Chapter 13
A Framework to Understand Interspecific Multimodal Signaling Systems

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Abstract Continued interest in multimodal signaling systems has resulted in new frameworks to understand the evolution and use of these complex signals. Most of these studies have focused on multimodal communication within a species (sexual and agonistic signaling), but members of different species also benefit by communicating through both eavesdropping and evolved signals. Here we develop a framework to understand interspecific multimodal signaling systems that asks three questions: (1) Is there an ecological incentive to communicate? (2) Is interspecific communication mechanistically possible? and (3) Is there a fitness consequence to this communication? Many aspects of multimodal signaling systems are expected to be similar within and across species, and signal reliability underlies all signaling. However, we identify unique constraints that apply to interspecific signaling systems: the need for overlapping sensory systems, sensory thresholds and cognitive abilities between the two species. This new framework should help identify the processes shaping multimodal signaling evolution in interspecific signaling systems.

13.1 Introduction

Multimodal signaling occurs when signals consist of components from two or more sensory modalities. Multimodal signals are common within most animal signaling systems, and perhaps are the norm (Hebets and Papaj 2004; Partan and Marler 2005). For instance, the black-tailed prairie dog's (*Cynomys ludovicianus*) multifunction, contagious jump–yip contains a visual component (the jump) and an acoustic component (the yip) (Hare et al. 2014). However, given the inherent costs of producing and receiving signals, a fundamental question is how have these complex

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signals evolved (Bro-Jørgensen 2010)? Previous research has focused on trying to understand the benefits of multimodal communication; however, this research has focused predominantly on intraspecific signaling systems, specifically sexual and agonistic signals (Bro-Jørgensen 2010; Bro-Jørgensen and Dabelsteen 2008; Candolin 2003). Here we present a framework to explain the conditions under which multimodal signaling has evolved in *inter*specific signaling systems.

A number of hypotheses have been developed to explain the evolution of multimodal signals (reviewed in Bro-Jørgensen 2010). Many of the adaptive explanations for multimodal signaling in intraspecific signaling systems are likely to apply to interspecific signaling systems because there will be similar selection for increased robustness, content, and/or reliability. However, there are likely notable differences between intra- and interspecific multimodal signaling systems because of differences in ecology, sensory systems, and cognition that exist between different species.

13.2 A Brief Background of Multimodal Signaling

Multimodal signals are often classified as redundant or nonredundant depending on the information contained in the components of the signal (Partan and Marler 2005). Furthermore, the evolution of multimodal signals can be explained using two main mechanisms: content-driven selection for increased information (i.e., the multiple messages hypothesis; Johnstone 1996) and efficacy-driven selection for increased robustness (i.e., the backup signals hypothesis; Johnstone 1996; Hebets and Papaj 2004). To study receiver responses, each component of a multimodal signal is tested separately and then together to understand how the combination of the components alters response (Partan and Marler 2005). For example, male fruit flies (*Drosophila melanogaster*) that use both an acoustic and a chemical component in their female courtship display have more successful matings than males that use only acoustic or chemical components (Rybak et al. 2002). This illustrates redundant enhancement (Partan and Marler 2005), where both components provide information to assess male suitability (redundant), but when combined males have significantly more matings than from either component presented alone (enhancement).

Prior work and existing frameworks fail to distinguish between intraspecific and interspecific signaling systems. The majority of empirical examples of multimodal signaling have focused on intraspecific signaling systems (Bro-Jørgensen and Dabelsteen 2008; Candolin 2003; Partan and Marler 2005; Wilkins et al. 2015). Recently, however, frameworks and hypotheses that enable the analysis of a signaling system as a whole have been proposed (Bro-Jørgensen 2010; Hebets et al. 2016; Wilkins et al. 2015). These frameworks use network and systems approaches that account for dynamic selection and consider the possibility of interactions between components across contexts (i.e., inter-signal interaction; Hebets and Papaj 2004). Although, these new frameworks and hypotheses aim to better understand a signaling system as a whole, again no distinction has been formally made between intraspecific and interspecific signaling systems.

13.3 Interspecific Signaling and Communication

Kostan (2002) developed a framework for the evolution of interspecific communication that exists along a gradient of reciprocity: eavesdropping by one species, both species eavesdropping on one another, asymmetrical communication where one species is intentionally signaling to the other, or mutualistic communication where both species produce signals that alter the behavior of the other (Kostan 2002). Interspecific communicative interactions can occur within any of these categories and in a variety of contexts that include (but are not limited to) predator–prey interactions, habitat selection, resource acquisition, and species recognition.

Regardless of the category of communication, it is important to understand the costs and benefits of the exchange for both a signaler and a receiver (Westrip and Bell 2015). In eavesdropping situations, the receiver benefits from the information in the signal and the sender can either be negatively affected (sender −, receiver +; as seen when a predator eavesdrops on prey; Rhebergen et al. 2015) or not affected at all (sender 0, receiver +; as seen when one species eavesdrops on the alarm calls of another species; Fallow and Magrath 2010). In mutualistic asymmetrical communication, both the sender and the receiver benefit (sender +, receiver +; as seen when flowers signal to their pollinators). The fitness benefits of both the sender and the receiver are important in order to understand the category of the signaling system and the mechanisms that maintain it.

We develop an integrative framework that specifies the conditions under which we expect to find multimodal signaling systems among species that is based on three broad questions: (1) Is there an ecological incentive for interspecific communication? (2) Is interspecific multimodal communication mechanistically possible? and (3) Is there a fitness consequence to multimodal communication?

13.4 An Interspecific Multimodal Framework (Fig. 13.1)

13.4.1 Is There an Ecological Incentive to Communicate?

In order for interspecific communication to evolve, at least one species in a pair should gain fitness benefits from communicating with the other (e.g., two species share predators, share food, or there is a predator–prey relationship; Murray and Magrath 2015). Some species have more opportunities for interactions than others. For instance, increased ecological similarity between species should lead to greater potential for interactions and perhaps stronger selection for communication to evolve.

If there is an ecological incentive to communicate, then are there aspects of each species’ ecology that favor multimodal signals over unimodal or multicomponent signals? In intraspecific systems, it is hypothesized that selection for increased content, reliability, or robustness (i.e., content- and efficacy-driven selection) leads

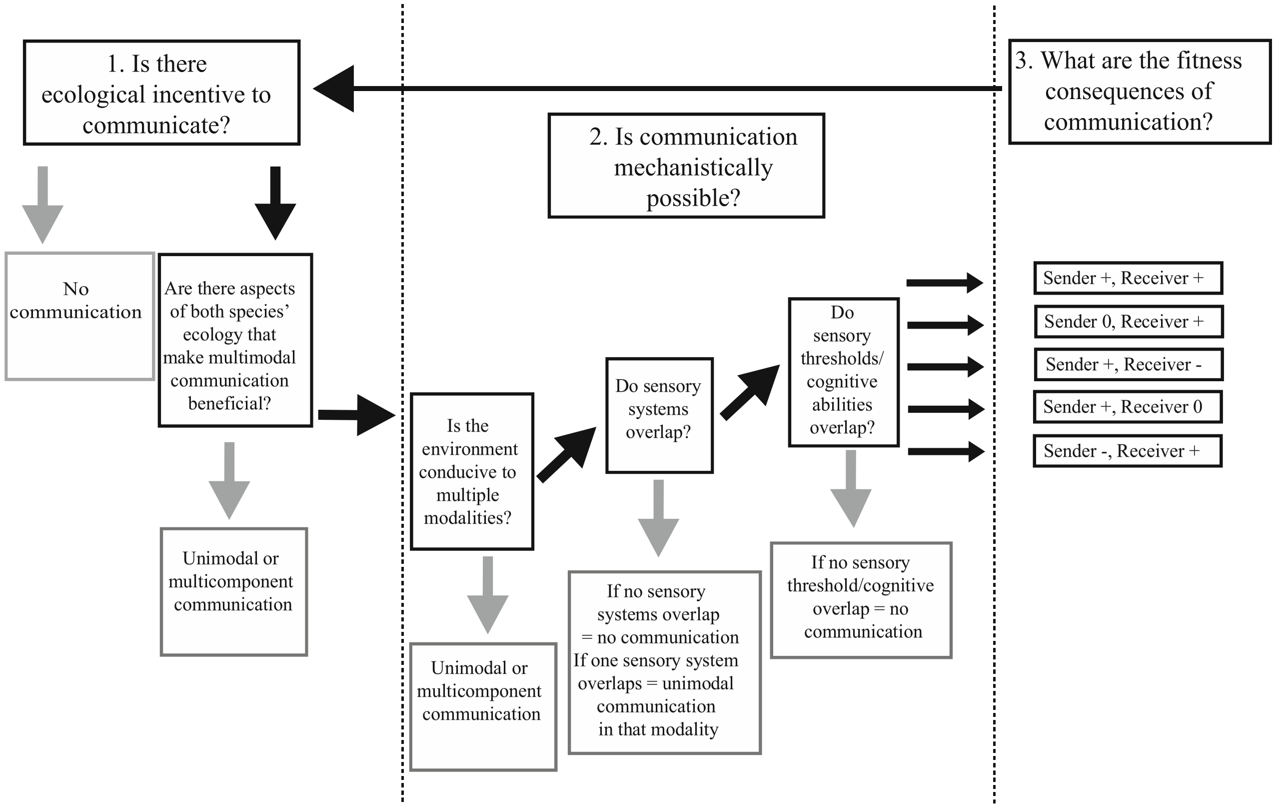

Fig. 13.1 Conceptual framework for understanding how and why multimodal signaling systems evolve in interspecific signaling systems. Black arrows indicate a "yes" response to the question posed in the boxes, where a gray arrow indicates a "no" response

to multimodal signals over unimodal or multicomponent signals, and similar selection may exist for interspecific signaling systems. For example, aposematic signals are often multimodal and combine visual, acoustic, and often olfactory components to deter predators. One hypothesis for the use of multimodal signals rather than unimodal or multicomponent signals is that the multimodal signals aid in learning and associating a defended prey with unpalatability (Rowe and Halpin 2013).

13.4.2 Is Interspecific Multimodal Communication Mechanistically Possible?

Sensory drive suggests that the relationship between the environmental conditions, the sensory systems, and signals together drive the evolution of signaling systems (Endler 1992; Tobias et al. 2010). Following this, we ask three main questions to identify the mechanisms behind interspecific multimodal signaling: (1) Do the environmental conditions favor specific modalities? (2) Do the species' sensory modalities overlap? and (3) Do the species' sensory thresholds and cognitive abilities overlap? The answers to these questions highlight the main differences between intraspecific and interspecific communication.

Do the environmental conditions favor specific modalities? Environments influence communication signals in two ways: the environment can influence the transmission and diffusion properties of a potential signal, and the environment can influence the ability of the receiver to detect the signal above the background noise (Bradbury and Vehrencamp 2011; Endler 1992). Environmental influences differ across signal modalities because of inherently different transmission and diffusion rates. For example, both acoustic and chemical signals can be used for short- and long-distance communication, but acoustic signals are generally short-term signals, while chemical signals can persist for a longer time (Weissburg et al. 2014). However, the environment can influence transmission and diffusion rates in other ways. For example, an acoustic signal travels further in water than in air (Bradbury and Vehrencamp 2011). Furthermore, habitats are not always stable (Bro-Jørgensen 2010). For example, there may be seasonal variation in the transmission properties of a habitat type. Great tit (*Parus major*) song transmits differently in a deciduous forest habitat before and after foliation (Blumenrath and Dabelsteen 2004). In addition, within a habitat type, variation in sounds produced by other species, abiotic features, and anthropogenic sources will further modify or mask signal transmission. For example, Uy and Safran (2013) found that the habitat density influences the use of the components of a multimodal signal used for species recognition. A subspecies of *Monarcha* flycatcher found in dense habitats used the acoustic and visual components sequentially, with the acoustic signal acting as a long-range signal and the visual signal acting as a close-range signal. Whereas another subspecies found in more open habitats used both acoustic and visual signals simultaneously (Uy and Safran 2013).

Do the sensory modalities overlap? Receivers can influence signal evolution through how they perceive and process signals (Rowe 1999). Therefore, the receiver's sensory system can be a selective force on the evolution of signals, including multimodal signals. In interspecific signaling systems, this means that the species must have overlapping sensory modalities: the sender needs to produce signal components in modalities the receiver possesses. For example, California ground squirrels (*Spermophilus beecheyi*) produce a multimodal signal to one predator and not another because of the predator's sensory systems (Rundus et al. 2007). Squirrels augment their antipredator tail waving behavior with infrared radiation when confronted with infrared-sensitive rattlesnakes (*Crotalus oreganus*), but do not when confronted with infrared insensitive gopher snakes (*Pituophis melanoleucus*). Furthermore, when rattlesnakes are exposed to tail waving and infrared radiation signals they shift from predatory to defensive behavior more often than when confronted with tail waving alone. The rattlesnake pit organs, which are responsible for detecting infrared radiation, make the rattlesnake an exceptional rodent predator; however, the California ground squirrel has exploited this adaptation to put rattlesnakes on the defensive.

Do the sensory thresholds and cognitive abilities overlap? Beyond possessing overlapping sensory systems, the signals must also be within the receiver's detection thresholds and cognitive processing abilities (Murray and Magrath 2015). For example, Murray and Magrath (2015) found responses to conspecific and heterospecific mobbing calls in superb fairy-wrens (*Malurus cyaneus*) and white-browed scrubwrens (*Sericornis frontalis*) differed because of reduced recognition of heterospecific calls. They concluded that there may be constraints on eavesdropping, such as the lack of perceptual specializations to detect heterospecific mobbing calls despite a large ecological overlap between the two species (Murray and Magrath 2015). This suggests that ecological overlap alone does not guarantee communication, but that sensory thresholds are important in signal use.

The opportunity for overlapping sensory modalities, sensory thresholds, and cognitive abilities is the key difference between intraspecific and interspecific communication systems. In general, conspecifics share similar sensory systems and thresholds (but see Gall and Lucas 2010). However, different species may not necessarily have the same sensory systems, the same sensory sensitivity or thresholds within a given sensory system, the same cognitive abilities, or the same information processing abilities. Therefore, it is imperative when investigating the possibility of interspecific multimodal communication to account for the sensory system as a whole (modalities, thresholds, and cognitive abilities). Overlap can be accomplished through the coevolution of sender and receiver, such as seen in plant–pollinator signaling systems (e.g., sensory drive; Endler 1992) or through sensory exploitation of sensory systems evolved for another purpose, such as seen in California ground squirrels exploiting the rattlesnakes' infrared sensory system to deter predation (Rundus et al. 2007; Ryan 1998).

Asking whether multimodal communication is mechanistically possible between species reveals important and unique constraints on the evolution of such communication because of the need for overlapping sensory modalities, sensory thresholds, and cognitive abilities between species. Although receiver psychology (including sensory thresholds and cognitive abilities) has been acknowledged as important in intraspecific signaling systems (Rowe 1999), it may be even more crucial in interspecific signaling systems because of the greater chance of a mismatch between sensory modalities, sensory thresholds, or cognitive/processing abilities. Therefore, future research into interspecific multimodal signaling systems needs to address the sensory systems of receivers in order to completely understand how the signaling system functions.

13.4.3 Is There a Fitness Consequence to Interspecific Multimodal Communication?

Like intraspecific signaling systems, the fitness consequences of signaling are dictated by the costs and benefits of signaling for both senders and receivers. These costs and benefits may also be driven by selection for increased robustness (efficacy-driven selection) or increased information or reliability (content-driven selection). Furthermore, there may be an adaptive reason to signal or the signaling system may be a by-product of another process (e.g., sensory exploitation). Finally, the costs and benefits of signaling between a sender and receiver can act as an ecological incentive to interact. Below, we present examples for three of the cost/benefit situations between sender and receiver using our framework: both sender and receiver benefit (sender +, receiver +), sender benefits (sender +, receiver −), or receiver benefits (sender −, receiver +).

Signaler +, Receiver +: Plant–Pollinator Signaling Systems

Most plant–pollinator signaling systems are asymmetrical communication systems (Kostan 2002) that involve an olfactory component and a visual component. The ecological incentive to communicate is the mutual benefit to both sender and receiver: plants get pollinated (sender +) and pollinators get an energy reward (receiver +). Selection for increased information and reliability about the nutritional reward (content-driven selection; Leonard et al. 2011) and robustness against a noisy background with multiple olfactory and visual signals bombarding pollinators (efficacy-driven selection; Leonard and Masek 2014) may drive the need for multimodal signals over unimodal signals. Communication is mechanistically possible because these systems are thought to coevolve, with plant multimodal signals coevolving with the sensory and perceptual systems of their pollinators (Haverkamp et al. 2016; Leonard and Masek 2014). For example, the evening primrose (*Oenthera neomexicana*) and hawkmoth (*Manduca sexta*) plant–pollinator system uses both olfactory and visual signals (Raguso and Willis 2002). Hawkmoths require both a visual component and an olfactory component from evening primrose in order to elicit feeding behavior (i.e., proboscis extension). Decoupling the visual and olfactory stimulus will elicit approach but not feeding.

Signaler +, Receiver −: Predators Manipulating Their Prey

Some asymmetrical signaling systems (Kostan 2002) are deceptive or manipulative where the signaler benefits and the receiver does not. For example, painted redstarts (*Myioborus pictus*) are flush-pursuing birds (Jabłoński and Lee 2006). Redstarts use visual signals accompanied by substrate vibrations to exploit their insect prey escape responses so they can pursue them in aerial chases. The ecological incentive to signal is a benefit to the sender in a predator–prey context. The use of a multimodal signal (visual + substrate vibrations) over a unimodal signal may result from sensory exploitation where the two components together flush prey more often or successfully than a unimodal signal. Another possibility is the signals are linked through morphology and one cannot be produced without the other. If sensory exploitation is involved in this system, then the signal will be in the modalities, thresholds, and cognitive abilities that the prey evolved for other purposes. This is conjecture because the necessary experiments have not been completed. Yet, sensory exploitation seems reasonable to expect since the visual stimulus alone has been linked to sensory exploitation (Jablonski 2001).

Signaler −, Receiver +: Predators Eavesdropping on Their Prey

Some signaling systems are characterized by eavesdropping receivers that benefit at the cost to the sender. Predators often eavesdrop on their prey's signals to locate them (Halfwerk et al. 2014; Rhebergen et al. 2015; Roberts et al. 2007). For example, male Túngara frogs (*Physalaemus pustulosus*) produce acoustic signals to attract females and compete with other males. A by-product of these acoustic signals is the visual signal of the inflating vocal sac. Females in this system prefer males with a linked acoustic and visual signal (Taylor and Ryan 2013; Taylor et al. 2011). Fringe-lipped bats (*Trachops cirrhosus*) also prefer the acoustic and visual components to aid in localizing their prey (Halfwerk et al. 2014; Rhebergen et al. 2015). Therefore, in this system, the multimodal signal evolved as a sexual signal, but is being eavesdropped on by predators. Male frogs use a multimodal signal over a unimodal signal because of intraspecific sexual selection (Taylor et al. 2011; Taylor and Ryan 2013). For the predators, the multimodal signal improves prey localization under various acoustic environmental conditions, suggesting the environment that these signals are produced in favors multimodal over unimodal because Túngara frogs call in choruses (Rhebergen et al. 2015). Finally, the bats have the capacity to hear the acoustic signals and use echolocation on the vocal sac to aid in localizing prey (Rhebergen et al. 2015), which is interesting because the bats are not using their visual sensory system for the visual component, but instead are using their unique sensory system (echolocation).

13.5 Conclusions

The literature on intraspecific multimodal signaling and communication is rapidly expanding. This has been driven by clearly articulated frameworks that help us understand the multimodal signaling system as a whole. We hope that by developing a similar framework for interspecific multimodal signaling systems researchers will better understand the costs and benefits that influence the adaptive value of interspecific multimodal signaling systems. Potential information is everywhere and for many species, particularly those with overlapping sensory and cognitive systems, there may be clear benefits from acquiring and using information produced by other species. And, there is often strong selection on species to exploit other species' sensory abilities for their own benefit. We hope that this framework provides structure to help understand empirical examples and provides predictions that can be empirically tested in future work. Finally, understanding interspecific multimodal signaling puts us in a better position to assess and understand how anthropogenic changes that effect multimodal signaling systems will influence these important interspecific relationships (Halfwerk and Slabbekoorn 2015; Partan 2017).

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