REVIEW ARTICLE

Eavesdropping on visual secrets

Nicholas C. Brandley · Daniel I. Speiser · Sönke Johnsen

Abstract   Private communication may benefit signalers by reducing the costs imposed by potential eavesdroppers such as parasites, predators, prey, or rivals. It is likely that private communication channels are influenced by the evolution of signalers, intended receivers, and potential eavesdroppers, but most studies only examine how private communication benefits signalers. Here, we address this shortcoming by examining visual private communication from a potential eavesdropper's perspective. Specifically, we ask if a signaler would face fitness consequences if a potential eavesdropper could detect its signal more clearly. By integrating studies on private communication with those on the evolution of vision, we suggest that published studies find few taxon-based constraints that could keep potential eavesdroppers from detecting most hypothesized forms of visual private communication. However, we find that private signals may persist over evolutionary time if the benefits of detecting a particular signal do not outweigh the functional costs a potential eavesdropper would suffer from evolving the ability to detect it. We also suggest that all undetectable signals are not necessarily private signals: potential eavesdroppers may not benefit from detecting a signal if it co-occurs with signals in other more detectable sensory modalities. In future work, we suggest that researchers consider how the evolution of potential eavesdroppers' sensory systems influences private communication. Specifically,

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we suggest that examining the fitness correlates and evolution of potential eavesdroppers can help (1) determine the likelihood that private communication channels are stable over evolutionary time, and (2) demonstrate that undetectable signals are private signals by showing that signalers benefit from a reduction in detection by potential eavesdroppers.

Keywords Private communication · Co-evolution · Vision · Eavesdropping · UV signals

Introduction

Organisms rarely signal in environments that lack potential eavesdroppers. While signalers may benefit if they communicate with intended receivers, they may suffer if their communication is detected by eavesdroppers such as parasites, predators, potential prey or rivals (Cade 1975; Endler 1980; Tuttle and Ryan 1981; Stauffer and Semlitsch 1993; Wagner 1996; Zuk and Kolluru 1998; Peake et al. 2001; Peake 2005; Kim et al. 2009; Clark et al. 2012). However, because sensory perception often varies both between species (Munz 1958; Lythgoe 1968; Menzel 1979; Marshall et al. 1999; Briscoe and Chittka 2001; Frentiu and Briscoe 2008) and among conspecifics (e.g. Jacobs 1984; Gumm et al. 2012), signalers can lower the costs imposed by potential eavesdroppers—while maintaining the benefits of communication to intended receivers—if they communicate privately with a signal that is less apparent to potential eavesdroppers than intended receivers. Because of the benefits of avoiding detection by potential eavesdroppers, private signals have been suggested in nearly every signaling modality (e.g. Williams and Dodson 1972; Hopkins and Heiligenberg 1978; Payne et al. 1986; Narins 1990; Stoddard 1999; Nakano et al. 2008; Romer et al. 2010). Notably, much of this work has focused on color signals (Denton et al. 1970; Hinton 1976, Endler 1978, 1980, 1991; Guilford and Harvey 1998; Cummings et al. 2003; Stevens and Cuthill 2007; Siebeck et al. 2010; Bybee et al. 2012) and polarization signals (Shashar et al. 1996; Chiou et al. 2008; Mathger et al. 2009; Brady and Cummings 2010). Recently, communication of this sort has gone by a variety of names including "concealed" (Shashar et al. 1996), "covert" (Warrant 2010), "hidden" (Stevens and Cuthill 2007), "private" (Endler 1983), "privileged" (Cronin et al. 2003), "secret" (Chiou et al. 2008), and "shielded" (Hastad et al. 2005); while the names are different, all of these papers discuss the biological process that we refer to here as private communication.

Most studies on private communication have focused on how private communication benefits a signaler, but private communication channels are almost certainly influenced by the evolution of signalers, intended receivers, and potential eavesdroppers. Examining a potential eavesdropper's evolution and fitness correlates can (1) help determine the likelihood that private communication channels are stable over evolutionary time, and (2) demonstrate that a signal is adaptively private, not simply less detectable to potential eavesdroppers for non-adaptive reasons. From the perspective of a potential eavesdropper, a private communication channel may pose two different selective pressures. First, such as in species-specific sex pheromone signaling (Lewis and Cane 1990) and some pollination mutualisms (e.g. Williams and Dodson 1972; Schaefer et al. 2004; Chen et al. 2009; Svensson et al. 2010), both signalers and potential eavesdroppers may benefit from private communication. Eavesdroppers may benefit in these situations by not responding to irrelevant signals. In these cases, we expect selection on potential eavesdroppers to favor the formation and persistence of private communication channels. In the second case, such

as in predator–prey interactions, potential eavesdroppers may be harmed by private communication if not detecting a signal leads to fitness-related consequences such as missed meals (Endler 1980; Cummings et al. 2003) or increased attacks by signalers (Hinton 1976). Here, we expect selection on potential eavesdroppers to oppose the formation and persistence of private communication channels. Thus, we term private communication detrimental to potential eavesdroppers as *protected private communication* to emphasize that if a signal is to remain undetectable over time, potential eavesdroppers must face evolutionary barriers that make it unlikely for them to evolve the ability to detect it.

In this review, we examine protected private communication from the perspective of potential eavesdroppers. Throughout, we integrate physiological and behavioral studies on private communication with those on the evolution of sensory systems in potential eavesdroppers. To elucidate our points, we use case studies involving vision, specifically as it relates to the detection of color and polarization signals. Visual signals tend to be displayed more continuously than other types of signals and are thus more likely to inadvertently reveal a signaler's location (e.g. Endler 1980; Lloyd and Wing 1983; Bruce et al. 2001). Signalers can voluntarily discontinue acoustic, electric, or mechanical signals, for example, when eavesdroppers are nearby, but this is less commonly the case for non-bioluminescent visual signals. Thus, we argue that signalers that depend on visual cues are particularly likely to benefit from private communication. Additionally, many researchers have studied the evolution of vision, allowing us to connect what we know about private signals to what we know about the evolution of the visual systems of potential eavesdroppers.

As a first step towards examining how the evolution of potential eavesdroppers may influence private communication channels, we discuss barriers that may allow visual protected private communication to remain private over evolutionary time scales. Although certain signals could remain private over time because of rapidly changing ecological interactions or co-evolutionary arms races, neither of these possibilities are currently supported by published research. Thus, in parts I and II of this paper, respectively, we focus our discussion on the evolutionary constraints and functional costs associated with potential eavesdroppers evolving the ability to detect particular private signals. When considering our findings from parts I and II, as well as evidence that certain potential eavesdroppers have cracked communication channels previously considered private (Stevens and Cuthill 2007; Turner et al. 2009), we conclude that it is necessary for researchers to demonstrate that signalers benefit from less detectable communication before they declare that a signal is private. In part III, we discuss how signals that are less apparent to potential eavesdroppers than intended receivers are not necessarily private, as they may contain information detectable through other sensory channels. In part IV, we describe how researchers may manipulate potential eavesdroppers to demonstrate that a signal that is less apparent to potential eavesdroppers than it is to intended receivers actually functions as protected private communication. We argue that it is important to demonstrate that a proposed protected private signal's reduced detectability is adaptive, i.e. that reduced detection by potential eavesdroppers benefits the signaler. To do this, researchers need to ask a question fundamentally different from those asked previously. Instead of only asking what a potential eavesdropper can detect, we need to ask *if a potential eavesdropper could detect the signal more clearly (up to as clearly as an intended receiver), would the signaler face fitness consequences*?

Constraints on potential eavesdroppers

Evolving extreme-wavelength sensitivity

Many researchers have suggested that signals in the ultraviolet (<400 nm; UV) or red (>570 nm) portions of the UV–visible spectrum are protected private signals (Denton et al. 1970; Hinton 1976; Guilford and Harvey 1998; Cummings et al. 2003; Siebeck 2004; Michiels et al. 2008; Bybee et al. 2012). In cases where signalers and eavesdroppers have photoreceptors with peak sensitivities to different wavelengths of light (referred to as λ_{max}), such extreme-wavelength signals can be used for protected private communication if the signal has smaller differences in luminance (achromatic contrast) or color (chromatic distance) when viewed by potential eavesdroppers than when viewed by an intended receiver (Fig. 1).

Whether a protected private signal has reduced detectability predominantly via luminance or color determines how a potential eavesdropper's visual system would need to evolve in order to better detect the signal. Because the luminance of a signal is often related to its color, many hypothesized private signals provide luminance cues that an intended receiver can detect more clearly than a potential eavesdropper. In this case, a lineage of potential eavesdroppers only needs to evolve a single appropriately sensitive photoreceptor class to crack the private signal (Fig. 1a–d). If a private signal has a similar color to its background, such as a UV marking on a violet field or an orange spot on a yellow wing, the signal cannot be detected through luminance differences. In such cases, a potential eavesdropper needs to be able to discern the color of the signal in order to detect it. To detect a color-private signal, a potential eavesdropper would need two sets of
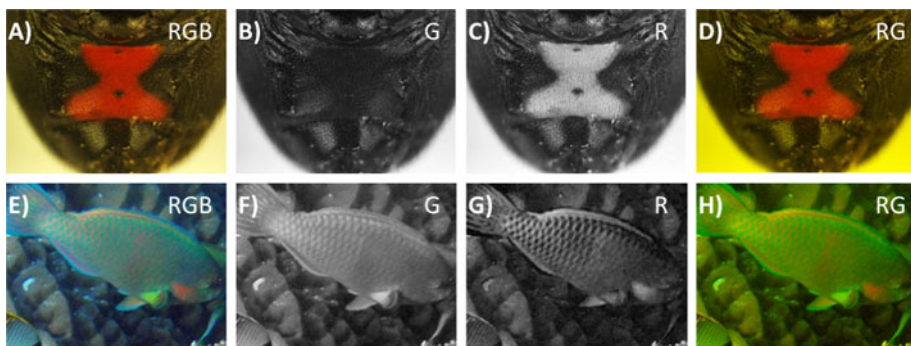
Fig. 1 Examples of a possible luminance-private and color-private signal viewed by different photoreceptor classes and combinations. *Letters* on the *top left* of each image indicate photoreceptor classes present (R = red, G = green, B = blue). *Top panels* (**a–d**) A possible luminance-private channel, the hourglass of a southern black widow spider (*Latrodectus mactans*). Note that shifting the peak sensitivity of a green photoreceptor (**b**) to longer wavelengths (**c**) reveals the signal. The color information (**d**) largely duplicates the achromatic information. *Bottom panels* (**e–h**) A possible color-private channel demonstrated by the surf parrotfish (*Scarus rivulatus*). Note that shifting a green photoreceptor (**f**) to longer wavelengths (**g**) does not reveal all of the information found in (**h**) and (**e**). In comparison, dichromatic vision (**h**) makes the patterning of the fish obvious to a viewer. Adding a third photoreceptor class (**e**) reveals even more spatial information. **a** and **e** are unmodified images. Other images were modified in Adobe Photoshop by removing the relevant channels. Because camera sensors generally have a much narrower spectral absorbance curve than biological photoreceptors, the effects of privacy are exaggerated by the images. The intent of the figure is to show the differences in the evolutionary pressures imposed on potential eavesdroppers, and not to suggest that formal modeling suggests that either of the examples used are actually private signals

photoreceptors that differ in peak sensitivity, yet are simultaneously sensitive to both signal and background (Fig. 1e–h). Evolving two sensitive photoreceptor classes usually involves opsin genes that duplicate and then diverge so that the photopigments they encode have different spectral sensitivities (Yokoyama 1994, 2000; Dulai et al. 1999; Spaethe and Briscoe 2004; Parry et al. 2005). Alternatively, previously existing opsins may be co-opted for new functions (Plachetzki and Oakley 2007).

Spectral sensitivity can by shifted by relatively small evolutionary changes (Table 1). For example, single amino acid substitutions can shift the spectral sensitivity of opsins enough to change the perception of some protected private signals in the UV or red wavelengths. In birds (415–368 nm; Yokoyama et al. 2000) and fruit flies (414–359 nm; Salcedo et al. 2003), a single amino acid substitution can shift peak sensitivity into the UV and possibly reveal private signals based on UV wavelengths. Likewise, in both invertebrates (e.g. Briscoe 2001; Frentiu et al. 2007) and vertebrates (e.g. Neitz et al. 1991; Chan et al. 1992; Yokoyama and Radlwimmer 2001), three to six amino acid substitutions can shift a green ($\lambda_{max} = \sim 530$ nm) sensitive photopigment towards wavelengths ($\lambda_{max} = \sim 560$ nm) that will improve red discrimination. Extreme-wavelength vision can also evolve through changes to a photoreceptor's chromophore or through the addition of filters that restrict the wavelengths of light reaching certain photoreceptors. Some animals, including the winter crayfish (*Procambarus clarkii*; Girard, 1852), firefly squid (*Watasenia*

Table 1 Examples of spectral sensitivity changes from a variety of taxa

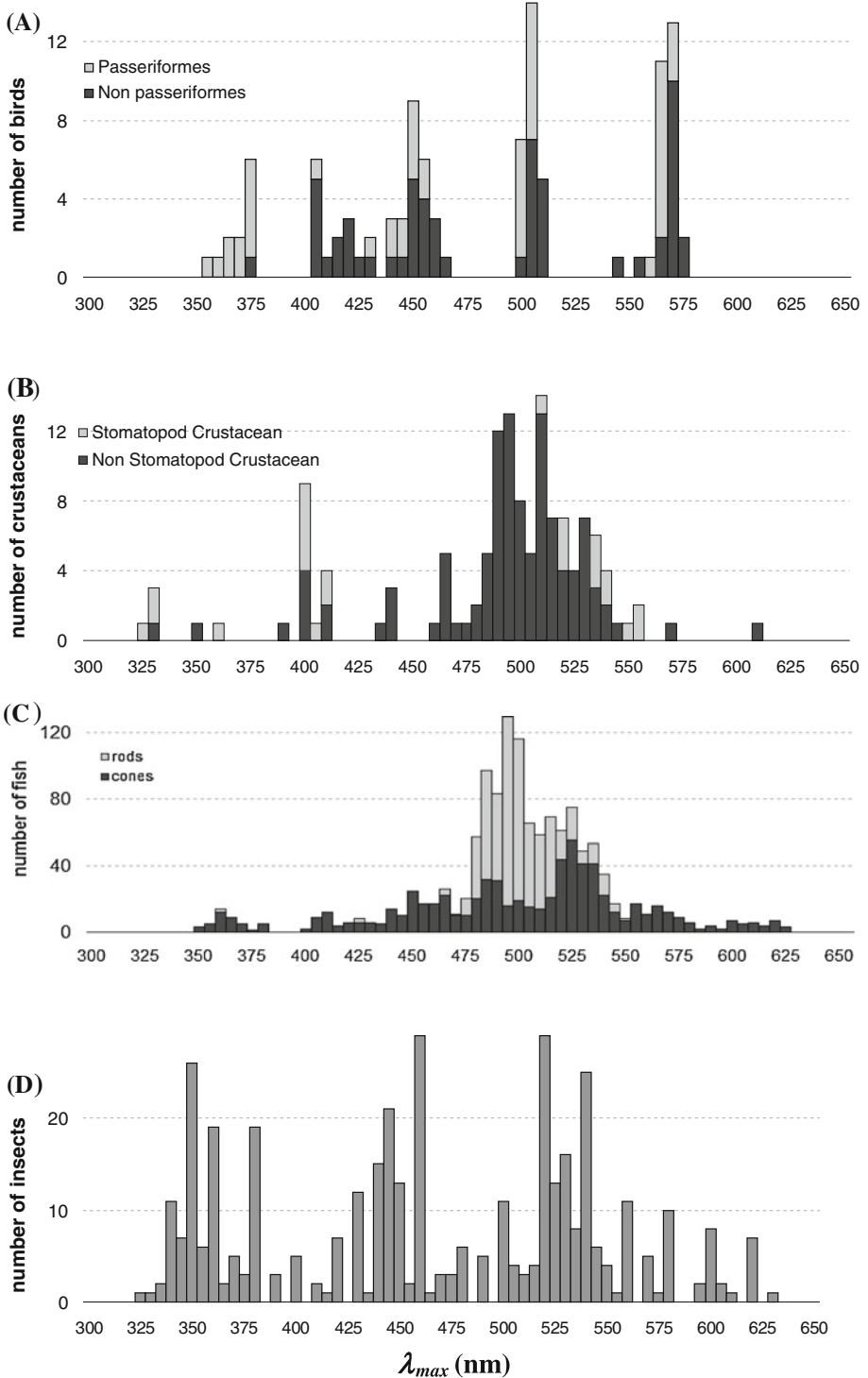| Type	λ_{max}	λ_{max}'	Note	Species	Reference
Opsin change					
Single amino acid substitution	415	369 (1)	V-UV switch	*Gallus gallus*	Yokoyama et al. (2000)
Single amino acid substitution	347	420 (1)	V-UV switch	*Drosophila melanogaster*	Salcedo et al. (2003)
Multiple amino acid substitutions	359	414 (1)	V-UV switch	*Mus musculus*	Shi et al. (2001)
Three amino acid substitutions	530	562 (2,3)	G-R switch	*Homo sapiens*	Neitz et al. (1991)
Multiple amino acid substitutions	520	575 (3)	G-R switch	*Papilio xuthus*	Briscoe (2001)
Chromophore change					
Chromophore substitution	484	470, 500 (2)		*Watasenia scintillans*	Seidou et al. (1990)
Chromophore substitution	533	567 (2)	G-R switch	*Procambarus clarkii*	Zeiger and Goldsmith (1989)
Chromophore substitution	498	515 (2)		*Salaria pavo*	White et al. (2004)
Filter					
Screening pigment	360	400 (2)	UV-V switch	*P. xuthus*	Arikawa et al. (1999)
Screening pigment	500	550 (2)	G-R switch	*W. scintillans*	Michinomae et al. (1994)

Changes in opsin, chromophore, or filter can result in a shift to red sensitivity, while changes to opsin or loss of a filter can result in UV vision. V = violet, G = green, R = red. λ_{max} and λ_{max}' represent two different sensitivities found in (1) experimental mutants, (2) different photoreceptor classes in the same species or (3) different species

scintillans; Berry, 1911), and peacock blenny (*Salaria pavo*; Risso, 1810), combine different chromophores with the same opsin protein to shift the λ_{max} of photoreceptors by 20–35 nm (Table 1). Animals may also use filters (e.g. lens compounds, oil droplets, or overlying photoreceptors) to alter the spectral sensitivity of photoreceptors (Bowmaker and Knowles 1977; Douglas and Marshall 1999). As with changes to opsin proteins or chromophores, changes in filters may reveal private signals by shifting a photoreceptor's λ_{max} to the red or UV portions of the visible light spectrum (Table 1).

Comparative surveys of species-rich lineages provide additional evidence that the spectral sensitivities of photoreceptors often shift in ways that can potentially reveal extreme-wavelength protected private signals. For example, four recent meta-studies demonstrate that photoreceptors that are primarily sensitive to UV or red light can be found in birds (Frentiu et al. 2007), crustaceans (Marshall et al. 1999), fish (NESCent working group on the evolution of vertebrate visual systems), and insects (Briscoe and Chittka 2001) (Fig. 2). UV vision ($\lambda_{max} < 400$ nm) is also found in all five classes of vertebrates [amphibians (e.g. Deutschlander and Phillips 1995); birds (reviewed in Frentiu and Briscoe 2008); fish (reviewed in Losey et al. 1999); mammals (e.g. Jacobs et al. 1991); and reptiles (e.g. Ammermuller et al. 1998)]. Further, researchers have shown that UV sensitivity has been lost or gained at least eight times in birds alone (Carvalho et al. 2007; Odeen et al. 2011). UV vision is also common in invertebrates, as it is found in most insects (Briscoe and Chittka 2001), some arachnids (e.g. Devoe 1975; Walla et al. 1996), certain crustaceans (Frank and Case 1988; Marshall et al. 1999; Frank et al. 2012), the giant clam *Tridacna maxima* Röding, 1798 (Wilkens 1984) and the annelid worm *Torrea candida* Delle Chiaje, 1841 (Wald and Rayport 1977). Similarly, red-sensitive photoreceptors ($\lambda_{max} > 550$), although less common, occur in all vertebrate classes, including amphibians (Perry and McNaughton 1991), birds (Frentiu and Briscoe 2008); fish (Loew and Lythgoe 1978), mammals (Neitz et al. 1991), and reptiles (Loew et al. 2002). Red-sensitive photoreceptors are also found in numerous invertebrates, such as insects (Briscoe and Chittka 2001), certain arachnids (Yamashita and Tateda 1976), certain crustaceans (Marshall et al. 1999), and annelids (Wald and Rayport 1977). Evidence thus suggests that a wide range of metazoans see in the extreme-wavelengths and that potential eavesdroppers may face few lineage-specific evolutionary constraints to detecting extreme-wavelength protected private signals.

In certain cases, researchers have shown that separate eavesdropping lineages have cracked the same protected private signal through different mechanisms. One case study involves the detection of the bioluminescence produced by three separate genera of predatory dragonfish (*Aristostomias*, *Malacosteus*, and *Pachystomias*). These species produce far red ($\lambda_{max} \approx 700$ nm) bioluminescence that may function both as a protected private signal between conspecifics and as a private searchlight to detect prey in the deep sea where red light is uncommon (Denton et al. 1970; Levine et al. 1980; Widder et al. 1984; Partridge and Douglas 1995). However, more than 40 years after a private function for the far red bioluminescence of dragonfish was first suggested, researchers have found evidence that at least two different fish species preyed upon by dragonfish have possibly

(A) number of birds — Passeriformes, Non passeriformes

(B) number of crustaceans — Stomatopod Crustacean, Non Stomatopod Crustacean

(C) number of fish — rods, cones

(D) number of insects

λ_{max} (nm)

cracked the private signal. The first species, *Myctophum nitidulum* (Garmin 1899), has red-shifted a visual pigment (to a λ_{max} of 522 nm) via a chromophore substitution coupled with a change in the opsin protein (Hasegawa et al. 2008). A visual pigment maximally sensitive to 522 nm light is not ideal for detecting the far red bioluminescence of dragonfish, but models show that the red-sensitive photoreceptors can detect far red bioluminescence at distances up to one meter away (Turner et al. 2009). The second potential eavesdropper species, *Bolinichthys longipes* (Brauer 1906), detects far-red bioluminescence using the same mechanism employed by the dragonfish themselves—a chlorophyll-derived sensitizing pigment with a λ_{max} of ≈ 670 nm (Turner et al. 2009).

Over evolutionary time, the spectral sensitivities of photoreceptors appear to be relatively unconstrained within the UV-visual spectrum. However, the long-wavelength end of this spectrum deserves special attention: no known photoreceptors have a λ_{max} greater than ~630 nm, even though long-wavelength light is abundant in many habitats (Johnsen 2012). This upper limit on spectral sensitivity may be due to thermal noise—the activation of photoreceptors by heat and not light (De Vries 1943; Barlow 1956; Ala-Laurila et al. 2004a). In general, there is an inverse relationship between the λ_{max} of a photopigment and its activation energy: photopigments sensitive to long-wavelength light have a relatively low activation energy and are thus more susceptible to thermal noise (Ala-Laurila et al. 2004a, b; Pahlberg et al. 2005; Luo et al. 2011). Because animals cannot discriminate between photoreceptors triggered by light and photoreceptors triggered by heat, thermal noise may make photoreceptors sensitive to long-wavelengths too unreliable for vision.

Concerning protected private communication, we hypothesize that animals differ in their ability to limit thermal noise (Ala-Laurila et al. 2004b) in ways that influence whether or not they can gather information about long wavelength light. If we are correct, signalers may be able to exploit differences between themselves and potential eavesdroppers in ways that make protected private communication stable over evolutionary time. We hypothesize that one species could detect long-wavelength light that another species could not due to differences in any of the following: (1) opsin protein structure (Ala-Laurila et al. 2004a, b, Luo et al. 2011), (2) body temperature [hotter eyes generally have more thermal noise (Ashmore and Falk 1980; Aho et al. 1988, 1993; Reilly and Thompson 2007)], or (3) eye size [smaller eyes are generally more susceptible to thermal noise because they have worse signal to noise ratios (Warrant and Locket 2004)]. We predict that small eyes operating at high temperatures will have the most trouble with thermal noise and will thus be the least likely to contain photoreceptors sensitive to long-wavelength light. However, more work is needed to test this hypothesis and to examine if temperature-related constraints on spectral sensitivity may be exploited for protected private signals involving far-red light.

Evolving polarization sensitivity

Signals involving polarized light are potentially effective for protected private communication because photoreceptor morphology differs between invertebrates and vertebrates in ways that give only invertebrates an innate potential for polarization sensitivity (Moody and Parriss 1961; Land and Nilsson 2002; Horváth and Varjú 2004; Appendix A in ESM). Based on typical photoreceptor geometry, researchers have hypothesized that organisms may be able to signal privately to polarization-sensitive invertebrate receivers without polarization-insensitive vertebrates being able to evolve the ability to detect the signal (Shashar et al. 1996; Mathger and Hanlon 2006; Douglas et al. 2007; Mathger et al. 2009; Brady and Cummings 2010).

Polarization sensitivity appears to be far more common in invertebrates than vertebrates, but it has been reported that certain vertebrates [e.g. amphibians (Adler and Taylor

1973; Auburn and Taylor 1979), birds (Kreithen and Keeton 1974; Muheim 2011), and fish (Waterman and Forward 1970; Kamermans and Hawryshyn 2011)] may detect the polarization of light through a variety of mechanisms (Table 2). Despite these reports, researchers have yet to reach a consensus on how many vertebrates are polarization-sensitive because behavioral investigations of polarization sensitivity are prone to intensity artifacts that may cause false positive reports (Horváth and Varjú 2004), and research on polarization signals has typically been biased towards invertebrates. Polarization sensitivity has, however, been demonstrated convincingly in at least one vertebrate family (Engraulidae; Fineran and Nicol 1976; Flamarique et al. 1998; Flamarique and Harosi 2002). Because some of the mechanisms through which vertebrates may obtain polarization sensitivity require relatively complicated optics, we predict that vertebrates may pay higher functional costs for polarization vision than invertebrates. In this sense, vertebrates may not be constrained from evolving polarization sensitivity, but constraints on photo-receptor morphology may lead to greater costs of polarization sensitivity in vertebrates than in invertebrates (part II; Table 2).

Conclusion

In this section, we suggested that published studies find few taxon-based constraints that would keep potential eavesdroppers from evolving the ability to detect common visual protected private signals. Many lineages of animals have separately evolved both red and

Table 2 Although invertebrates often possess an innate polarization sensitivity that vertebrates lack, vertebrates have been reported to detect polarization by a variety of different mechanisms

Proposed mechanism	Proposed in	Possible additional functional costs relative to mechanism I	Reference
I. Alignment of opsins (and thus the associated chromophores) within fingerlike projections of cell membrane	Invertebrates		Moody and Parriss (1961)
II. Polarizing (i.e. dichroic) filters between incident light and photoreceptors	Universal	Negligible	Johnsen (1994)
III. Tilted photoreceptors that mimic the mechanism found in invertebrates	Anchovies (*Anchoa*)	Requires more retinal space	Fineran and Nicol (1976)
IV. Polarization-dependent reflections within double cones	Amphibians, birds, fish, reptiles	Requires more retinal space, heightens metabolic demands	Cameron and Pugh (1991)
V. Polarization-dependent reflections within double cones that direct light toward a third photoreceptor	Rainbow trout (*Oncorhynchus mykiss*)	Requires more retinal space, heightens metabolic demands, reduces photon-catch	Flamarique et al. (1998)
VI. Alignment of opsins in photoreceptors, presumably mediated by cytoskeletal components	Universal	Negligible	Roberts et al. (2011)

In comparison to the most common mechanism used by invertbrates to detect polarized light (I), many of the potential vertebrate mechanisms may impose higher functional costs

UV vision, and polarization sensitivity has been documented in a wide range of invertebrates and satisfactorily demonstrated in at least one vertebrate family. Thus, we suggest that although potential eavesdroppers could be constrained from detecting a visual private signal in certain cases, many potential eavesdroppers may be able to evolve the ability to detect certain proposed private communication channels.

Functional costs of detecting protected private signals

Regardless of evolutionary constraints, a signal may remain private over evolutionary time if the ability to detect it is associated with net functional costs to potential eavesdroppers. In general, new visual abilities come with functional costs: improvements to one aspect of vision generally cause detriments to others. For example, the evolution of color vision can lower sensitivity (Clarke 1936; Munz 1958), coarsen spatial resolution (Lind and Kelber 2011), and require compensation for longitudinal chromatic aberration (Blest et al. 1981; Kroger et al. 1999; Kroger and Gislen 2004). Some of these costs are reduced in larger eyes. With a larger eye, certain visual abilities can be added or improved without detriment to others (Land and Nilsson 2002). However, larger eyes may require (among other demands) larger optical lobes for information processing, a larger head, and increased amounts of ATP (Laughlin et al. 1998; Laughlin 2001; Niven et al. 2007). Thus, potential eavesdroppers likely face functional costs if they evolve the ability to detect a protected private signal. If these costs outweigh the benefits a potential eavesdropper would gain from detecting a signal, the signal may remain private over evolutionary time.

Three particular functional costs merit further discussion because they may tend to pose a greater evolutionary hurdle for potential eavesdroppers than for intended receivers, and thus may be exploited for protected private communication. These costs are associated with: (1) vertebrates detecting polarized light; (2) UV vision; and (3) animals detecting signals that rarely occur in nature, such as circularly polarized light.

Costs of polarization vision may vary by evolutionary lineage

Vertebrates may pay a higher cost to detect private polarization signals because polarization sensitivity may rely on more complicated optics in vertebrates than in invertebrates (part I). These heightened costs may include increased retinal area, lower photon-catch, and higher metabolic demand (Table 2). However, if vertebrates can achieve polarization sensitivity by aligning photopigments along a common e-vector in their photoreceptors (Roberts et al. 2011) or by placing polarization filters in front of certain photoreceptors (Johnsen 1994), the costs of polarization sensitivity may be similar for both vertebrates and invertebrates. No vertebrate has yet been shown to achieve polarization sensitivity by these means, making the lineage specific costs associated with evolving polarization sensitivity an intriguing issue for future research.

UV-specific costs

UV-specific costs have led some researchers to suggest that UV light may be used as a protected private signal more often than red light (Cummings et al. 2003; Siebeck 2004). Evolving UV vision not only imposes the general costs associated with adding a new color channel, but may incur additional costs associated with radiation damage and UV-scattering (Leech and Johnsen 2009). For example, costs associated with color vision, such as

longitudinal chromatic aberration, may be heightened for detecting UV light when compared to detecting light with longer wavelengths because UV light tends to be farther away from the peak sensitivity of most animal's photoreceptors than long wavelength light. These costs are best illustrated by animals such as primates (Wood and Truscott 1993) and some fish (Siebeck and Marshall 2001) that have UV-absorbing filters that prevent light with wavelengths shorter than $\sim$400 nm from entering their eyes. These filters are even found in cases where animals possess photoreceptors with some sensitivity to UV radiation (such as the blue-sensitive cones in the human eye).

UV radiation can damage eyes by inhibiting protein synthesis and causing cataract formation (Zigman and Bagley 1971; Ham et al. 1976; Collier et al. 1989; De Mora et al. 2000). However, such damage requires substantial amounts of UV radiation, so UV costs are highest in terrestrial or shallow aquatic habitats where UV radiation is abundant. Because UV damage is cumulative, animals with longer lifespans likely suffer more from UV radiation than short-lived animals. This might allow an individual to use a UV signal to communicate privately with short-lived receivers without longer-lived potential eavesdroppers evolving the ability to detect it. In cases where top predators live longer than other species (Shuter et al. 2005), this may allow species lower on the food chain to use a stable protected private signal against top predators.

In addition to radiation damage, the physical properties of UV light may reduce eavesdropping in two distinct ways. First, in certain environments, UV light is attenuated more quickly than visible light. In these environments, UV signals may degrade quickly with distance; thus, individuals could communicate with organisms nearby without fear of those farther away detecting the signal (Siebeck 2004). Second, if UV light enters the eye, the visual contrast of all signals may decrease if the photoreceptors of the eye also receive spacelight—i.e. photons originally emitted from the signal's background that were then scattered into the path of the signal (e.g. Fig. 5 in Johnsen 2007). If an eye does not restrict UV light from reaching the retina, all photoreceptors would respond to UV spacelight because all photoreceptors have a secondary sensitivity peak in the UV in addition to their primary sensitivity peak (Govardovskii et al. 2000).

In certain habitats, however, the UV-specific contrast attenuation described above may not be significant over distances at which potential eavesdroppers can detect signalers. For example, if an animal in dry air views a target 100 meters away, similar amounts of UV (97.5 %; 400 nm) and long-wavelength photons (98.8 %; 700 nm) reach its eyes (Bass and Optical Society of America 1995). In this case, it is likely that the slightly increased attenuation of UV light is irrelevant. In some aquatic environments, the wavelength-dependent bias in attenuation may be greater, both because attenuation at all wavelengths is greater and because light absorption is often far higher at UV wavelengths than at other wavelengths. Because natural waters vary in how much light they scatter and absorb, it is necessary to examine each environment separately before assuming that UV signals will not propagate as far as longer-wavelength signals. In some cases, underwater contrast may actually be higher at UV wavelengths due to the spectrum of the illumination, the spectral reflectance and size of the signal, and—for viewing in directions other than horizontal—the wavelength dependence of the difference between the diffuse and beam attenuation coefficients (Lythgoe 1968; Lythgoe and Partridge 1991; Marshall 2000; Johnsen 2002).

Net costs vary by the rarity of signal properties

Evolving the ability to detect a particular protected private signal may provide additional benefits for an eavesdropper. For example, if a predatory bird evolves UV vision in order to

better detect the UV plumage of a prey bird, this new ability may also benefit the predatory bird by making the urine of rodents (Viitala et al. 1995) and the plumage of other birds (Hastad et al. 2005) more obvious. Conversely, a protected private signal that uses a form of information found rarely in nature may minimize the net benefit a potential eavesdropper may gain from evolving the ability to detect it. Thus, we hypothesize that the ability to detect a novel sensory signal might be relatively costly to an eavesdropper when it cannot be used for other tasks.

Circularly polarized light is one example of a signal that is rarely encountered in nature. Circularly polarized light has only been identified in light reflected from the exoskeletons of certain arthropods, such as stomatopod crustaceans and scarab beetles (Neville and Caveney 1969; Chiou et al. 2008), the bioluminescence of some *Photuris* fireflies (Wynberg et al. 1980), and in minor amounts at water–air interfaces (Horváth and Varjú 2004). Potential eavesdroppers might be less likely to evolve sensitivity to circularly polarized light because this ability lacks value for other visual tasks. To date, researchers have only demonstrated sensitivity to circularly polarized light in two groups of animals—stomatopod crustaceans (Chiou et al. 2008) and scarab beetles (Brady and Cummings 2010)—and have suggested a protected private communication function for circularly polarized light in both.

Conclusion

If a lineage of potential eavesdroppers improves their detection of a private signal, they likely will increase their functional costs relative to prior to being able to detect the private signal. While evolving the ability to detect any private signal may increase functional costs, the costs associated with polarized signals, UV signals, and signals found rarely in nature (such as circularly polarized light) may provide protection against some potential eavesdroppers evolving the ability to detect a protected private signal. However, increased costs in these three cases may not always apply, and researchers should examine their specific system with care.

Multimodality of protected private signals

Regardless of the constraints and functional costs associated with evolving the ability to detect a protected private signal, certain hypothesized private signals may not be private because they provide eavesdroppers with detectable information via other sensory modalities. When producing an acoustic signal, for example, a signaler may also move or vibrate (e.g. Parri et al. 1997; Taylor et al. 2007). Even if an eavesdropper cannot detect the acoustic signal, the byproducts of signaling may give an eavesdropper all the information that it needs to detect the signaler. This scenario is especially likely if the eavesdropper only needs to locate a signaler and does not need to interpret other pieces of information carried by the signal. While in some cases the signal may be much more obvious than its byproducts, in other cases researchers need to treat a signal as multimodal and examine all channels through which potential eavesdroppers may detect both the signal and the act of signaling.

Extreme-wavelength signals are one example of a multimodal signal. Like all color signals, extreme-wavelength signals may provide information about both luminance and color. Their privacy will depend on both parameters: an extreme-wavelength signal may be private when either its luminance contrast or color contrast is lower to a potential

eavesdropper than an intended receiver (Fig. 1). In songbirds, for example, Stevens and Cuthill (2007) noted that although the UV plumage regions modeled by Hastad et al. (2005) provide color differences that may be more apparent to conspecifics than potential predatory eavesdroppers, the UV plumage also provides luminance differences that are easily detectable by non-UV sensitive predators. Because different colors may provide different luminance levels, we need to simultaneously consider the color and luminance of hypothesized protected private signals; just because a potential eavesdropper cannot discriminate a certain color does not mean they cannot detect a signal via luminance differences.

Like extreme-wavelength signals, polarized signals may be detected through multiple channels: the structures that produce polarized signals (Land 1972; Seago et al. 2009) often simultaneously produce saturated colors that may provide potential eavesdroppers with detectable color and luminance cues (e.g. Fig. 3; Sweeney et al. 2003; Douglas et al. 2007). If polarized signals are used by signalers to reduce the likelihood of detection by potential eavesdroppers, these polarized patterns must not co-occur with detectable color or luminance patterns. At the very least, the color or luminance patterns should be less obvious to potential eavesdroppers than the polarization patterns.

The neotropical butterfly *Heliconius cydno* (Doubleday, 1847) is one example of an animal with a polarized signal that potentially provides information in multiple channels.
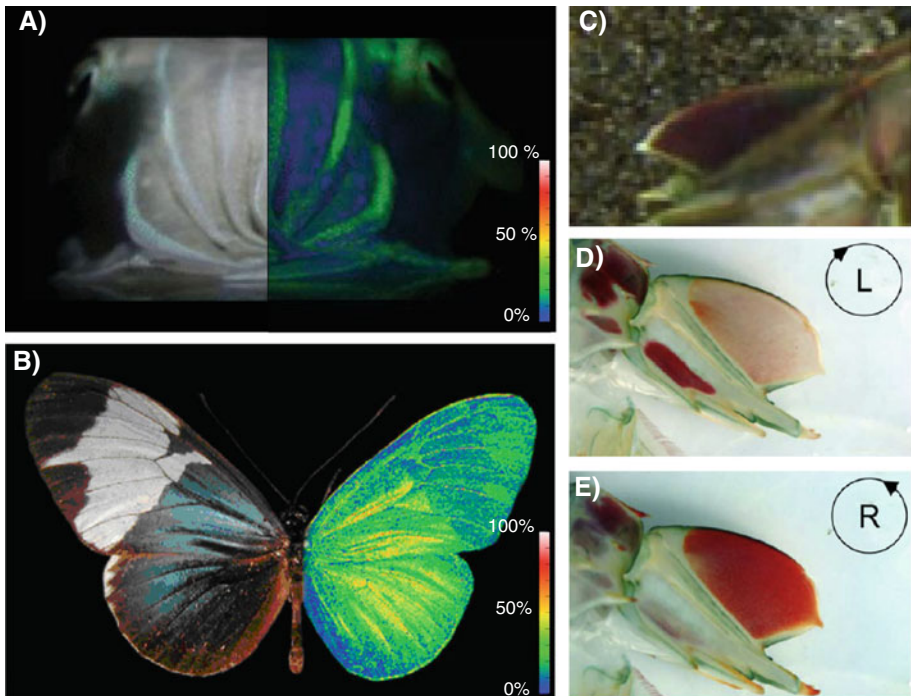

Fig. 3 The color components of polarized signals. Images of **a** the cephalopod *Sepia officinalis* and **b** the butterfly *H. cydno*. The *left hand side* of each image shows a color photograph of the animal, while the right is a false-colored polarization image that shows degree of polarization. **c–e** The circularly polarized keel of a stomatopod crustacean, viewed under normal conditions and left- and right-handed polarized light. Note that in all three animals strong chromatic or achromatic components accompany polarized reflectance. Images from **a** (Chiou et al. 2007), **b** (Douglas et al. 2007), **c–e** (courtesy of Christine Huffard)

H. cydno likely uses both its color (Mallet 1993) and polarization (Sweeney et al. 2003) patterns as a signal to mates (Fig. 3b); however, researchers have suggested that the polarization component may function as a private signal that predatory birds cannot detect (Douglas et al. 2007). To test a single case of the chromatic components of polarized signals, we modeled the polarization distance, color distance, and luminance contrast between two regions of the wings of the neotropical butterfly *H. cydno* (For full methods and definitions see Appendix B in ESM). If the polarized signal is private and reduces detection by potential eavesdroppers, we would expect the polarization pattern to be more distinct than both the color and luminance patterns. However, when viewing isolated components of *H. cydno's* appearance (Fig. 4), we find that the wing's polarization pattern (Fig. 4b; polarization distance = .276) is accompanied by color patterns (Fig. 4c; color distance = .176) and luminance differences (Fig. 4d; ∼2.5 times brighter). These color and luminance differences make it unlikely that *H. cydno* utilizes polarized reflectance as a protected private signal.

The example of *H. cydno* suggests that some polarization-blind eavesdroppers may be able to detect certain polarized signals. In order to signal privately via polarized signals, an animal needs to match its polarized signal's chromatic and achromatic reflectance to the background. For example, the scarab beetle *Chrysina gloriosa* (LeConte 1854), has a green exoskeleton that produces polarized reflections that may spectrally match the juniper foliage on which this animal lives (Brady and Cummings 2010). While the privacy of some polarized signals may be limited to specific backgrounds, certain cephalopod mollusks (e.g. squid, octopus, and cuttlefish) possess anatomical features that could produce private polarized signals against a variety of backgrounds. Many cephalopods have two different layers of cells that control their dermal coloration. The inner layer, packed with iridophores, reflects polarized light at short wavelengths (Mathger et al. 2009). These iridophores are covered by an outer cell layer that contains chromatophores—pigment-containing sacs that expand and contract via neural control (Florey 1969). Notably for protected private communication, light passing through the chromatophores changes in color, but not polarization (Mathger and Hanlon 2006). Theoretically, a cephalopod's iridophores could produce polarized signals whose color could be altered by the chromatophores to match different substrates (Mathger et al. 2009). While it is an intriguing hypothesis, researchers currently lack behavioral data demonstrating (1) that cephalopods actually mask the chromatic components of polarized signals and (2) that the ability to mask polarized signals in this manner is adaptive.

Demonstrating an adaptive value for reduced detection of a signal

In order to show that a signal is private, we need to demonstrate that its secrecy is adaptive. Here we discuss four ways to test whether the reduced detection of a proposed private signal benefits a signaler. These methods include: (1) manipulating the signal; (2) manipulating a potential eavesdropper's perception of the signal; (3) removing potential eavesdroppers from a population of signalers and measuring whether selective pressures on the signaler decrease; or (4) manipulating the numbers of potential eavesdropper in different populations of signalers and comparing how the signal changes over time between populations (Table 3). Note that for many of these methods, researchers need to follow signalers or potential eavesdroppers over long periods of time. The exact lengths of time required will depend on whether the expected changes occur via phenotypic plasticity or are evolved responses.
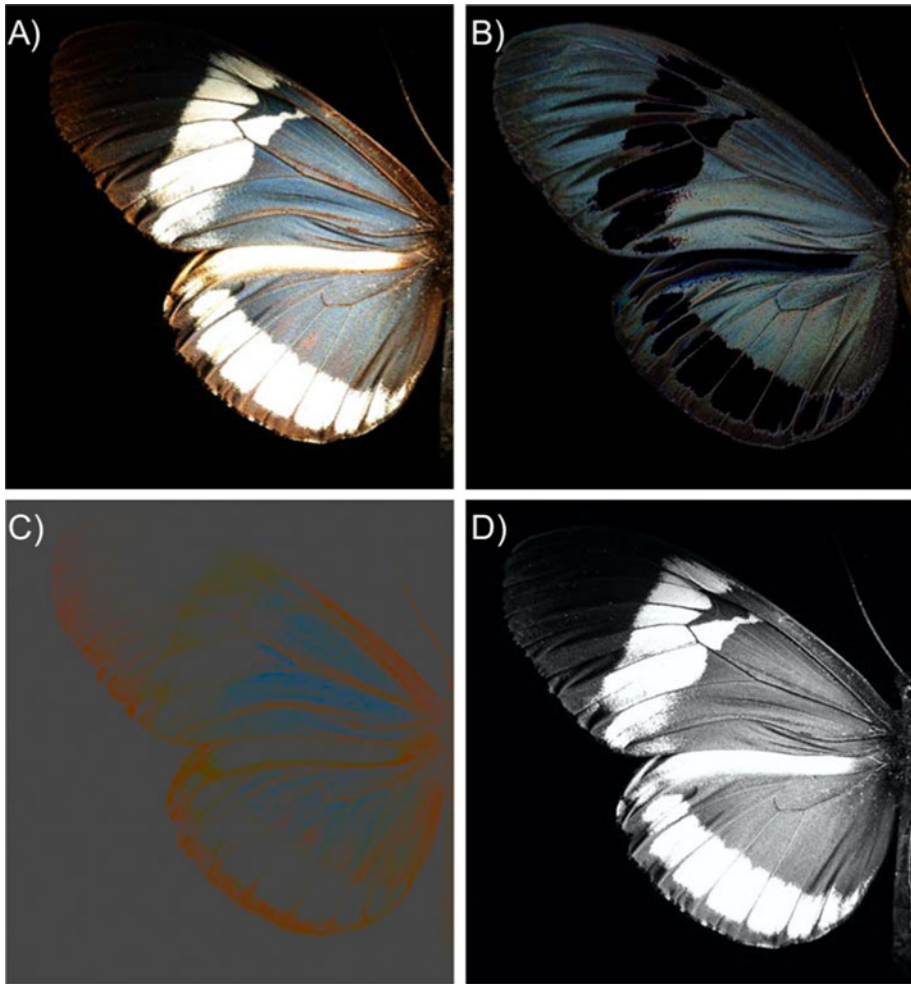
Fig. 4 Multiple channels of reflectance information in *H. cydno*. **a** An unmodified wing of *H. cydno*. **b** Polarization image of *H. cydno* multiplied by the normal image to show degree of polarization as a function of color. Full polarization views as white, 0 % polarization is *black*. **c** Color-only image where achromatic information has been removed. **d** Achromatic-only image (*black–white*). Note that the wing's polarization differences (**b**) strongly correlate with achromatic differences (**d**) that would be detectable by a polarization-blind eavesdropper. Original photo adapted from Sweeney et al. (2003)

Via signal manipulation experiments, we can alter a proposed private signal to make it more obvious to a potential eavesdropper. Instead of only asking what a potential eavesdropper can detect, manipulating the signal asks: if a potential eavesdropper could detect a signal more clearly (up to as clearly as an intended receiver), would the signaler face fitness consequences? Depending on the modality of the signal and the sensory processing of the potential eavesdropper, the exact methods will vary. If a signaler suffers from increased eavesdropping after its signal has been manipulated, we would conclude that the signal has an adaptive private value. However, the above methods may give us false negative results: potential eavesdroppers may need time to either learn, or evolve, the behavioral capacity (independent of physiology) to use the information present.

Table 3 Researchers can use a variety of methods to demonstrate that the reduced detection by eavesdroppers of a hypothesized protected private signal is adaptive

Method	Expectation if signal is private	Pros	Cons
1. Manipulate the signal	More conspicuous signals negatively impact factors associated with a signaler's fitness	Signals can be switched from one modality to another. Can fully demonstrate that the privacy of a signal is adaptive	May give false negative results if potential eavesdroppers do not respond to an unfamiliar modified signal, or do not have enough time to evolve the ability to detect it
2. Manipulate the potential eavesdropper's perception	If a potential eavesdropper and intended receiver have the same sensory abilities, the signaler's fitness will decrease	Can demonstrate an adaptive function for a private signal	Requires knowledge of the underlying sensory genetics of the potential eavesdropper
3. Remove the potential eavesdropper	A signal will become more genetically and/or phenotypically diverse when potential eavesdroppers are absent	May be less intensive than methods 1 and 2	May give false negative results if other forces are maintaining the signal's form. Dependent on generation time of signaler. Cannot fully rule out other factors responsible for a signal's form. Pleiotropy may lead to false results
4. Compare and manipulate different populations containing signalers	Signals will be more obvious to potential eavesdroppers in populations where potential eavesdroppers are absent	May be less intensive than methods 1 and 2	Cannot fully rule out other factors responsible for a signal's form. Pleiotropy may lead to false results

If signals in differing modalities are processed in similar ways, we could convert a signal from one modality to another. For example, we could utilize the similarities between polarization and color processing to convert a polarized signal into a color signal. This is feasible because it appears that color and polarization processing are similar in that both can be represented as the responses of two or more photoreceptor classes to a stimulus (Bernard and Wehner 1977; Glantz 2001; Kleinlogel et al. 2003). However, differences between color and polarization processing could alter the results. Additionally, no signal is completely isolated from its environment. A polarization signal may contrast highly with its background relative to other polarization signals in the scene. If this polarization signal is then converted into a chromatic one, however, the new signal may have a low contrast relative to the contrasts occurring in the environmental background.

Instead of manipulating signals, researchers may soon be able to modify a potential eavesdropper's ability to detect a particular signal. For example, molecular biologists can already manipulate the spectral sensitivities of photopigments through targeted alterations to the amino acid sequences of opsin proteins (e.g. Yokoyama and Radlwimmer 2001). Given decreased costs associated with gene discovery and improved methods for altering

gene expression in vivo, it soon may be possible to create potential eavesdroppers with sensory abilities that mimic those of intended receivers. Doing so would require: (1) identifying the genes in a potential eavesdropper responsible for detecting a particular signal; (2) modifying these genes so that the resulting proteins have the desired functional characteristics; and (3) expressing the new genes in place of the old ones in living individuals. These modified eavesdroppers could then be used in behavioral experiments to determine if signalers suffer fitness consequences when their signals are viewed by potential eavesdroppers with sensory capabilities similar to intended receivers.

In a third method for testing whether the reduced detection of a particular signal by eavesdroppers is adaptive, we propose that researchers track how signals change over time when potential eavesdroppers are removed from an environment. If a signal is private and relevant eavesdroppers are absent, we have removed the selective pressure on the signal to remain less detectable. Without this pressure, genetic drift (or natural selection if the private qualities of a signal are associated with fitness costs) and differences in expression may cause signals to become more detectable than they were when potential eavesdroppers were still present. Within a population, we would also expect that microhabitats without potential eavesdroppers contain a greater variation in signals than environments where potential eavesdroppers are still present (McShea and Brandon 2010). However, this method may fail to support an existing private function for a signal if other selective pressures (such as sexual selection) maintain the signal's form. Additionally, for many animals with long generation times, researchers may need to observe populations (and constantly ensure potential eavesdroppers are still not present) for longer than is experimentally feasible in order to detect a change in a potentially private signal.

Finally, researchers can combine a comparative approach with potential eavesdropper manipulation to provide evidence that a particular signal is private (e.g. Endler 1980). This fourth experimental method requires both (1) comparing natural populations to establish the private function of a signal in nature, and (2) experimental manipulations that examine whether potential eavesdropper occurrence, and not another factor, is the mechanism responsible for the reduced detectability of a signal. For example, if the occurrence of an eavesdropping predator varies between isolated populations of signalers, we would first compare signals between isolated populations. On average, we would expect signals to be less detectable to potential eavesdroppers in populations where potential eavesdroppers are present than where they are absent. However, this method does not rule out other factors (e.g. temperature, other eavesdroppers, and habitat) that may differ by population and could be correlated with both the presence of potential eavesdroppers and the detectability of the signal. To partially rule out these factors, we could introduce potential eavesdroppers to some isolated prey populations. In populations where potential eavesdroppers were introduced, we would expect selection to favor signals that have reduced conspicuousness in characteristics that potential eavesdroppers can detect. This approach does not necessarily prove that a signal is private. Potential eavesdroppers may alter their environment in other ways besides eavesdropping, such as changing the total species composition (Paine 1966). Therefore, differences observed between treatments may be a result of these factors and not to reduced rates of eavesdropping.

In short, by manipulating potential eavesdroppers and/or signalers, researchers can test whether a proposed protected private signal benefits the signaler because of a reduction in detection by potential eavesdroppers (Table 3). Unfortunately, each possible method has its own drawbacks, and all of them are daunting tasks. However, we feel that the benefits of demonstrating an adaptive value for a proposed private signal outweighs these difficulties;

without demonstrating that a proposed protected private signal is actually private, we may confuse actual private signals with signals that are undetectable for non-adaptive reasons.

Conclusion

Protected private communication relies on physiological and evolutionary asymmetries between potential eavesdroppers and intended receivers. Protected private signals can remain private over evolutionary time through four different mechanisms: (1) evolutionary constraints, (2) functional costs to detection, (3) relationships between signalers and potential eavesdroppers that change faster than selection can act, or (4) a co-evolutionary arms race. If no constraints apply, a potential eavesdropper's lineage may be able to evolve the ability to detect a protected private signal. In a variety of animal taxa, studies suggest that spectral sensitivity has often changed in ways that would reveal protected private signals using UV and red wavelengths (Table 1). Similarly, studies suggest that vertebrates may be able to detect the polarization of light by a variety of mechanisms, but that some of these mechanisms may be associated with greater functional costs than those generally employed by invertebrates (Table 2).

If a potential eavesdropper evolves the ability to detect a formerly private channel, they may suffer functional costs because optical principles imply tradeoffs between color vision, polarization vision, sensitivity, and acuity. No eye can improve all visual parameters at once without increasing in size and metabolic demand. However, costs to sensory abilities are only one part of a potential eavesdropper's net fitness, and it is the net fitness of a potential eavesdropper (along with the fitness of signalers and intended receivers) that will determine whether a protected private signal remains private over evolutionary time. Many other variables, such as the rate of occurrence of the signal and the benefit of its detection, will also determine the prevalence of protected private communication. Often, net fitness may not be experimentally measurable or may involve too many variables to be modeled with reasonable accuracy. For instance, if a falcon could detect UV light, would the benefit of detecting a song bird's UV plumage outweigh the loss of acuity from scattered light, increased UV damage to the eye, and the need to correct for additional chromatic aberration? To predict this we would need to know: (1) how often the passerine and the hawk interact, (2) the per occurrence increase in successful predation resulting from the hawk seeing the private signal, (3) the occurrence of other prey, (4) the per occurrence decrease in successful predation of other prey because of the loss of acuity from light scattering, (5) the fitness costs from UV radiation damage to the eye, and 6) the costs of shifting a violet pigment into the UV on optical sensitivity and the visual contrast of other relevant objects. Needless to say, these are daunting tasks. An alternative, possibly simpler, method is to demonstrate that an undetectable signal benefits the signaler because of its secrecy (Table 3).

It is important to note that differences in behavior, rather than physiology, can also lead to communication free from eavesdroppers. In some cases, these behaviors may be less evolutionarily labile in potential eavesdroppers than certain aspects of their sensory physiology. For example, the fiddler crab *Uca tangeri* (Eydoux, 1835) may use differences in microhabitat to signal to potential mates with parts of its body (e.g. its mouth parts or the bottoms of its claws) that are camouflaged from predators approaching from above, such as birds (Cummings et al. 2008). It is unlikely, although not impossible, that a bird would benefit if it foraged with its head held against the ground to detect the crabs at their most conspicuous viewing angle. Similarly, some coral reef fish may use contrasting stripes that blur together to match the background when viewed by a predator at a distance (Marshall

2000). A predator could increase the distance at which it could detect such fish by evolving better spatial resolution (at the cost of either lower sensitivity or a larger eye). However, if these coral reef fish are often near intended receivers, but far from predators, the eye size required by the predator to detect its prey may incur maintenance costs that outweigh its benefits. Signalers can also switch from signaling in one modality to another as the cost-benefit ratio of these signals change with environmental conditions. For example, when bat predators pose a higher risk during the full moon, certain neotropical katydids (Family Pseudophyllinae) switch their signaling from acoustic songs to substrate vibrations (Romer et al. 2010). In order to detect the vibrations, predatory bats would have to forage by landing on each katydid's individual plant.

To date, no hypothesized protected private signal has been shown to benefit the signaler because of the signal's reduced detection by potential eavesdroppers. We do not consider it a coincidence that two of the oldest proposed protected private communication channels, the far-red bioluminescence of dragonfish and the UV plumage of passerines, have been cracked by certain likely eavesdroppers (Stevens and Cuthill 2007; Turner et al. 2009). Future studies on private signaling need to demonstrate that an undetectable signal is adaptive, and not undetectable for non-adaptive reasons.

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