

## Review

## Visual Acuity and the Evolution of Signals

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**Acuity, the fineness with which sensory systems perceive and parse information, limits the information that organisms can extract from stimuli. Here, we focus on visual acuity (the ability to perceive static spatial detail) to discuss relationships between acuity and signal form and evolution. Research suggests that acuity varies by orders of magnitude across species, and that most animals have much lower acuity than humans. Thus, hypotheses regarding the function of spatial patterns must account for the acuity of relevant viewers. New data quantifying acuity in a range of taxa allow us to examine correlations between acuity and ecology, elucidate the selective forces that receiver acuity places on signal evolution, and examine how signals might appear to viewers with different acuities.**

### Sensory Acuity

Animal behavior is influenced by the information that an organism can perceive and process, which is in turn mediated by sensory systems. Thus, studies of how animals interact with both other animals and with the environment must consider the relevant perceptual systems. One way that individuals can extract information is via signals, which also form the basis for communication [1]; thus, signals are fundamental to the behavior and fitness of organisms. Though many definitions of ‘signal’ exist, one criterion is that they be perceptible by the receiver [2]. Because of close causal relationships between signal form, signaling behavior, receiver perception, and decision-making, receiver sensory systems can be an important selective force on numerous aspects of the signaling process [3]. In addition, many signals have been under selection to be species-specific, signature-like, or honest advertisements of mate quality, leading to elaboration of signal form [4]. Crucially, for elaborate signals to be effective, receivers must possess both the necessary sensory machinery and the cognitive power to decipher them. Despite this, acuity, or how finely receivers can parse and perceive information, is an understudied aspect of receiver sensory capability.

Many well-studied examples of elaborate signals are visual, involving complex spatial patterns and color combinations, making vision a useful modality in which to study receiver acuity and perception of signals. Additionally, unlike higher-dimensional senses (e.g., chemoreception, touch), visual patterns are more readily parameterized and analyzed, and numerous visual signals are comprised of pattern elements, meaning that one can study relationships between acuity and signal perception in a wide range of taxa. Though **visual acuity** (see [Glossary](#)) is also an important component of motion perception, here we address only the spatial component of visual acuity and its relationship to resolving detail. Thus, for our purposes, we define visual acuity (hereafter acuity) as the ability of an animal to perceive static spatial detail ([Box 1](#)). However, many of these ideas can be extended and applied to other sensory modalities, such as the perception of motion or sound.

### Incorporating Visual Acuity into Studies of Signaling

Including acuity in studies of animal signaling is important for several reasons. First, humans have exceptionally high acuity, surpassed only by a few predatory bird species, and thus researchers sometimes develop hypotheses regarding signal function that do not reflect what is seen by the

### Highlights

Recent increased interest in visual acuity, the ability to perceive static spatial detail, has shown that acuity is highly variable, ranging over four orders of magnitude across species with image-forming eyes.

Human visual acuity is some of the highest in the animal kingdom, meaning that researchers may develop hypotheses regarding the function of spatial patterns that do not account for the relevant viewer’s sensory capabilities.

Signals can potentially exploit differences in visual acuity between species, which may arise due to differences in eye type, eye size, and/or viewing distance.

Because acuity can vary between two viewers of the same scene, it represents a promising yet understudied channel for private communication.

Small animals, particularly those with compound eyes, have low acuity and thus can only perceive fine patterns over very short distances.

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intended viewer. Second, because acuity dictates what patterns can and cannot be resolved, it determines the spatial information that can be extracted from visual scenes by signal receivers (hereafter ‘viewer’). Third, acuity is likely an important selective force on signal evolution because visual signals often incorporate spatial patterns. Fourth, acuity varies significantly across species, spanning at least four orders of magnitude in animals with image-forming eyes. Such large variation in acuity between species might allow signalers to exploit differences in sensory capabilities to produce signals that are more apparent to certain viewers than to others. For example, signals could vary in their conspicuousness to viewers that differ in acuity as a result of differences in eye size, eye type, viewing distance, or a combination of these factors (Box 2).

Here, we examine whether signal structure can exploit between-species differences in acuity by discussing trends in acuity across animals, laying out predictions for how variation in acuity can influence signal evolution, and using specific systems as examples. In particular, we discuss three signaling scenarios where potential viewers have varying acuities, resulting in signals that are likely to be differentially apparent to: (i) conspecifics versus heterospecifics, (ii) certain heterospecifics versus others, and (iii) near versus far viewers.

Throughout, we portray the viewer-specific spatial information available using the R package AcuityView [30]. Importantly, these images do not show us what the animal actually ‘sees’. Rather, they show us the spatial information content of a scene given acuity and viewing distance. It is likely that further edge enhancement and other forms of higher-order processing occur in many animals, though such postprocessing cannot add information to an image, but only act on information that is above the acuity limit.

#### Box 1. Anatomical Features that Limit Acuity

##### Camera and Compound Eyes

Although there are 10 recognized optical eye types [5], here we focus on camera and apposition compound eyes. Camera eyes are the principal eye type of vertebrates, although they are also found across some invertebrate taxa (gastropods, scallops, arachnids, cubozoa, alciopid polychaetes, and certain copepods) [5]. They comprise a single image-forming unit, an internal lens and a typically external cornea, that focuses an image onto a retina comprised of photoreceptor cells. Compound eyes are found across insects and crustaceans, as well as some chelicerates, annelids, and bivalve mollusks. Apposition compound eyes are comprised of multiple optical units, known as ommatidia, which are tubular structures consisting of at least one lens that funnels light to a group of photoreceptor cells.

##### Inter-Receptor Angle and Acceptance Angle

Two anatomical factors place an upper limit on acuity. The first is inter-receptor angle ( $\Delta\phi$ ; Figure 1), or the angular separation of photoreceptors, which is determined by the density of photoreceptors per degree of visual angle [6,7]. The more sampling stations that view a scene per unit angle, the higher acuity can potentially be; thus, small values of  $\Delta\phi$  correspond to higher acuity. Importantly, photoreceptor spacing and density usually vary across the eye, often resulting in areas of higher acuity in regions that view important areas of visual space. For example, the photoreceptors in a human fovea are more densely packed than anywhere else in the eye, conferring high acuity in the center of our vision, with acuity falling off rapidly into the periphery. Male march flies (*Dilophus febrilis*) have upward-facing acute zones in eye regions that track potential mates against the sky [8] (a representative example of the fact that in insects, the sexes sometimes differ in acuity), and fiddler crabs, [9], rabbits [10], and some benthic sharks [11] have horizontal bands of increased acuity for viewing the horizon.

The second factor that limits acuity is ‘acceptance angle’ ( $\Delta\rho$ ; Figure 1), or the angular width of the region viewed by each photoreceptor. In some eyes, such as those of deep sea fish,  $\Delta\rho$  is larger than  $\Delta\phi$ , so many photoreceptors view the same region of space, increasing sensitivity at the expense of acuity. Diffraction in compound eyes with small facets can also make  $\Delta\rho$  larger than  $\Delta\phi$ , which is the primary factor limiting acuity in this eye type (Box 2). However, in most diurnal eyes,  $\Delta\rho \cong \Delta\phi$  [5,6], and the upper limit of acuity can therefore be estimated using  $\Delta\phi$ .

#### Glossary

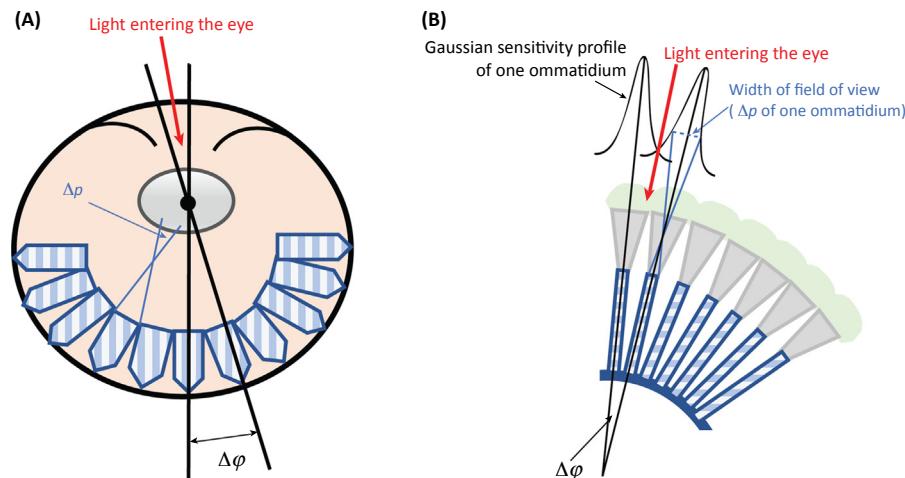
**Cycles per degree (cpd):** a measure of visual acuity; the number of black and white stripe pairs that an organism can discriminate within a single degree of visual angle.

**Minimum resolvable angle:** ( $\alpha_{\min}$ ) another measure of visual acuity; the angular width of the narrowest black and white stripe pair that can be discerned. When given in degrees, its inverse is cpd.

**Visual acuity:** the ability of a visual system to resolve static spatial detail.

**Other Factors That Impact Acuity**

Acuity can be affected by numerous other factors beyond anatomy. The best estimates of acuity take factors such as optics, diffraction, and spatial summation (a process by which multiple photoreceptors are tied together into one ‘super pixel’) into account. Acuity for color patterns is typically lower than for brightness-based patterns. Not all photoreceptors are sensitive to all wavelengths of light, and color vision requires a comparison between multiple receptors, making a functionally larger ‘pixel’ for sampling color patterns. Therefore, between-species differences in color vision may also contribute to differences in how spatial patterns are perceived. Lastly, acuity is distance-dependent, so when holding the viewer’s acuity constant, different levels of detail are discriminable from different distances, with finer details becoming less apparent from farther away. In air, this occurs as a result of both geometry (detail becomes finer as distance increases) and light scattering. In water, the effects of distance on ability to resolve detail are even more pronounced, since detail can be obscured by an intervening murky medium (see [12]).



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**Figure 1. The Inter-Receptor Angle  $\Delta\phi$  and Acceptance Angle  $\Delta\rho$  in (A) Camera and (B) Apposition Compound Eyes.** Each photoreceptor does not collect light from only straight ahead; rather, it has a sensitivity function based on the angle of incidence of a photon upon the photoreceptor. The sensitivity function is roughly Gaussian, as illustrated here, meaning that photoreceptors are most sensitive to photons from straight ahead, and sensitivity decreases as photons strike from angles off-center. The Gaussian sensitivity profiles of individual ommatidia overlap with those of neighboring ommatidia. The width of the field of view of a single ommatidium ( $\Delta\rho$ ) occurs at 50% sensitivity of the Gaussian sensitivity profile. For clarity, this is shown only in the apposition compound eye, though the photoreceptors in camera eyes have analogous sensitivity profiles.

**Evolutionary Consequences of Acuity for Signaling****The Effect of Eye Size and Type on the Perception of Signals in Interspecies Interactions**

Interspecies interactions, from mutualism to parasitism to predation, are often mediated by signals. However, assumptions about which viewers can resolve the details of a signal are often untested. In interspecies interactions, heterospecifics can impose selection pressure on signals that impact the success or efficiency of an interaction [31]. In the common case where two animals interact but have different acuities (Box 3), signals can be more distinguishable by heterospecifics but not conspecifics, or vice versa. Two examples of such signaling systems are those involving: (i) cleaner shrimp and client fish, and (ii) aposematic butterfly species and avian predators. In both systems, invertebrates with compound eyes display patterns composed of many elements which are small relative to body size, which might serve as signals to conspecific or heterospecific viewers, or both.

**Box 2. What Can Make Acuity Higher?****Focal Length and Photoreceptor Diameter**

In the typical contiguous retina, photoreceptors are packed so tightly together that they touch. In such cases,  $\Delta\phi = d/f$  (in radians), where  $d$  is the inter-receptor distance and  $f$  is the eye's focal length (the distance from the point in the lens through which light rays pass without being bent to the image on the retina) [5].

This formula shows that one way to obtain a smaller  $\Delta\phi$ , and thus higher acuity, is to increase focal length. This can be achieved by increasing the size of either the entire eye or only the longitudinal axis, as occurs in eyes that are tubular in shape [13]. Across species, the primary driver of variation in acuity is the longitudinal diameter of the eye: acuity is typically higher in larger eyes (Figure 1), and thus (through correlations between eye size and body size) generally higher in larger animals (birds [14], mammals [14,15], bees [16], and fish [17]).

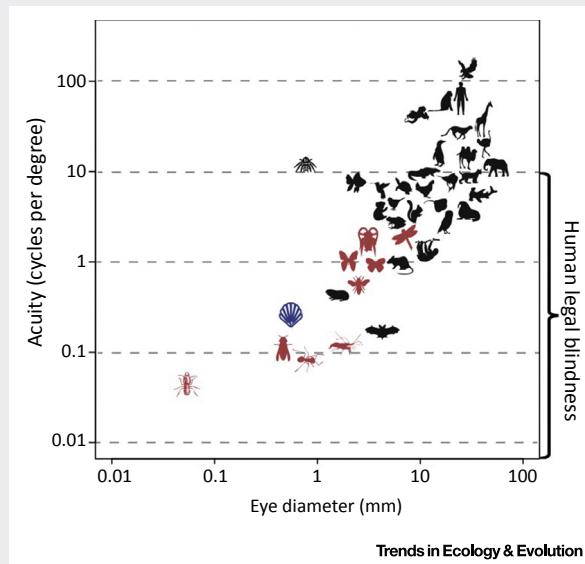
Acuity also increases when photoreceptors narrow (smaller  $d$ ). Narrower photoreceptors, however, collect light over a smaller area and thus gather less light, leading to an acuity–sensitivity trade-off. This trade-off is especially apparent in nocturnal animals, many of which have low acuity because they have relatively short eyes longitudinally and large-diameter lenses, to focus brighter images on the retina [5,7]. Crepuscular and nocturnal animals also often exhibit spatial summation [5], in which multiple photoreceptors pool together to collect light over a larger area. Functionally, this makes them a single visual sampling unit [18], increasing sensitivity at an acuity cost. Thus, acuity tends to be higher in diurnal versus nocturnal species (mammals [15], marsupials [19–21], strepsirrhine primates [22], birds [23]).

**Eye Type**

Acuity is higher in camera eyes than in compound eyes of the same size. This is because the small lenses of compound eyes are particularly affected by diffraction, a form of image blurring that arises from the wave nature of light [7]. For acuity to increase in compound eyes, each lens must be enlarged and more lenses must be added; thus, compound eyes are acuity-limited by their potential size. In fact, for a compound eye to mimic human acuity, it would need to be a startling 1 meter in diameter [24].

**Ecological Factors**

Together, differences in eye size and eye type account for the majority of variation in acuity. However, acuity also tends to be higher in predatory versus nonpredatory species (mammals [15], reef fish [25,26], insects [27], elasmobranchs [28], but see [17]) and species that live in spatially complex habitats (fishes [17,25,26], cichlids [29], elasmobranchs [28]).



**Figure 1. Acuity versus Eye Diameter across Species with Camera (Black), Compound (Red), and Mirror (Blue) Eyes.** The center of the icon has been placed at the acuity and eye size values. Of note is the fact that human values are likely derived from foveal vision and behavioral measures are recorded on alert, attentive subjects, and thus may represent a slight overinflation of acuity values. Values below 10 cpd are considered legally blind in humans, as indicated on the right side of the diagram. Acuity and eye diameter values, as well as citations, are found in Table S1 (in the supplemental information online).

**Box 3. Acuity across Species**

Although several eagles, vultures, and falcons have acuities that are higher than (or equivalent to) that of humans (~60 cpd [5]), beyond raptors, the maximum published acuity in birds is only 41 cpd (the laughing kookaburra *Dacelo novaeguineae* [41]). A compilation of acuity values from 93 bird species (Table S2 in the supplemental information online) shows that acuity in adult birds ranges from only 4 cpd (the barn owl *Tyto alba pratincola* [42]) up to 138 cpd (the eagle *Aquila audax*). However, the median acuity in birds is 11 cpd, and 84% of acuity estimates in birds are below 30 cpd.

Acuity is similarly variable across mammals and ray-finned fishes [28,38]. Acuity in non-human mammals ranges from a high in the chimpanzee (*Pan troglodytes*, 64 cpd [43]) to a low in mouse-eared bats (*Myotis* spp., 0.1 cpd [J. Eklöf, PhD thesis, Göteborg University, 2003]). The highest acuities among fishes are in large predatory species, including the rock bass (*Ambloplites rupestris*, 40 cpd [44]) and Atlantic sailfish (*Istiophorus albicans*, 32 cpd [45]), while the lowest is found in the Japanese rice fish (*Oryzias latipes*, 0.56 cpd [46]). Among elasmobranchs, acuity ranges from a low in the bamboo shark (*Chiloscyllium punctatum*, 2.0 cpd) up to a high in the bigeye thresher shark (*Alopias superciliosus*, 11 cpd) [11]. Beyond birds, fish, and mammals, little is known about acuity in other vertebrate groups, such as reptiles (but see [47] and references therein) and amphibians (but see [48]).

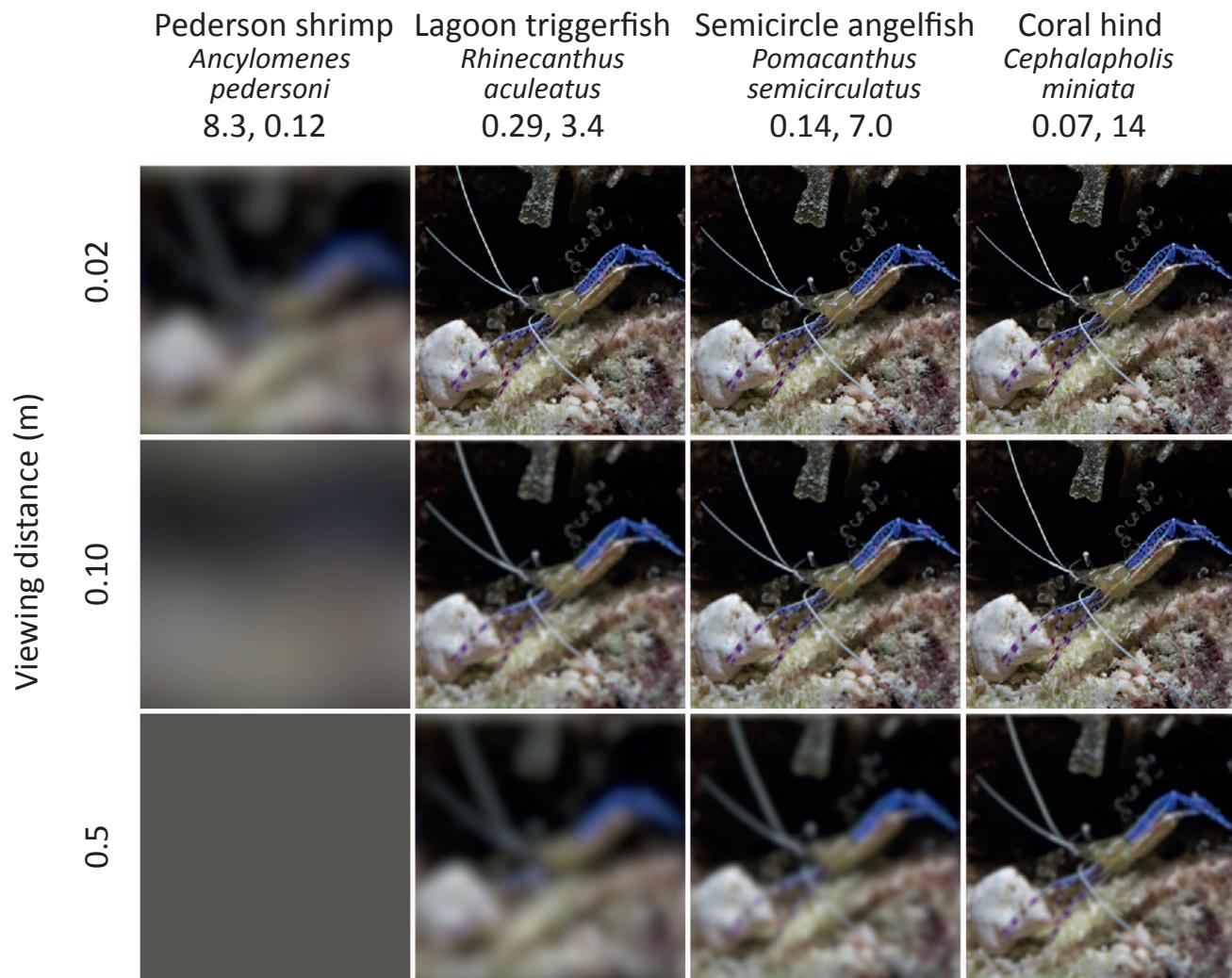
Among invertebrates, the highest known acuities occur in animals with camera eyes, for example gastropods, cephalopods, spiders, and scorpions [5]. The octopus *Octopus vulgaris* has acuity on par with large fish (46 cpd [49,50]). Certain spiders have exceptionally high acuity for their size, for example, the jumping spider *Portia fimbriata* has acuity on par with passerine birds, at 13 cpd [7]. Most known acuities in compound eyes come from insects (Table S3 in the supplemental information online), the highest of which occurs in the dragonfly *Anax junius* (2 cpd [27]). However, 98% of published acuity values for insects are below 1.0 cpd and the median acuity among measured insects is only 0.25 cpd. Outside of insects, eye morphology in 96 species of decapod crustaceans suggests that acuity ranges only up to 0.4 cpd [51]. Although a handful of other data points exist, little is known about acuity in other invertebrates. Overall, however, the majority of species have acuity that is far lower than that of humans.

The cleaner shrimp *Ancylomenes pedersoni* provides cleaning services to visiting client fish by removing and eating ectoparasites and dead skin [32]. *A. pedersoni* displays bright color patterns consisting of fine spots, as well as long, thin, white antennae that they typically whip about in a stereotyped fashion in the presence of clients. One hypothesis, based on the appearance of these shrimp to human viewers, is that their color patterns and antennae-whipping behavior serve as intraspecific signals related to group dynamics. An alternative hypothesis is that they serve as a signal directed only at client fish, which have large camera-type eyes and therefore acuity that is one to two orders of magnitude higher than the shrimp.

Accounting for acuity shows that conspecific viewers likely cannot resolve one another's color patterns, even from distances as close as 2 cm (Figure 1), suggesting they are not an intraspecific signal [33]. However, both their color patterns and antennae are visible to fish viewers of various acuities from a distance of at least 10 cm (Figure 1), a typical interaction distance between cleaners and clients [34]. Thus, these distinctive color patterns and antennae-whipping behaviors likely serve as signals directed at clients, despite the inability of cleaner shrimp themselves to distinguish them.

A second class of invertebrate signals directed at vertebrates are the aposematic warning colors of many insects. These colorful and high-contrast patterns serve to advertise to predators that a potential prey item is defended, unpalatable, or toxic [35–37]. It has also been suggested, however, that the fine-scale details of these color patterns might serve additional mate detection functions (e.g., [38]), and thus that some aspect of color pattern is resolvable by conspecifics.

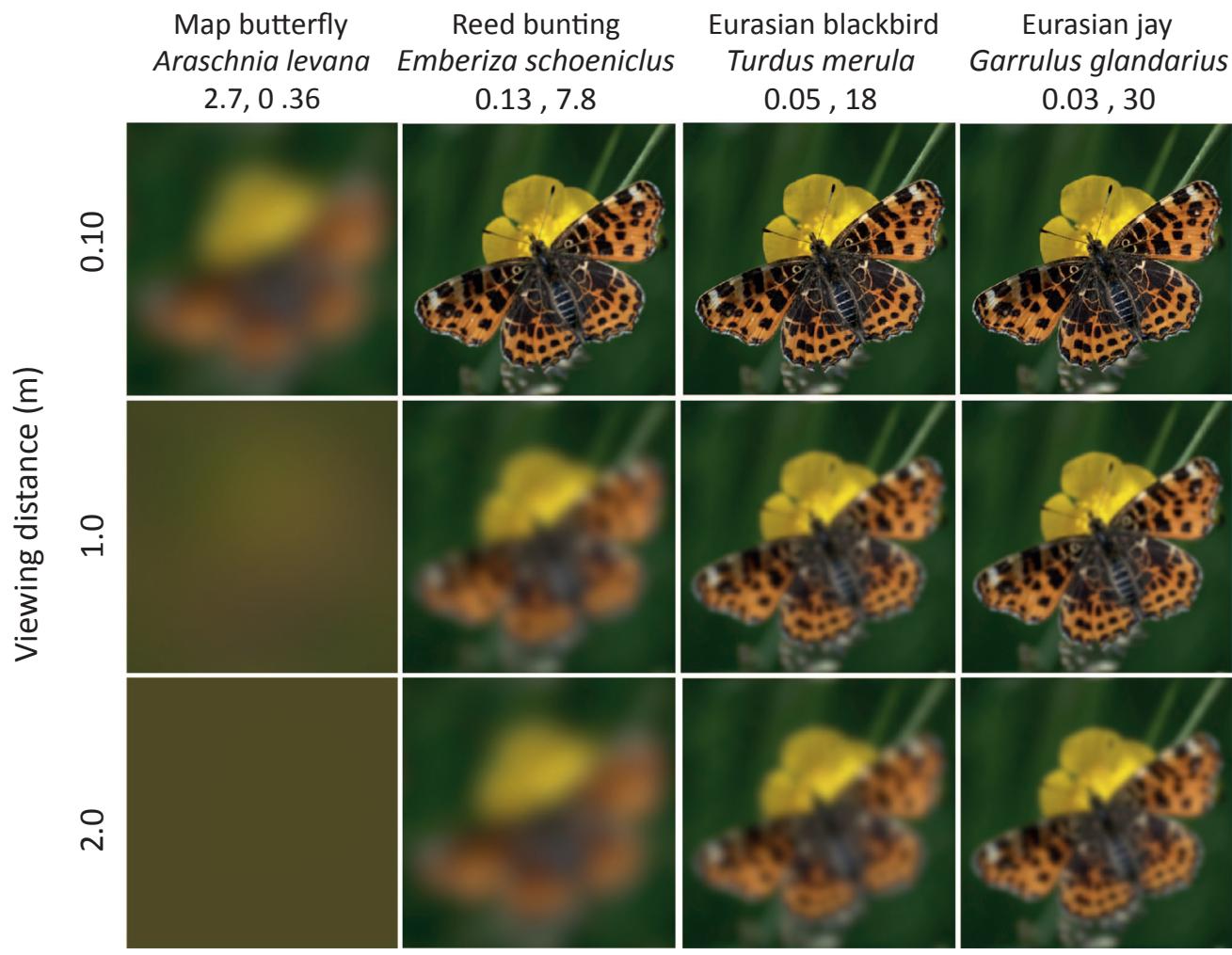
As an example, the aposematic color patterns of the butterfly *Araschnia levana* might signal conspecifics and/or potential predators (insectivorous birds) [39]. Conspecifics have low acuity, because they have small compound eyes, whereas birds have relatively high acuity, because of



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Figure 1. The cleaner shrimp *Ancylomenes pedersoni*, as the spatial aspects of the scene might appear from three different viewing distances to four different coral reef dwellers: a conspecific cleaner shrimp [33], the triggerfish *Rhinecanthus aculeatus* [87], the angelfish *Pomacanthus semicirculatus* [88], and the coral hind *Cephalapholis miniata* [88]. Column labels show  $\alpha_{\min}$ , acuity (in degrees and cycles per degree, respectively). Here, we assume that the shrimp is 4 cm across. To create images that contain only spatial information above the resolving power of a viewer of given acuity, we used the R package AcuityView [30]. Briefly, AcuityView Fourier transforms an image, and then multiplies the Fourier transform by a visual-system-relevant modulation transfer function, and then recovers an image in which all spatial information at spatial frequencies greater than the acuity of the organism has been removed. Image of shrimp from Wikimedia Commons.

their large camera eyes. Figure 2 shows that the color patterns of *A. levana* are visible to birds with a range of acuities from distances as far away as 1 m. At greater distances, birds on the lower end of the avian acuity range lose the ability to resolve the fine-scale details of these color patterns, but other birds do not. However, even from distances as close as 10 cm, *A. levana* cannot resolve discrete pattern elements of conspecifics. Importantly, aspects of whole-body coloration are still resolvable, and thus can function as an intraspecific signal. For example, behavioral studies have shown that a combination of color and pattern predicts both predator deterrence and mate attraction in the aposematic butterfly *Heliconius erato* [38], which has



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Figure 2. The aposematic butterfly *Araschnia levana*, as the spatial aspects of the scene might appear from three different viewing distances to a conspecific [89], as well as three sympatric, insectivorous birds that could be potential predators: the reed bunting *Emberiza schoeniclus* [90], the blackbird *Turdus merula* [90], and the jay *Garrulus glandarius* [91]. Column labels show  $\alpha_{\min}$  acuity (in degrees and cycles per degree, respectively). We assume that *A. levana* has a wingspan of 4 cm. Image of *A. levana* from Wikimedia Commons (photographer: Guido Gerding).

much larger patterns. Further studies that incorporate acuity can elucidate how and whether pattern and color traits are relevant to different viewers.

These examples underscore that fine-scale patterning does not always serve a conspecific signaling function. Because of constraints on the acuity of compound eyes (Box 2), insects and crustaceans can only perceive spatial patterns when they are either large or viewed at a very short distance. As a result, the precise patterning found on many animals with compound eyes might be nonfunctional or directed at species with higher acuities, or fine-scale patterns might blur into larger patterns that serve their own signaling function.

The low acuity of most insects and crustaceans should constrain the types of information that can be extracted from signals, meaning that they are more likely able to perceive and assess

larger color patterns or whole-body coloration. Importantly, even if certain color patterns cannot be resolved, aspects of coloration should still be visible as color patterns blur together. Thus, because of differences in viewer acuity, fine-scale patterns could be salient to certain viewers, while other viewers can only resolve, and thus assess, larger color pattern traits that arise as finer patterns blur together. For example, human acuity is roughly 60 **cycles per degree (cpd)** in the center of our gaze (fovea) but drops quickly away from the fovea, to one-tenth of that at only seven degrees away from the fovea. One hypothesis is that Leonardo da Vinci exploited this difference when painting the Mona Lisa, whose smile is more visible to low acuity vision than high acuity vision. Thus, looking elsewhere on the painting and viewing her mouth with peripheral vision, she appears to smile, whereas when one looks directly at her mouth, her smile is much less pronounced [40].

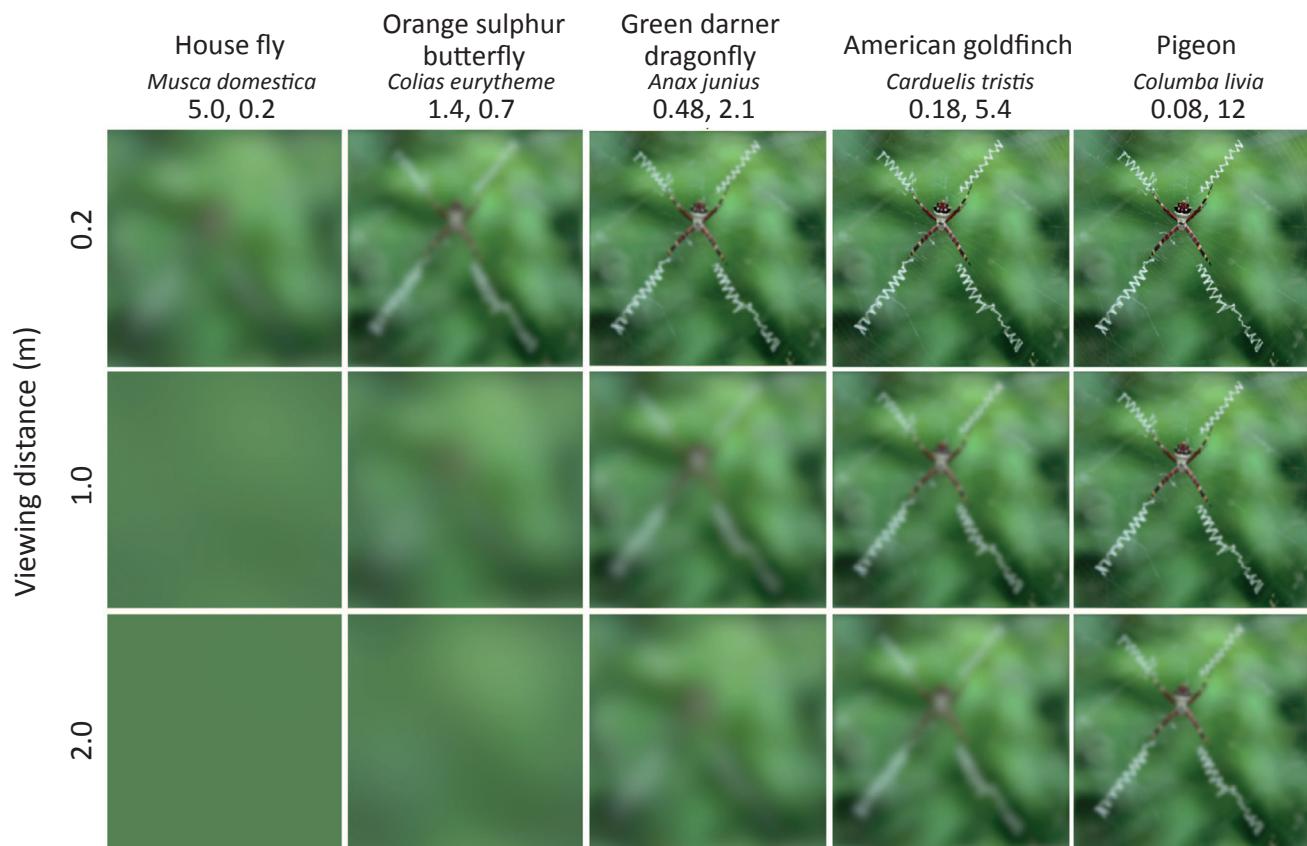
#### Acuity and Private Communication

Signals are often received by both intended and unintended viewers. Signal detection by intended viewers is, by definition, beneficial, but signal detection by unintended viewers can range from benign to costly for sender and/or receiver; for example, if a signal is detected by a potential prey animal, competitor, parasite, or predator (e.g., [52–55]). One way to reduce these costs is to communicate via signals that are less apparent to the sensory systems of unintended viewers than intended viewers by using what is known as a private communication channel. Private communication has been found in systems that exploit variation in viewer spectral sensitivity (for example private communication in ultraviolet [56] and near-infrared portions of the spectrum [57]), as well as in other visual modalities such as polarization [58,59]. However, private communication resulting from differences in viewer acuity has not been explored.

A common scenario in which we might predict private communication to function occurs when signalers wish to be less apparent to potential prey to ensure successful prey capture, but also apparent to another party, for example to attract potential mates, warn potential predators, or defend a structure from accidental harm. This can arise by signalers exploiting differences in viewer acuity. As case studies, we discuss spider web decorations (stabilimenta) and the pigmented stinging tentacles of some jellyfish.

Stabilimenta are silk decorations found on the webs of some orb-web spider species [60]. Although their function has inspired debate, two widely-tested theories imply visual functions for the stabilimenta, including: (i) a web protection function whereby stabilimenta deter animals large enough to accidentally destroy a web [61]; and (ii) a prey attraction function, whereby they lure prey [62]. Thus, the first of these hypotheses predicts that stabilimenta be perceptible by animals that could destroy the webs (primarily birds), while the second predicts that they are perceptible by the spider's arthropod prey. Although there have been studies correlating the spectral properties of web silk to bird and insect vision [63], no studies have yet accounted for acuity when viewing stabilimenta.

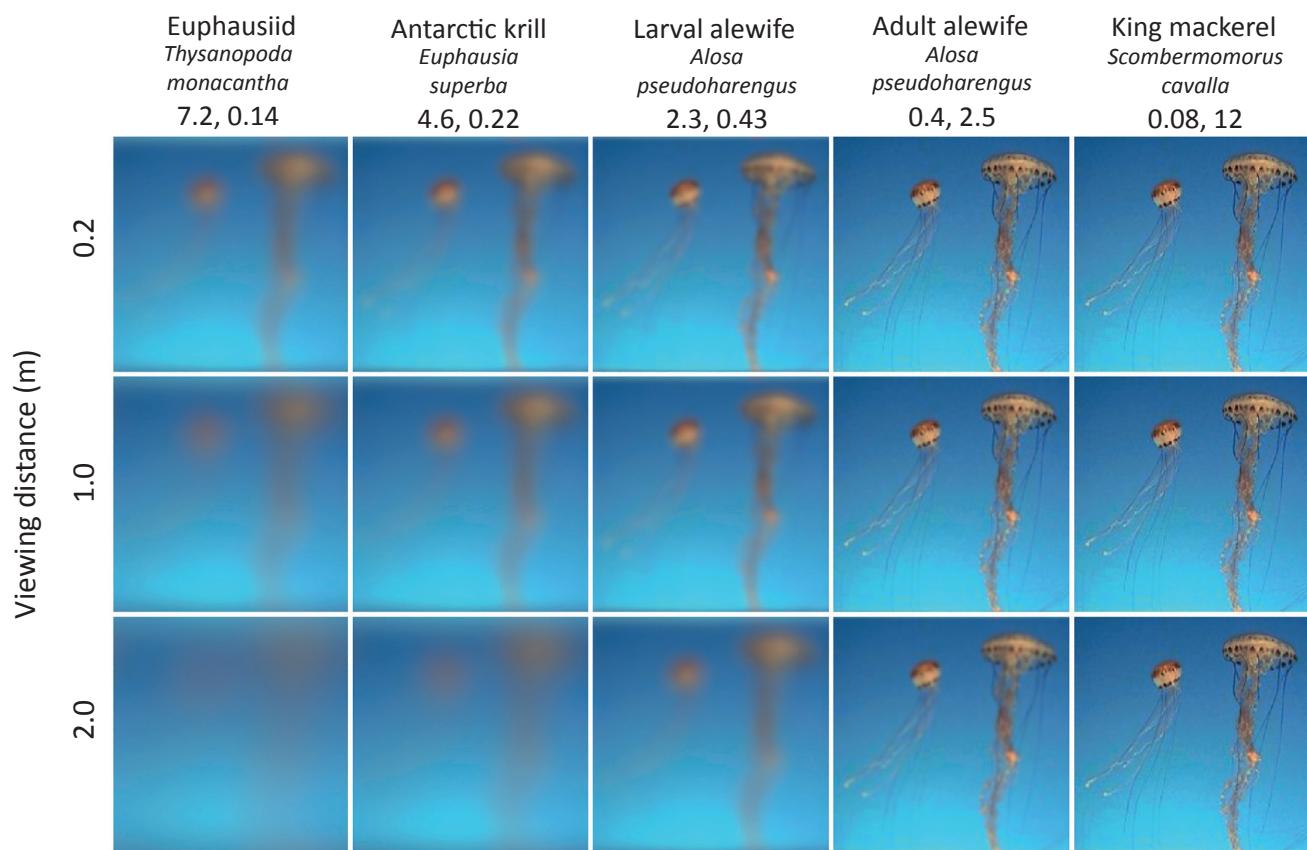
Figure 3 shows the appearance of web stabilimenta to representative insect and avian viewers, and illustrates that they are not distinguishable to smaller insects even from close distances. They are more apparent to insects with the highest acuities from distances that could allow them time to change course and avoid being caught. However, web stabilimenta are resolvable by a variety of birds from as far as 2 m, which should allow them time to avoid the web. Thus, the visibility of stabilimenta by different potential viewers lends support to the hypothesis that they privately communicate web location to birds while not alerting insects.



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Figure 3. Cruciate web stabilimentum, as the spatial aspects of the scene might appear from three different viewing distances to potential prey items (the house fly *Musca domestica* [27], the orange sulphur butterfly *Colias eurytheme* [92], and the green darner dragonfly *Anax junius* [93]), chosen to represent the range of ecologically relevant insect acuity, and two birds large enough to destroy a delicate web (the American goldfinch *Carduelis tristis* [94] and the pigeon *Columba livia* [95]), chosen to illustrate the low and high ends of relevant passerine acuity. Column labels show  $\alpha_{\min}$ , acuity (in degrees and cycles per degree, respectively). We assume the stabilimentum here is 15 cm wide. Image of the stabilimentum from Wikimedia Commons (photographer: Daniel Schwen).

The stinging tentacles of some jellyfish are also structures whose function is to capture small prey with low acuity. The diets of jellyfish are comprised of a range of marine creatures, some of which, including shrimp and small fish, have image-forming eyes. Paradoxically, the tentacles of some species are strongly pigmented and thus potentially more obvious, which should be detrimental to prey capture. However, the delicate nature of tentacles means that they are vulnerable to being destroyed by large fish. Considering the acuity of the potential viewers including pelagic crustaceans (krill), larval fish, and adult pelagic fish, however, we can see that adult fish can resolve the tentacles and thus likely avoid encountering and destroying them from at least 2 m away (Figure 4). However, the tentacles are far less apparent to animals with lower acuity, such as crustaceans and larval fishes, allowing them to effectively serve their prey capture function. Thus, as with web stabilimenta, the tentacles of jellyfish might exploit differences in acuity to signal privately to large fish while minimizing detection by smaller prey.



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Figure 4. Pigmented jellyfish tentacles, as the spatial aspects of the scene might appear from three different viewing distances to three potential prey items (the euphausiid *Thysanopoda monacantha* [96], the Antarctic krill *Euphausia superba* [96], and the larval alewife fish *Alosa pseudoharengus* [84]) and two fish large enough to destroy tentacles (the adult alewife *Alosa pseudoharengus* [84] and the king mackerel *Scomberomorus cavalla* [45]). Column labels show  $\alpha_{\min}$ , acuity (in degrees and cycles per degree, respectively). The larger jellyfish and its tentacles were assumed to be 1 m in length. Image of jellyfish from Wikimedia Commons (photographer: Chris Ruvolo).

These examples both show how fine-scale structures can potentially exploit differences in acuity to communicate privately. Notably, in both cases prey lineages are constrained by their eye type and size from detecting the structure. Thus, they are unlikely to be able to increase acuity over evolutionary time, which would require either evolving camera eyes, or increasing eye size, which comes at an energy cost, is constrained by morphology, and requires cognitive ability sufficient to process and analyze high-resolution images. Thus, unlike private communication based on exploiting differences in color vision [64], prey lineages are unlikely to ever break into acuity-based private communication channels. This makes these private communication channels fundamentally different from those based on spectral sensitivity, and thus a promising avenue of future research.

#### Acuity and Signal Active Space

The concept of a signal active space, or the area over which a signal can propagate and be detected by a receiver, was initially introduced to describe the distance over which insect pheromones are detectable [65]. For both chemical and auditory signals, it is intuitive to think of signals dissipating to the point of no longer being detectable. However, visual signals also have

an active space, which is the distance over which a signal is distinguishable, barring any obstructions between the signal producer and the viewer [66]. The distance dependence of acuity (Box 1) means that acuity limits what details can be perceived and from what distance. Thus, viewer acuity should influence the active space of a visual signal, and in turn, the distances at which individuals can perceive and recognize one another, interaction distance, and/or the size of their territories.

Several studies have explicitly incorporated viewer acuity to examine either from what distance a given scene becomes discriminable by a certain viewer, or to examine the relationship between viewer acuity and signaling distance (e.g., [47,67]). For example, animals with bright, conspicuous color patterns have long puzzled biologists, because their apparent conspicuity should make them particularly susceptible to predation. However, considering viewer acuity and viewing distance can help elucidate how bright colors can serve both a communication and a camouflage function.

Reef fishes, for example, are famous for their bright patterns; yellow and blue coloration in particular is widespread among reef fishes. This color combination should be especially conspicuous, because their spectral composition means that they retain their color underwater both over long distances and at depth [68,69], and they form a high-contrast pattern. However, incorporating measures of viewer color vision and acuity has shown that, though colorful and conspicuous to near viewers, yellow and blue patterns fade rapidly as the colors mix at distances beyond 1–5 m (for various fish viewers) to create a combined spectrum that matches that of the background water [68]. Fish, as relatively large animals with camera eyes, have high acuity. Blurring of color patterns would occur at much shorter distances for many other marine animals, particularly crustaceans. Thus, some brightly colored animals can be both conspicuous and camouflaged without changing their physical appearance, but rather depending on the distance to the viewer.

In zebras, another animal famous for its stripes, the high acuity of large carnivores means that the stripes remain resolvable to predators at distances of up to 50 m in daylight conditions. Thus, zebra stripes likely do not confer anti-predator camouflage during the day [70]. In twilight, and on moonless nights, however, the distance at which they can be resolved decreases to 30 m and 9 m, respectively, underscoring that acuity can change with ambient light (often via spatial summation; see Box 2).

The distance-dependent effects of acuity also mean that different aspects of the same signaling structure might vary in saliency depending on viewing distance. As an example, in the paper wasp *Polistes fuscatus*, large facet size (an indicator of high acuity) coevolves with fine facial markings [71] that mediate individual recognition [72]. Pattern variation is primarily restricted to the face, suggesting these color patterns are useful during close range, face to face, encounters [72]. In support of this, Tibbetts and colleagues estimated *Polistes* to have an interommatidial angle of approximately 1 degree [27,72], or a **minimum resolvable angle** of 2 degrees. Facial markings range from 0.25 to 0.5 mm in width and 1 to 2 mm in length [72], so wasps should be able to resolve a midsize marking (0.35 mm in width) from a distance of 1 cm, and the largest marks (2 mm in width) from a distance of 5.7 cm. Thus, acuity might constrain wasps to individually recognize one another only during close encounters, excluding them from individual recognition from far away or while flying.

If acuity limits a visual signal's active space, it might influence other aspects of an animal's behavior such as territory size, nest spacing, or the distance at which individuals assess one

another. For parasites and specialist predators that need to identify particular species, acuity can limit the distance at which they can do this, impacting foraging ability. These constraints will of course operate differently between species; individual recognition in *Polistes* wasps could be constrained to occur over short distances, whereas larger animals with individual recognition

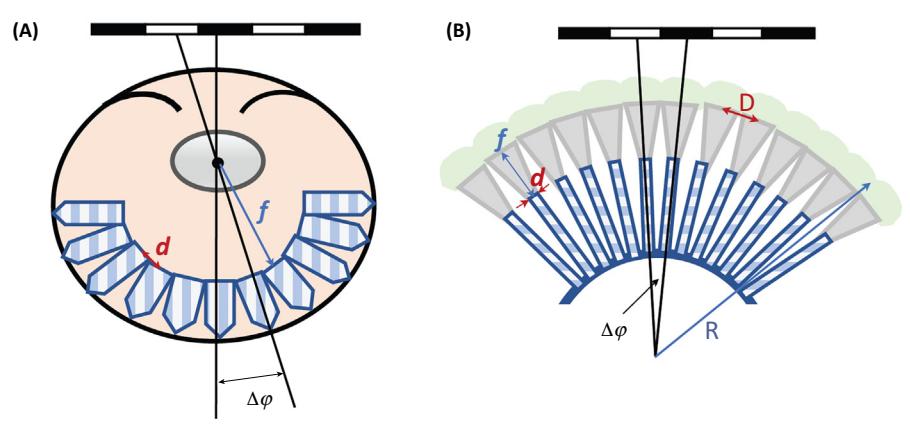
#### Box 4. Measuring Acuity Anatomically and Behaviorally

To estimate acuity anatomically in camera eyes, one can measure inter-photoreceptor distance ( $d$ ) and focal length ( $f$ ) to calculate  $\Delta\phi$  (Figure 1A), which is then multiplied by two and converted to degrees to give  $\alpha_{\min}$  (minimum resolvable angle). Typically, acuity is measured in the region of highest photoreceptor density. However, the peak density of the retinal ganglion cells (RGCs; found only in vertebrate eyes), or the size of their receptive field, is likely a better estimate of acuity (e.g., [73]) because numerous photoreceptors can feed information to a smaller number of RGCs [74,75].

In compound eyes,  $\Delta\phi$  is the angle between neighboring ommatidia (interommatidial angle). Because ommatidial diameter often varies across an eye, one should calculate the local interommatidial angle [76], which equals  $D/R$  (radians).  $D$  is the eye facet diameter in the area of interest, and  $R$  is the local radius of curvature of the eye (Figure 1B).

To behaviorally estimate acuity, animals can be trained to discriminate vertical from horizontal gratings [77,78] or from a uniform gray target with the same average luminance [79,80]. Alternatively, one can use the optomotor response, a stereotyped behavior elicited by placing an animal inside a rotating drum lined with vertical black and white stripe pairs [81], which the animal will track with its eyes or body. In both cases, the width of the stripes is made smaller until the animal can no longer distinguish the targets from each other, or ceases to track stimulus rotation. For the finest stripes the animal can reliably distinguish,  $\alpha_{\min}$  is the angle subtended at the eye by the black and white stripe pair (Figure 1). Using optomotor, however, necessarily involves stimulus motion, and the optomotor response itself is driven by units in the periphery of an eye that perceive motion [81]. Thus, optomotor likely does not yield estimates of an animal's highest acuity, especially in species that possess a fovea.

Unfortunately, different measures of acuity, even in the same species, yield different estimates, though the scale of this intraspecific variation is small compared with variation between species. Anatomical measurements provide a theoretical upper limit of acuity, and factors such as optical aberrations and spatial summation make behavioral acuity lower than predicted by anatomy. Thus, behavioral estimates may better represent visual function, but also can depend on external factors such as light level, motion, motivation, etc. Some studies find that behavioral and anatomical estimates align fairly closely [82–86], while others find behavioral estimates to be much lower than anatomical estimates [33,73].



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**Figure 1.** The inter-receptor angle  $\Delta\phi$ , inter-receptor distance  $d$ , and focal length  $f$  in camera type eyes (A), and rhabdom diameter  $d$ , focal length  $f$ , and interommatidial angle  $\Delta\phi$  (facet diameter  $D$  divided by local radius of curvature  $R$ ) in compound eyes (B). As shown by the black and white striped grating,  $\alpha_{\min}$  is the angle subtended by a black and white stripe pair in which the middle of a white stripe strikes one photoreceptor and the middle of a neighboring black stripe strikes a neighboring photoreceptor, meaning that the angular period of this finest resolved grating is  $2\Delta\phi$ .

ability, for example primates, can do so from further away. Small animals, even those that travel far and have large territories like some flying insects, are likely constrained to visually interact with one another using fine-scale patterns over just short distances, due to their low acuity. Because our acuity is often orders of magnitude higher than many species, we should be cautious not to overestimate the active space of most visual signals.

### Concluding Remarks and Future Directions

The human ability to both see and process spatial patterns is elite in the animal kingdom. Our high acuity allows us to resolve fine-scale details that are likely not resolvable by the vast majority of animal viewers, and at far greater distances. The examples presented here are by no means exhaustive, and illustrate the importance of considering acuity when making hypotheses about the function of animal visual signals. For example, predictions that deserve further attention include that: (i) larger animals will have signals with more complex and detailed color patterns; (ii) signals with fine pattern information should be presented to the viewer in the part of the visual field with the highest acuity; and (iii) signals presented by stationary animals will have signals with more complex patterns than those presented by moving animals.

Further studies that measure acuity in new species (Box 4) will continue to add invaluable data points to comparative studies of acuity across species. Additionally, numerous and exciting avenues of future research on acuity exist (see Outstanding Questions). There is a particular need for research that elucidates relationships between acuity, ecology, and cognitive capacity; increases our understanding of how acuity interacts with higher-order processes, as well as other modalities such as motion and temporal acuity; and examines relationships between acuity and signal form in nonvisual modalities (see Outstanding Questions). Such studies will help us to achieve a more complete understanding of the structure and function of animal signals.

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### Supplemental Information

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### Outstanding Questions

How does visual acuity of static pattern information interact with motion acuity (the minimum motion pattern that can be detected) and temporal acuity (the minimum speed of motion that can be detected)?

How do behavioral and anatomical measures of acuity within a species relate to one another?

How do texture, contrast, spatial frequency, and color vision, etc., combine to create the perception of a spatial pattern?

How does variation in acuity correlate with the capacity to process spatial information (i.e., cognitive ability)?

How much of pattern processing involves peripheral versus central perceptual processes?

How does acuity interact with higher-order perceptual processing, in particular, whether higher-level cognitive processes sharpen or amplify certain information?

How does acuity in other modalities, such as sound, limit the signal active space?

Visual acuity varies over orders of magnitude between species; how does acuity in other modalities vary between species?

How is acuity used for private communication across modalities?

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