes. *Chem Senses* 31:93–105.
- Koehl MAR, Koseff JR, Crimaldi JP, McCay MG, Cooper T, Wiley MB, Moore PA. 2001. Lobster sniffing: antennule design and hydrodynamic filtering of information in an odor plume. *Science* 294:1948–51.
- Kong WN, Hu RS, Zhao ZG, Li J, Zhang ZW, Li SC, Ma RY. 2014. Effects of trap height, location, and spacing on pheromone-baited trap catch efficacy for oriental fruit moths (Lepidoptera: Tortricidae) in a peach orchard. *Can Entomol* 146:684–92.
- Land MF. 1969a. Structure of the retinae of the principal eyes of jumping spiders (Salticidae: Dendryphantinae) in relation to visual optics. *J Exp Biol* 51:443–70.
- Land MF. 1969b. Movements of the retinae of jumping spiders (Salticidae: Dendryphantinae) in response to visual stimuli. *J Exp Biol* 51:471–93.
- Land MF. 1999. Motion and vision: why animals move their eyes. *J Comp Physiol A Sensory Neural Behav Physiol* 185:341–52.
- Land MF, Nilsson D-E. 2012. *Animal eyes*. Oxford: Oxford University Press.
- Larsen ON, Dabelsteen T. 1990. Directionality of blackbird vocalization. Implications for vocal communication and its further study. *Scand J Ornithol* 21:36–45.
- Letelier JC, Marin G, Sentis E, Tenreiro A, Fredes F, Mpodozis J. 2004. The mapping of the visual field onto the dorso-lateral tectum of the pigeon (*Columba livia*) and its relations with retinal specializations. *J Neurosci Methods* 132:161–68.
- Long KD, Rosenqvist G. 1998. Changes in male guppy courtship distance in response to a fluctuating light environment. *Behav Ecol Sociobiol* 44:77–83.
- Losos DN, Weaver JBR, Fies TW, Herrel A, Fabre AC, Losos JB. 2017. The curious case of the left-sided dewlap: directional asymmetry in the Curaçao anole, *Anolis lineatus*. *Breviora* 553:1–7.
- Marshall AH, Meyer J. 1985. The directivity and auditory impressions of singers. *Acta Acust united with Acust* 58:130–40.
- Marshall NJ. 2000. Communication and camouflage with the same “bright” colours in reef fishes. *Philos Trans R Soc B Biol Sci* 355:1243–48.
- Mcgregor PK, Horn AG, Leonard ML, Thomsen F. 2013. *Animal communication and noise*. Animal communication and noise. Vol. 2. Berlin/Heidelberg Germany: Springer.
- McLean DJ, Skowron Volponi MA. 2018. trajr: an R package for characterisation of animal trajectories. *Ethology* 124:440–48.
- Meadows MG, Butler MW, Morehouse NI, Taylor LA, Toomey MB, McGraw KJ, Rutowski RL. 2009.

- Iridescence: views from many angles. *J R Soc Interface* 6 (Suppl 2):S107–13.
- Melo N, Wolff GH, Costa-da-Silva AL, Arribas R, Triana MF, Gugger M, Riffell JA, DeGennaro M, Stensmyr MC. 2020. Geosmin attracts *Aedes aegypti* mosquitoes to oviposition sites. *Curr Biol* 30:127–134.e5.
- Mhatre N, Balakrishnan R. 2008. Predicting acoustic orientation in complex real-world environments. *J Exp Biol* 211:2779–85.
- Mhatre N, Malkin R, Deb R, Balakrishnan R, Robert D. 2017. Tree crickets optimize the acoustics of baffles to exaggerate their mate-attraction signal. *elife* 6:e32763.
- Miles M, Fuxjager MJ. 2019. Phenotypic diversity arises from secondary signal loss in the elaborate visual displays of toucans and barbets. *Am Nat* 194:704088.
- Miller GL, Loudon C, Freed S. 2007. Position around a tree: consequences for pheromone detection. *J Chem Ecol* 33:541–54.
- Mohorović M, Krofel M. 2020. The scent world of cats: where to place a urine scent mark to increase signal persistence? *Anim Biol* 1:1–18.
- Moore P, Crimaldi J. 2004. Odor landscapes and animal behavior: tracking odor plumes in different physical worlds. *J Mar Syst* 49:55–64.
- Morehouse NI, Buschbeck EK, Zurek DB, Steck M, Porter ML. 2017. Molecular evolution of spider vision: new opportunities, familiar players. *Biol Bull* 233:21–38.
- Muller-Schwarze D. 2006. *Chemical ecology of vertebrates*. Cambridge: Cambridge University Press.
- Muller BS, Bovet P. 1999. Role of pinnae and head movements in localizing pure tones. *Swiss J Psychol* 58:170–179.
- Müller R. 2015. Dynamics of biosonar systems in horseshoe bats. *Eur Phys J Spec Top* 224:3393–3406.
- Naguib M, Wiley RH. 2001. Estimating the distance to a source of sound: mechanisms and adaptations for long-range communication. *Anim Behav* 62:825–37.
- Nath T, Mathis A, Chen AC, Patel A, Bethge M, Mathis MW. 2019. Using DeepLabCut for 3D markerless pose estimation across species and behaviors. *Nat Protoc* 14:2152–76.
- Nehring V, Wyatt TD, d’Ettorre P. 2013. Noise in chemical communication. *Animal communication and noise*. Berlin/Heidelberg, Germany: Springer. p. 373–405.
- Nelson BS, Beckers GJL, Suthers RA. 2005. Vocal tract filtering and sound radiation in a songbird. *J Exp Biol* 208:297–308.
- Nelson XJ, Fijn N. 2013. The use of visual media as a tool for investigating animal behaviour. *Anim Behav* 85:525–36.
- Olea PP, Casas F, Redpath S, Viñuela J. 2010. Bottoms up: great bustards use the sun to maximise signal efficacy. *Behav Ecol Sociobiol* 64:927–37.
- Oren M, Nayar SK. 1995. Generalization of the Lambertian model and implications for machine vision. *Int J Comput Vis* 14:227–51.
- Otto JC, Hill DE. 2016. Males of a new species of *Jotus* from Australia wave a paddle-shaped lure to solicit nearby females (Araneae: salticidae: euophryini). *Peckhamia* 122:1–39.
- Ottway DS, Pankhurst SJ, Waterhouse JS. 2005. A possible function for female enurination in the mara, *Dolichotis patagonum*. *Chem Signals Vertebr* 10:101–9.
- Padgham M. 2004. Reverberation and frequency attenuation in forests—implications for acoustic communication in animals. *J Acoust Soc Am* 115:402–10.
- Patricelli GL, Dantzker MS, Bradbury JW. 2007. Differences in acoustic directionality among vocalizations of the male red-winged blackbird (*Agelaius phoeniceus*) are related to function in communication. *Behav Ecol Sociobiol* 61:1099–1110.
- Patricelli GL, Dantzker MS, Bradbury JW. 2008. Acoustic directionality of red-winged blackbird (*Agelaius phoeniceus*) song relates to amplitude and singing behaviours. *Anim Behav* 76:1389–1401.
- Patricelli GL, Krakauer AH. 2010. Tactical allocation of effort among multiple signals in sage grouse: an experiment with a robotic female. *Behav Ecol* 21:97–106.
- Patricelli GL, Uy JAC, Walsh G, Borgia G. 2002. Male displays adjusted to female’s response. *Nature* 415:279–80.
- Payne R, Webb D. 1971. Orientation by means of long range acoustic signaling in baleen whales. *Ann NY Acad Sci* 188:110–41.
- Peckmezian T, Taylor PW. 2015. A virtual reality paradigm for the study of visually mediated behaviour and cognition in spiders. *Anim Behav* 107:87–95.
- Pegram KV, Lillo MJ, Rutowski RL. 2013. Iridescent blue and orange components contribute to the recognition of a multicomponent warning signal. *Behaviour* 150:321–36.
- Pegram KV, Rutowski RL. 2014. Relative effectiveness of blue and orange warning colours in the contexts of innate avoidance, learning and generalization. *Anim Behav* 92:1–8.
- Persons MH, Fleishman LJ, Frye MA, Stimphil ME. 1999. Sensory response patterns and the evolution of visual signal design in anoline lizards. *J Comp Physiol A Sensory Neural Behav Physiol* 184:585–607.
- Phillips DP, Calford MB, Pettigrew JD, Aitkin LM, Semple MN. 1982. Directionality of sound pressure transformation at the cat’s pinna. *Hear Res* 8:13–28.
- Pokorny T, Vogler I, Losch R, Schlütting P, Juarez P, Bissantz N, Ramírez SR, Eltz T. 2017. Blown by the wind: the ecology of male courtship display behavior in orchid bees. *Ecology* 98:1140–52.
- Querubin A, Hie RL, Provis JM, Bumsted OK. 2009. Photoreceptor and ganglion cell topographies correlate with information convergence and high acuity regions in the adult pigeon (*Columba livia*) retina. *J Comp Neurol* 517:711–22.
- Rafson JP, Bee MY, Sacks GL. 2019. Spatially resolved headspace extractions of trace-level volatiles from planar surfaces for high-throughput quantitation and mass spectral imaging. *J Agric Food Chem* 67:13840–47.
- Richards DG, Wiley RH. 1980. Reverberations and amplitude fluctuations in the propagation of sound in a forest: implications for animal communication. *Am Nat* 115:381–99.
- Riffell JA, Abrell L, Hildebrand JG. 2008. Physical processes and real-time chemical measurement of the insect olfactory environment. *J Chem Ecol* 34:837–53.
- Rodríguez C, Amézquita A, Ringler M, Pašukonis A, Hödl W. 2020. Calling amplitude flexibility and acoustic spacing in the territorial frog *Allobates femoralis*. *Behav Ecol Sociobiol* 74: 1–10.
- Römer H, Schmidt AKD. 2016. Directional hearing in insects with internally coupled ears. *Biol Cybern* 110:247–54.

- Rosenthal GG. 2007. Spatiotemporal dimensions of visual signals in animal communication. *Annu Rev Ecol Evol Syst* 38:155–78.
- Rutowski RL, Macedonia JM, Merry JW, Morehouse NI, Yturalde K, Taylor-Taft L, Gaalema D, Kemp DJ, Papke RS. 2007. Iridescent ultraviolet signal in the orange sulphur butterfly (*Colias eurytheme*): spatial, temporal and spectral properties. *Biol J Linn Soc* 90:349–64.
- Ryan MJ, Cummings ME. 2013. Perceptual biases and mate choice. *Annu Rev Ecol Evol Syst* 44:437–59.
- Salva O, Regolin L, Mascalonzi E, Vallortigara G. 2012. Cerebral and behavioural asymmetries in animal social recognition. *Comp Cogn Behav Rev* 7:110–38.
- Santos SICO, De Neve L, Lumeij JT, Förschler MI. 2007. Strong effects of various incidence and observation angles on spectrometric assessment of plumage colouration in birds. *Behav Ecol Sociobiol* 61:1499–1506.
- Schindelin J, Arganda-Carreras I, Frise E, Kaynig V, Longair M, Pietzsch T, Preibisch S, Rueden C, Saalfeld S, Schmid B, et al. 2012. Fiji: an open source platform for biological image analysis. *Nat Methods* 9:676–82.
- Schneider CA, Rasband WS, Eliceiri KW. 2012. NIH Image to ImageJ: 25 years of image analysis. *Nat Methods* 9:671–75.
- Scholes E. 2008a. Evolution of the courtship phenotype in the bird of paradise genus *Parotia* (Aves: Paradisaeidae): homology, phylogeny, and modularity. *Biol J Linn Soc* 94:491–504.
- Scholes E. 2008b. Courtship ethology of Wahnes' parotia *Parotia wahnesi* (Aves: Paradisaeidae). *J Ethol* 26:79–91.
- Settles GS, Kester DA, Dodson-Dreibelbis LJ. 2003. The external aerodynamics of canine olfaction. In: Barth FG, Humphrey JAC, Secomb TW, editors. *Sensors and sensing in biology and engineering*. Vienna: Springer. p. 323–35.
- Sih A, Chang AT, Wey TW. 2014. Effects of behavioural type, social skill and the social environment on male mating success in water striders. *Anim Behav* 94:9–17.
- Sih A, Sinn DL, Patricelli GL. 2019. On the importance of individual differences in behavioural skill. *Anim Behav* 155:307–17.
- Simpson RK, McGraw KJ. 2018a. It's not just what you have, but how you use it: solar-positional and behavioural effects on hummingbird colour appearance during courtship. *Ecol Lett* 21:1413–22.
- Simpson RK, McGraw KJ. 2018b. Two ways to display: male hummingbirds show different color-display tactics based on sun orientation. *Behav Ecol* 29:637–648.
- Slabbekoorn H, den Boer-Visser A. 2006. Cities change the songs of birds. *Curr Biol* 16:2326–31.
- Snowdon CT, Hodun A. 1981. Acoustic adaptation in pygmy marmoset contact calls: locational cues vary with distances between conspecifics. *Behav Ecol Sociobiol* 9:295–300.
- Steinberg DS, Leal M. 2013. Sensory system properties predict signal modulation in a tropical lizard. *Anim Behav* 85:623–29.
- Stevens M. 2007. Predator perception and the interrelation between different forms of protective coloration. *Proc R Soc B* 274:1457–64.
- Stevens M, Parraga CA, Cuthill IC, Partridge JC, Troscianko TS. 2007. Using digital photography to study animal coloration. *Biol J Linn Soc* 90:211–37.
- Stowers JR, Hofbauer M, Bastien R, Griessner J, Higgins P, Farooqui S, Fischer RM, Nowikovsky K, Haubensak W, Couzin ID, et al. 2017. Virtual reality for freely moving animals. *Nat Methods* 14:995–1002.
- Temple SE. 2011. Why different regions of the retina have different spectral sensitivities: a review of mechanisms and functional significance of intraretinal variability in spectral sensitivity in vertebrates. *Vis Neurosci* 28:281–93.
- Templeton JJ, Mountjoy DJ, Pryke SR, Griffith SC. 2012. In the eye of the beholder: visual mate choice lateralization in a polymorphic songbird. *Biol Lett* 8:924–27.
- Tullberg BS, Merilaita S, Wiklund C. 2005. Aposematism and crypsis combined as a result of distance dependence: functional versatility of the colour pattern in the swallowtail butterfly larva. *Proc Biol Sci* 272:1315–21.
- Umbers KDL, Symonds MRE, Kokko H. 2015. The mathematics of female pheromone signaling: strategies for aging virgins. *Am Nat* 185:417–32.
- Uy JAC, Endler JA. 2004. Modification of the visual background increases the conspicuousness of golden-collared manakin displays. *Behav Ecol* 15:1003–10.
- Vasey G, Lukeman R, Wyeth RC. 2015. Additional navigational strategies can augment odor-gated rheotaxis for navigation under conditions of variable flow. *Integr Comp Biol* 55:447–60.
- Vickers NJ. 2000. Mechanisms of animal navigation in odor plumes. *Biol Bull* 198:203–12.
- Voigt CC, von Helversen O. 1999. Storage and display of odor in male *Saccolaryx billineata* Emballonuridae. *Behav Ecol Sociobiol* 47:29–40.
- Von Campenhausen M, Wagner H. 2006. Influence of the facial ruff on the sound-receiving characteristics of the barn owl's ears. *J Comp Physiol A Neuroethol Sensory, Neural, Behav Physiol* 192:1073–82.
- Webster DR, Weissburg MJ. 2001. Chemosensory guidance cues in a turbulent chemical odor plume. *Limnol Oceanogr* 46:1034–47.
- Webster DR, Weissburg MJ. 2009. The hydrodynamics of chemical cues among aquatic organisms. *Annu Rev Fluid Mech* 41:73–90.
- Webster RJ, Callahan A, Godin JGJ, Sherratt TN. 2009. Behaviourally mediated crypsis in two nocturnal moths with contrasting appearance. *Philos Trans R Soc B Biol Sci* 364:503–10.
- Weissburg MJ. 2000. The fluid dynamical context of chemosensory behavior. *Biol Bull* 198:188–202.
- White TE, Zeil J, Kemp DJ. 2015. Signal design and courtship presentation coincide for highly biased delivery of an iridescent butterfly mating signal. *Evolution* 69:14–25.
- Whitehead JM. 1987. Vocally mediated reciprocity between neighbouring groups of mantled howling monkeys, *Alouatta palliata* palliata. *Anim Behav* 35:1615–27.
- Whitney HM, Reed A, Rands SA, Chittka L, Glover BJ. 2016. Flower iridescence increases object detection in the insect visual system without compromising object identity. *Curr Biol* 26:802–8.
- Wiebe KL, Chang AM. 2018. Seeing sunlit owls in a new light: orienting Snowy Owls may not be displaying. *IBIS (Lond 1859)* 160:62–70.
- Wilczynski W, Brenowitz EA. 1988. Acoustic cues mediate inter-male spacing in a neotropical frog. *Anim Behav* 36:1054–63.

- Wiley RH, Richards DG. 1978. Physical constraints on acoustic communication in the atmosphere: implications for the evolution of animal vocalization. *Behav Ecol Sociobiol* 3:69–94.
- Wiley RH, Richards DG. 1982. Adaptations for acoustic communications in birds: sound transmission and signal detection. In: Kroodsma DE, Miller EH, editors. *Ecology and evolution of acoustic communication in birds*. New York (NY): Academic Press. p. 131–81.
- Wilson DR, Hare JF. 2006. The adaptive utility of Richardson's ground squirrel (*Spermophilus richardsonii*) short-range ultrasonic alarm signals. *Can J Zool* 84:1322–30.
- Witte K, Farris HE, Ryan MJ, Wilczynski W. 2005. How cricket frog females deal with a noisy world: habitat-related differences in auditory tuning. *Behav Ecol* 16:571–79.
- Yorzinski JL, Patricelli GL. 2010. Birds adjust acoustic directionality to beam their antipredator calls to predators and conspecifics. *Proc R Soc B Biol Sci* 277:923–32.
- Yorzinski JL, Patricelli GL, Babcock JS, Pearson JM, Platt ML. 2013. Through their eyes: selective attention in peahens during courtship. *J Exp Biol* 216:3035–46.
- Zhuang Q, Müller R. 2006. Noseleaf furrows in a horseshoe bat act as resonance cavities shaping the biosonar beam. *Phys Rev Lett* 97:218701.
- Zimmermann MJY, Nevala NE, Yoshimatsu T, Osorio D, Nilsson DE, Berens P, Baden T. 2018. Zebrafish differentially process color across visual space to match natural scenes. *Curr Biol* 28:2018–2032.e5.