

SIGNALS, SIGNAL CONDITIONS, AND THE DIRECTION OF EVOLUTION

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Abstract.—There is a bewildering diversity of signals, sensory systems, and signaling behavior. A consideration of how these traits affect each other's evolution explains some of this diversity. Natural selection favors signals, receptors, and signaling behavior that maximize the received signals relative to background noise and minimize signal degradation. Properties of sensory systems bias the direction of evolution of the signals that they receive. For example, females may prefer males whose signals they can perceive more easily, and this will lead to the spread of more easily perceived male traits. Environmental conditions during signal transmission and detection also affect signal perception. Specific environmental conditions will bias the evolutionary direction of behavior, which affects the time and place of signaling as well as microhabitat preferences. Increased specialization of microhabitats and signaling behavior may lead to biased evolution of the sensory systems to work more efficiently. Thus, sensory systems, signals, signaling behavior, and habitat choice are evolutionarily coupled. These suites of traits should coevolve in predictable directions, determined by environmental biophysics, neurobiology, and the genetics of the suites of traits—hence the term “sensory drive.” Because conditions vary in space and time, diversity will be generated.

The immense diversity of species is intriguing. At least some of this variation in physical appearance is the result of the diversity of visual and other signals used in various forms of communication, including attracting and courting potential mates, maintaining territories, holding groups together, and minimizing predation. The diversity in appearance is rivaled by variation in the times and places where the signals are transmitted and in the designs of the devices used to receive them. Can any of this variation be explained or even predicted?

Natural selection favors signals, receptors, and signaling behavior that maximize the received signal relative to background noise and minimize signal degradation. Conditions during signal transmission and detection can affect the quality and effectiveness of received signals because both can alter the signal's perceived form. Therefore, a signal's effectiveness will depend on the signal's form, receiver design, and behavior that determines the environmental conditions during transmission. As a result, signals, receptors, and behavior are not suites of evolutionarily independent traits; they are functionally related and are therefore likely to influence the evolution of one another. The direction of the resulting joint evolution of signals, receptors, and signaling behavior is affected by environmental physics, biophysics, and neurobiology. The processes leading to these biases in the direction of evolution can be loosely called “sensory drive,” which suggests that sensory systems and sensory conditions “drive” evolution in particular di-

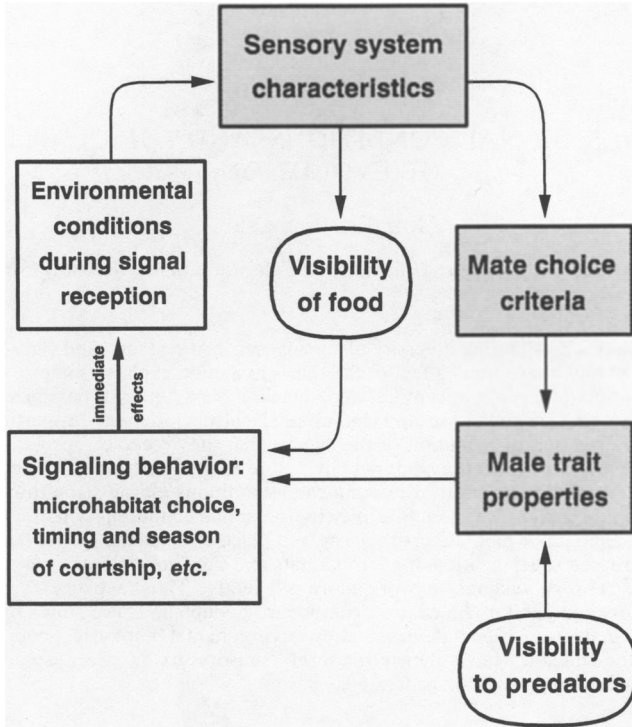


FIG. 1.—The essential processes of sensory drive. *Arrows indicate evolutionary influences, except for the one labeled "immediate effects."* The shaded portion is equivalent to Ryan's (1990) sensory exploitation model.

reactions (Endler and McLellan 1988; Endler 1989). The purpose of this article is to explore some aspects of sensory drive, to make a few predictions, and to encourage further work on the subject. I will summarize the process of sensory drive, give an example for visual communication, make predictions about visual systems, and then discuss some general implications for all sensory modes.

THE PROCESS OF SENSORY DRIVE

Figure 1 summarizes the main evolutionary relationships among sensory systems, signals, and the conditions under which they are sent and illustrates these relationships with the example of sexually selected male traits. Similar interactions should affect territorial, antipredator, and other kinds of signals.

The characteristics of the sensory system determine how male traits are perceived. Senses will affect the evolution of mate-choice criteria because they ensure that not all available male signals will be perceived equally well. If only some types or components of signals are able to be detected easily and perceived clearly, then these will be used as female choice criteria, whereas other, less easily perceived components will not be used. Thus, mate-choice criteria are

predisposed to evolve in the directions favored by sensory characteristics. In some cases, this predisposition may even lead to preferences for male traits that have not yet evolved (Basolo 1990). Mate-choice criteria determine, or at least strongly bias, the direction of evolution of male traits; preferred male traits spread at the expense of unpreferred traits. In a sense, the signal characteristics of the male traits evolve to “exploit” the signal-reception characteristics of females; signals that stimulate the sensory system most strongly have an advantage over those that result in less stimulation. Ryan (1990) termed this process (*shaded* in fig. 1) “sensory exploitation” and has provided much evidence for it in the auditory signals of frogs and other animals (Ryan 1990; Ryan and Rand 1990; Ryan and Keddy-Hector 1992). However, additional processes are also operating (fig. 1).

The signal’s evolution is also affected by predation, a fact well-known for both visual and auditory signals (Endler 1978, 1983; Tuttle and Ryan 1982). In general, the signal evolves as a local balance between the relative strengths of sexual selection and predation (Endler 1978, 1980, 1983). For example, if predation is relatively stronger than sexual selection, then color patterns will be more cryptic. If predation is relatively weaker, color patterns will be more conspicuous and closer to those predicted from the sensory exploitation model. If different elements of the signal are perceived differently, then they will reach different balances between the two selective factors. For example, if the predator is particularly sensitive to yellow and not very sensitive to red, then, even though both yellow and red may be equally bright to females, the balance between sexual selection and predation escape will favor male color patterns that emphasize red (Endler 1978, 1991).

The environment is spatially and temporally heterogeneous, and the physical properties of the environment affect the rates of attenuation and degradation of the signal (Lythgoe 1979; Wiley and Richards 1982; Halliday and Slater 1983; Ryan 1985, 1988*a*; Endler 1986, 1990). Most animals do not signal continuously but, rather, transmit at particular seasons, times, and in particular microhabitats; this has the immediate effect of ensuring a specific and predictable set of environmental conditions during transmission (fig. 1). For a species with a particular male signal, the signal can be transmitted effectively only at certain times and in certain places. Males that transmit at these times and in these places obtain more mates than males that transmit at times and in places where attenuation or degradation is greater. This is likely to favor increasing specialization of signaling behavior, which leads to better (less attenuation and degradation) and more predictable signaling conditions (fig. 1). This argument applies to the colors and scents of fruits and flowers as well as to animal signals; here, sensory drive will involve both the plant and its dispersers or pollinators. Specialized signaling behavior may also affect the general microhabitat choice of the species, particularly in animals.

If a species spends much of its time in a particular microhabitat and signals only under certain conditions, then the sensory system can evolve to best match the conditions. In fact, there is much evidence that sensory systems have evolved to be “tuned” to match the average characteristics of the environment. For

example, the spectral sensitivity of many unrelated fishes has converged to patterns specific to different classes of water color and ambient light conditions in which they live (Levine and MacNichol 1979; Lythgoe 1979; Lythgoe and Partridge 1991). Fish living in clear water (tropical marine and shallow fresh water) tend to be more blue sensitive than fish living in colored (green, brown, or reddish ["black"]) waters, and fish living in deep water (but still in the photic zone) tend to be less sensitive to reds than shallow-water species (Levine and MacNichol 1979). It is likely that the conditions under which sensory systems are used affect the evolution of those systems. Sensory conditions also affect the evolution of signals because they directly affect the form of received signals (Endler 1990, 1991) as well as indirectly affecting them through the evolution of sensory systems (fig. 1).

The sensory system's characteristics also affect how food is detected and perceived. Food items may be most easily detected at particular times and places, which will affect the evolution of microhabitat choice, timing, and season of activity of predators and prey. These changes will in turn affect the evolution of the sensory system (fig. 1). The detection of predators may depend on microhabitat choice, and this may also affect the evolution of sensory systems.

Figure 1 summarizes the major evolutionary interactions of sensory drive. There are a few intimately related processes that are also important, and these are shown in figure 2. First, microenvironmental specialization is likely to lead to changes in the visibility or detectability of food (v). Food detectability can change as a result of two different processes: (1) direct effects on conspicuousness caused by the interaction between the microenvironment and the sensory system and (2) natural selection on the food organism to minimize its visibility. These processes can result in food specialization and further habitat specialization, which in turn can affect sensory system evolution. Feeding success (fs) mediated by food visibility can also have direct effects on the evolution of sensory systems. Changes in microenvironment specialization affect the visibility or detectability (p) of the signals to predators, which also affects the signal design. As for food visibility, there are two processes arising from predation: (1) direct effects caused by interactions between the environmental conditions and the predator's sensory system and (2) natural selection acting on the predator to increase efficiency in that microenvironment. Both predators and food will affect the joint evolution of behavior, sensory systems, and signals.

Mating success and sexual selection also affect the process of sensory drive (fig. 2). Mating success (ms) can affect the evolution of sensory systems directly if mates are hard to detect or courtship rituals are very complex. Individuals with better senses may be more successful in finding mates than those with poorer senses, which would favor the evolution of sensory systems. In addition, sensory (and cognitive) systems with more signal-processing power may be able to assess mates more rapidly, which would reduce risk of predation during courtship or allow more matings per lifetime.

Sexual selection (ss) by female choice directly affects the evolution of mate-choice criteria (fig. 2), in addition to sensory drive. The direction of the Fisher process of sexual selection is unbiased with respect to the direction of evolution

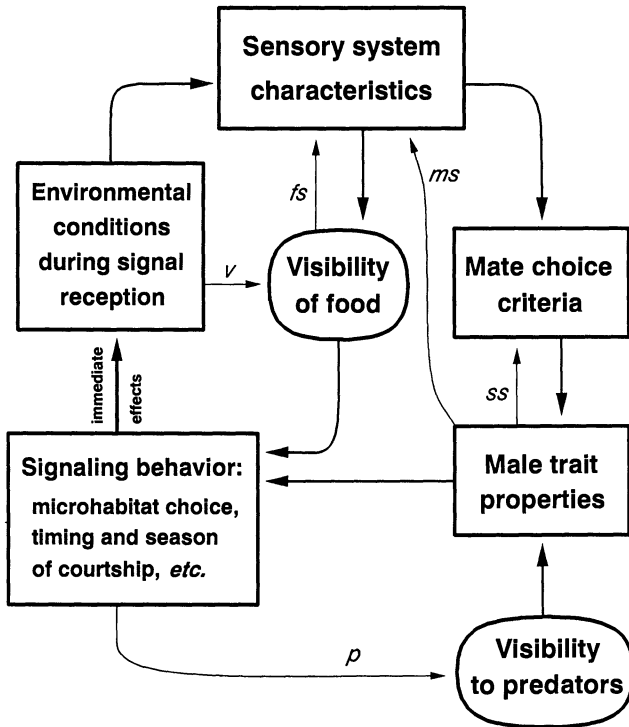


FIG. 2.—Sensory drive and other intimately related processes. *Thick arrows* are as in fig. 1; *thin arrows* indicate ancillary processes. v , Immediate effect of microenvironment on the visibility of prey, also natural selection acting on prey; fs , feeding success that directly affects the evolution of sensory systems; ms , mating success that might affect the evolution of sensory systems directly; ss , sexual selection (good genes or Fisher processes) that directly influences the evolution of mate-choice criteria; p , immediate effect of microenvironment on visibility to predators, and also natural selection caused by microenvironmental conditions acting on predator senses and behavior.

and requires some external factor to set its initial direction (Fisher 1930; Lande 1981; Kirkpatrick 1982). Sensory drive can easily set the initial direction of the Fisher process and thus can profoundly affect the direction of sexual selection. Various “adaptive,” “good genes,” or “handicap” systems of sexual selection favor kinds of traits that are good predictors of offspring fitness (Pomiankowski 1988; Grafen 1990), but the exact traits used may be determined by other factors, such as sensory drive. For example, carotenoid-based yellow and red colors may both indicate feeding success, but visual conditions and spectral sensitivity may favor the use of red. Sexual selection by intermale competition should also operate simultaneously with sensory drive; signals that males use to assess each other are subject to the same biophysical and neurobiological rules as other signals. It would be difficult for sexual selection to operate without sensory drive, and vice versa.

The major point of sensory drive, and of figures 1 and 2, is that the evolution

of sensory systems, signals, and behavior is coupled; changes in one suite of traits cause evolutionary changes in the others. These suites of traits must not be expected to evolve independently; they will coevolve. The evolution of these traits should not be random, but it should, in principle, be predictable from a knowledge of environmental physics and the biophysics and neurobiology of signal transmission and reception. Particular environmental conditions favor particular sensory characteristics. These characteristics favor specific mate-choice criteria, which in turn favor certain sexual signals. These signals are best sent under unique environmental conditions; thus, cycles of specialization of each suite of traits are established. A similar argument can be made for the traits involved in other kinds of signals.

SIGNAL CONTENT, STRUCTURE, AND CONSTRAINTS

Natural selection does not favor only signals that are efficient in transmission and reception. Guilford and Dawkins (1991) make an important distinction between the strategic and tactical "design" of signals. A signal's tactical design refers to its structure and efficacy: natural selection favors signals that are easily transmitted, received, detected, and discriminated from others, and those that are remembered most easily. For example, a particular sound pattern may be most easily heard under background noise conditions deficient in that frequency, and it may be easy to distinguish from other signals in the same frequency band if its temporal pattern is complex and unique. In contrast, a signal's strategic design refers to its purpose: natural selection favors signals that elicit a response in the receiver that increases or maintains the fitness of the sender. Thus, strategic design concerns signal content more than signal structure. Signals may contain true or false information about distance among neighbors (Morton 1982), social status, mate quality, and even the intentions of the signaler (Sebeok 1977; Halliday and Slater 1983; Pomiankowski 1988; Grafen 1990; Guilford and Dawkins 1991). Natural selection obviously affects both content and structure, but these often result from different processes. Sensory drive is primarily concerned with the structure or tactical design of signals; it does not address the content or strategic design of signals, although it may provide constraints as to what kinds of information can be sent.

Most of the theoretical and empirical literature on sexual selection is more concerned with signal content than structure. This is particularly true of the good genes, adaptive, or handicap approaches, in which females use signal content as a predictor of offspring quality (Pomiankowski 1988; Grafen 1990). In these approaches, the design constraints induced by sensory drive may limit or bias the kind of information that can be sent; for example, less information can be sent per unit of time under noisy conditions. Design constraints, however, can also be used to convey information. For example, if all territory holders send signals with the same sets of characteristics, and different parts of the signal degrade at different rates with distance, then the configuration of the received signal, in comparison with the "expected" signal, contains information about distance (Morton 1982) and also, perhaps, rate of movement. Such information

could help the receiver decide whether to approach, especially if travel costs are high. If higher-quality male territory holders are found at greater density, the same information might also be used to assess mate quality.

The Fisher models of sexual selection simply assume that females choose mates on the basis of the male trait (the received signal). If the Fisher process works by itself, the direction of sexual selection is not inherently biased relative to content, and sensory drive sets the direction of evolution of the traits. Sexual selection under the Fisher process is most likely to affect the structure of the signals rather than their content because it favors greater efficiency of signal reception and processing (which can also be favored directly by natural selection). Sexual selection under one of the good genes processes affects both structure and content. In the latter case, sensory drive affects the signal efficacy and constrains and biases the direction of the evolution of signal content.

Although I concentrate on signal structure in the rest of my article, I do not mean to imply that content is unimportant; in fact, both strategic and tactical factors should always affect the evolution of signals (fig. 2). In addition, signal structure will also evolve to be more efficient relative to events occurring in the brain. However, because little is actually known about the psychological aspects of communication and these aspects have already been explored by Guilford and Dawkins (1991), I consider only the processes occurring between transmission and reception. Genetic, phylogenetic, and physiological constraints also affect the evolution of signals, receptors, and behavior (i.e., in vision; Goldsmith 1990); however, except for the biases they may induce in the direction of evolution, I do not discuss constraints in this article. Again, this does not imply that these processes are unimportant, only that the purpose of this article is to explore the effects of signal design, reception, and associated behavior on the direction of evolution in these suites of traits.

A POSSIBLE EXAMPLE OF SENSORY DRIVE: VISUAL SIGNALS IN GUPPIES

The System

The color patterns of guppies (*Poecilia reticulata*) illustrate a possible example of the results of sensory drive for vision, visual signals, and behavior. Guppies are small poeciliid fishes of small mountain streams found in the tropical forests of northeastern South America. They are genetically polymorphic for color-pattern elements that vary in color (hue), brightness (total reflectance), size, and shape. The color patterns in a given population represent a compromise between sexual selection for conspicuousness and natural selection for crypsis (inconspicuousness), and the compromise varies geographically with predation intensity. A male guppy cannot be too conspicuous, or it will be eaten before it has a chance to mate, but it cannot be too cryptic, or it will not be attractive to females. Female preferences vary genetically among populations (Houde 1988*b*; Stoner and Breden 1988; Houde and Endler 1990), but, in general, females prefer males that are more conspicuous (Endler 1980, 1983; Kodric-Brown 1985; Houde 1987, 1988*a*, 1988*b*; Long and Houde 1989). Guppies vary with regard to the spectral

sensitivity of their long-wavelength-sensitive cones (Archer et al. 1987), which suggests a mechanism for variation in female preferences. If this variation is heritable, then direct natural selection of the visual system is possible. Guppies live in the company of a variety of combinations of diurnal visually hunting fish and invertebrate predators, and this geographically varying community structure results in predation-intensity gradients within streams. As diurnal visually hunting predation increases in space or time, those fish with greater average crypsis are favored (Endler 1978, 1980, 1983). There are differences in the timing of courtship relative to predation (Endler 1987), differences in visual conditions during courtship and predation, and differences in vision among guppies and some of their predators (Endler 1991). These factors reduce the compromise between sexual selection and crypsis, because they cause the same color pattern to be relatively conspicuous under some conditions and relatively cryptic under others (Endler 1991).

Ambient Light and Its Effects on Visual Signals

In order to describe sensory drive in guppies, it is first necessary to describe the environmental conditions during signaling and the effect of the ambient light on the appearance of the signal. These conditions and effects will also be used for the general predictions about visual signals.

Guppies live in streams that flow through tropical forests, which exhibit a mosaic of light environments (fig. 3). There are five different light environments—forest shade, woodland shade, small gaps, large gaps, and early/late—and these are determined by forest geometry, sun angle, and weather (J. A. Endler, unpublished manuscript). Forest shade results when most of the light reaching the surface of an animal or background has been transmitted through or reflected from vegetation; very little comes from the sky through canopy holes, and none comes directly from the sun (fig. 3). Forest shade is green or yellow-green because intermediate wavelengths are differentially reflected and transmitted by vegetation. Woodland shade results when a significant fraction of light comes from the open cloudless sky, the rest comes from vegetation, and none comes directly from the sun. Woodlands are forests with largely discontinuous canopy. Woodland shade is bluish or blue-gray, because the blue sky light overwhelms the light reflected from the vegetation. This light habitat is not limited to forests and occurs anywhere there is shade but where most of the sky is unobstructed by vegetation or clouds; this includes the shade of canopy emergents in a forest canopy and even the shade of boulders in the desert. Small gaps are patches of light with a diameter less than about 1 m (resulting from a canopy gap subtending less than about 1° solid angle). Small gaps tend to be relatively yellowish or reddish compared to full sunlight because virtually all of the ambient light comes directly from the sun; the sun is much richer in long wavelengths than the sky or vegetation. Large gaps yield “white” light and have essentially the same color as open areas because virtually all of the ambient light comes from the sun and open sky and little from the vegetation. Clouds are whiter than direct sunlight because they are simple diffusers of the blue sky and sun above them. When the sun is blocked by clouds and a large fraction of the sky is cloudy, then forest

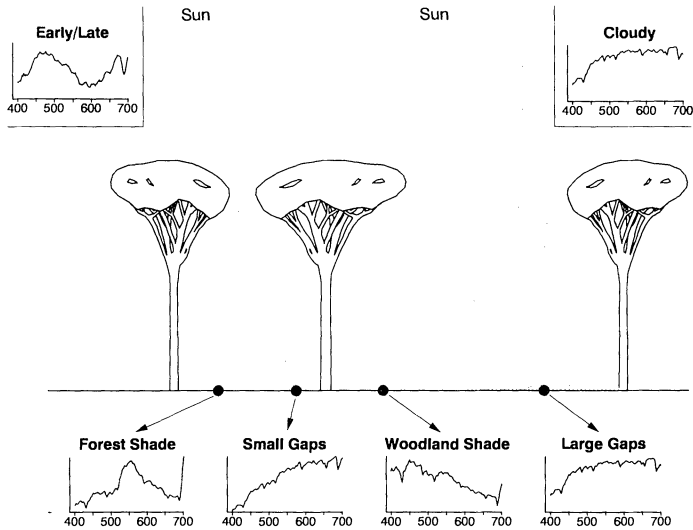


FIG. 3.—The major light environments of forest animals. The spectra shown are plots of the intensity of light as a function of wavelength (Endler 1990). *Forest Shade* is rich in middle wavelengths (green and yellow); *Small Gaps* are rich in longer (redder) wavelengths; *Woodland Shade* is rich in shorter (blue) wavelengths; *Large Gaps* exhibit essentially white light. When the sun is obscured by clouds (*Cloudy*), the spectra of these four habitats converge on that of large gaps or nonforested areas. In twilight conditions (*Early/Late*), the spectra of these habitats converge on a purplish light, deficient in middle wavelengths. If a forest canopy has taller emergent trees, then both woodland shade and large-gap environments will be found in the canopy.

shade, woodland shade, small gaps, and large gaps converge in color and are all “white,” as long as there are some holes in the canopy (fig. 3, *inset*). This convergence occurs for two reasons: clouds are brighter than blue sky and the radiance from vegetation, so they overwhelm these effects; and clouds are diffusers, so they increase the light coming through all canopy holes in all directions. As a result, heterogeneity in ambient light color disappears as soon as the sun is obstructed by a cloud. For this reason I refer to the white-colored habitat as “large gaps/open/cloudy,” or simply, “open/cloudy.” A fifth light habitat, early/late, appears when the sun is rising or setting, regardless of the weather. It is purplish (fig. 3, *inset*) because at those times intermediate wavelengths are differentially absorbed by ozone over the long light-path lengths. If there are clouds at those times, there may be a brief period of strongly reddish light caused by the reflection of long wavelengths off the clouds. In summary, depending on location, clouds, and time of day, a guppy (or any other forest animal) can be seen in greenish, bluish, reddish, whitish, or purplish light (forest shade, woodland shade, small gaps, open/cloudy, and early/late, respectively; fig. 3).

The color (spectral shape) of light reaching the viewer’s eye depends on the ambient light striking the color pattern, the reflectance spectrum of the color-pattern element (colored patch), and the spectral transmission properties of the water or air (Endler 1990). For example, a color pattern consisting of gray, blue,

yellow-green, and red patches shows high color and brightness contrast in white light (open or cloudy conditions; fig. 3), but under the yellow-green light of forest shade the yellow-green is very bright, whereas the blue and red patches are darker and duller. In woodland shade the blue is brightest (reflecting the greatest proportion of ambient light), whereas the other colors are duller. In small gaps the red patches are brightest, and the blues are the duller. In general, the patches whose reflectance spectra match the ambient light spectrum are the brightest, and those patches that mismatch are the duller, for a given total reflectance (Endler 1986, 1990, 1991). This affects both the brightness and color contrast of adjacent patches, thus affecting the overall conspicuousness of the color pattern (Endler 1991). The overall contrast is also affected by wavelength-specific absorption and scattering of light between the animal and the viewer. For example, in greenish water, blue and red patches attenuate more rapidly than yellow and green patches. Therefore, depending on the similarity between the radiance spectra of each patch and the water (or air) transmission spectra, the contrast can change markedly with distance (Lythgoe 1979; Endler 1986, 1990, 1991). Hence, even if the animal's pigment pattern remains constant, if it moves among different light environments, and if it is seen at different distances, its appearance can change dramatically (Lythgoe 1979; Endler 1986, 1990, 1991). By choosing when and where to court, a guppy or other animal can send very different visual signals in different environments (Endler 1991).

Sensory Drive in Guppies

The following situation is hypothetical but consistent with all our knowledge of guppies. Consider an ancestral guppy population with all color-pattern elements equally frequent (i.e., yellow is as common as blue and orange). A midday peak in predation favors most courtship early and late in the day and less courtship at midday (Endler 1987). Consequently, courtship takes place under different lighting conditions than those of maximum predation times (figs. 2, 3). There can also be a spatial shift because the different diurnal habitats (fig. 3) affect color conspicuousness in various ways (Endler 1991). Courtship and sexual selection favor color patches that reflect a greater fraction of the incident light during the times and places of maximum courtship activity and select against colors that reflect less light at those times and places. In general, the more light reflected, the greater the potential visual contrast. Because maximum courtship occurs under purplish light (rich in blue and red light; fig. 3), blues and oranges are favored, while yellows are at a disadvantage at this time of day. Predation selects against colors that reflect relatively more than other colors during times of maximum predation risk, and this makes yellow particularly disadvantageous. The conflicting effects of visibility to both mates and predators favor patches with maximum reflectance and contrast during courtship times and relatively little reflectance and contrast during predation. These differences are enhanced by differences in vision and viewing distances between guppies and their predators (Endler 1991). Visual differences favor colors that signal to other guppies at "private wavelengths," or at least those wavelengths to which predators such as the pike cichlid *Crenicichla alta* or the prawn *Macrobrachium crenulatum* are not

very sensitive (Endler 1978, 1991). As the color patterns become more and more efficient for courtship and less visible to predators at particular times and places, there is selection for microhabitat choice, because courtship, feeding, and other activities at other times and places result in lower mating success and greater predation risk. At times of predation risk, guppies become less visible to potential mates and more visible to predators (Endler 1991). All of these factors induce natural selection acting on the visual system for increased efficiency at particular times and places. The net effect is that the sensory system and sensory conditions can affect the visibility of male traits and, hence, mate-choice criteria (through visibility effects), color-pattern design, and microhabitat choice and timing of courtship; these factors, in turn, can affect the evolution of the sensory systems. This leads to a cycle of evolutionary interactions, as shown in figure 2.

SOME GENERAL PREDICTIONS FOR VISUAL SIGNALS

The example of sensory drive in guppies and the general scheme shown in figure 2 would be difficult to demonstrate directly. Yet it is possible to predict how suites of sensory, signal, and behavioral traits should jointly evolve and, hence, be distributed in nature. The predictions in the next section apply to conspecific visual signals and aposematic signals but not to crypsis. Note that these predictions are tentative and qualitative; specific and quantitative predictions would require a detailed knowledge of the vision, signals, environmental physics, and behavior of the animals concerned.

Maximizing Conspicuousness

In a particular light environment, a color pattern is most conspicuous if its adjacent color-pattern elements vary greatly in brightness (total reflectance) and chroma (saturation or color purity), and it is less conspicuous if it varies less in these parameters (Endler 1990, 1991). Spectra with high saturation have rapid transitions in intensity as a function of wavelength, whereas those with low saturation have only gradual transitions (Endler 1990). Unsaturated (low chroma) colors change with ambient light more than saturated colors; a perfectly unsaturated spectrum, such as white or silver, simply reflects the same colors that strike it.

There are four ways to maximize color-pattern conspicuousness. The simplest method is to have color patterns with light patches (white, light gray, or other highly reflective unsaturated colors) adjacent to dark patches (black, dark gray, or others with low reflectance and chroma). But color patterns with adjacent unsaturated colors of contrasting reflectance are disadvantageous in that they are conspicuous in nearly all light conditions to nearly all species, so any advantage in courtship may be offset by increased predation.

The second method of maximizing conspicuousness is to match the brightness of the ambient light and water (or air) transmission spectra. If the ambient light striking an animal is not white, then it consists of some high-intensity wavelengths and other low-intensity wavelengths. To be conspicuous, a color pattern should have colored patches that reflect high-intensity ambient wavelengths and these

patches should be adjacent to patches that reflect low-intensity wavelengths. For example, in bluish light, a blue patch would reflect most light striking it (bright spot), whereas a yellow or red patch would reflect very little light (dark spot), and a green patch would be intermediate, assuming the same total reflectance.

The third method of maximizing conspicuousness is to have adjacent patches with complementary colors, such as red and green or yellow and blue. Complementary colors are colors whose spectra have few or no wavelengths in common, for example, blue and yellow. The radiance spectrum of a blue spot is rich in wavelengths below 500 nm but radiates little light above 500 nm, and a yellow spot radiates much above 500 nm but little below 500 nm. Adjacent patches are the most conspicuous because their complementary radiance spectra stimulate combinations of wavelength-specific photoreceptors (cones) in opposite ways, which maximizes color contrast (Lythgoe 1979; Hurvich 1981). This maximization of contrast depends on the peak absorbance wavelengths of the cones relative to the cutoff wavelengths (the wavelength at which radiance changes from low to high, for example, at about 600 nm for an orange patch), as well as on the details of the neural connections in the retina and the brain. Thus, two patches that are complementary for one species may not be complementary for another, and so they will seem less bright to the latter species as compared to the former.

The fourth method of maximizing conspicuousness is to use complementary colors whose cutoff frequencies are centered in the region of the greatest ambient light intensity and water (or air) transmission. For example, in the bluish light of tropical marine water, blue and yellow are more conspicuous than red and green, whereas, in the greenish light of temperate lakes and ponds, red and green are more conspicuous than blue and yellow. This fact may explain the relative abundance of these pairs of colors in tropical marine and temperate lake fishes, respectively (Lythgoe 1979). As in the case of brightness matching, any change in ambient light and/or transmission spectra will change the relative contrast of pairs of colors that are complementary at different parts of the spectrum.

Divergence of Species and Populations

Closely related species that live in different light environments should exhibit the following differences: predictably different color-pattern characteristics, predictably different sensory characteristics, and predictably different behavior. These differences may also apply among populations of widespread species if they vary geographically in microhabitat and light environment. Because there are five major light environments in forests (fig. 3), these predictions can be made more specific. (These predictions are based on the four methods of maximization of contrast and conspicuousness described in the previous section.)

Color-pattern characteristics.—Species that live in forests with continuous canopy and that court in forest shade (fig. 3) should use primarily red and orange and a little blue for increased contrast within the color pattern. Species that live in woodlands or in the canopies of forests (geometrically equivalent to woodlands) and that court in shade (woodland shade; fig. 3) should use primarily blue, blue-green, and, if possible, ultraviolet patches, with a little red for increased contrast. Species that court in small gaps should use yellow or orange, with some purple

for increased contrast. There are no particular predictions for species that live in large gaps or court anywhere in forests or woodlands when the sun is obscured by a cloud (open/cloudy; fig. 3), because all wavelengths are roughly equally abundant; therefore, no colors would be more efficient than others in maximizing the signal conspicuousness. If one were to compare the color patterns of species living in evergreen tropical forests to those of species living in deciduous tropical forests, one would also expect to find, on the average, more use of ultraviolet, blue, and green in seasonal forests, because woodland shade would be more common there than forest shade. During the dry season there is very little continuous canopy (fig. 3) in tropical deciduous forests, but the canopies of tropical evergreen forests remain relatively continuous all year. Similarly, species that breed in the dry season should use blue and green in their visual signals more often than those that breed in the wet season. One has to know exactly where the species display when one tests these predictions. For example, the light environment at or near forest canopies is essentially the same as woodland: the canopy emergents form a discontinuous canopy resulting in a mosaic of woodland shade and large gaps immediately below the emergents. Consequently, we would expect a greater frequency of blue and green in canopy species than in forest floor and subcanopy species, all in forests with continuous canopy.

Because all forest light environments converge on large gaps or open areas during cloudy weather (fig. 3), these predictions should have greater accuracy in places and times with fewer cloudy days and should be least accurate in cloud forests. Because the relatively flat ambient light spectra of cloudy days in forests do not favor any particular combination of signaling colors, there should be a greater diversity of signaling colors in cloud forests than in other places with lower numbers of cloudy days per year. There are two common patterns in tropical rain forests during the wet season. In some places (such as Costa Rica) heavy rains come in the afternoon, but it is frequently sunny in the morning. In other places (such as Trinidad) there is no predictable pattern, and it may be cloudy all day. Thus, one would predict a greater diversity in the signaling colors of wet-season breeders in places where the cloudiness is unpredictable and common than in places where there are regular sunny periods in the wet season. These predictions should also be more accurate for species that are active only when the sun is out (tanagers, orioles, and many species of butterflies) and inactive as soon as the sun is obstructed by clouds. But they will be invalid for species that are usually active when the sun is obscured by clouds.

Visual characteristics.—The characteristics of the sensory system should match those of the environment in order to make the most use of available signals. Species displaying in forest shade should be relatively more sensitive to yellow-green and perhaps red than species displaying in the open or in large gaps. Species displaying in small gaps should be relatively more sensitive to longer wavelengths (yellow, orange, and red). Species displaying in woodland shade should be relatively more sensitive to blue and blue-green. In general, species found in continuous forest (forest shade and small gaps) should be more sensitive to longer wavelengths, whereas species found in woodlands (woodland shade and large gaps) should be more sensitive to shorter wavelengths. Once again, canopy species in

forests should be more similar to woodland species than either is to forest floor and subcanopy forest species. These predictions, like those for signaling colors, need to be modified to account for the frequency of cloudy weather.

Behavior.—Behavior involving visual signals to conspecifics or, if aposematic, signals to potential predators should also vary with the environment. Signals should be sent at the times and in the places and seasons in which their signal-noise ratio will be maximized. For example, if a bird uses blue to signal to conspecifics, it should do so in the shade of canopy emergents (effectively woodland shade) rather than in the dense shade found deeper in the forest (forest shade), and it should not be as active when the sun is obstructed by clouds. The need to signal to conspecifics while minimizing the signals to predators also affects places in which the animal forages. Thus, species found in shady microhabitats in forest canopies (woodland shade) are also found in woodland habitats, the edges of tree falls, and disturbed sites, whereas species found in shady habitats beneath continuous canopies (forest shade) are much more habitat specific. By the same logic, species specializing in small gaps may have a large height range within forests but probably will not go outside dense forests. The same arguments may apply also to single isolated shrubs for smaller insects, because the light environment varies with geometry in the same way as in forests, but on a much smaller scale. Species that signal when in the sun should have a greater range of habitats and microhabitats than those signaling in one of the shade microenvironments. Similarly, species that are active during cloudy conditions should also have a greater range of habitats and microhabitats than those that are active only when the sun is not blocked by clouds.

The evolution of behavior and color patterns should interact. If behavior is indeed selected to maximize the efficiency of signal transmission and reception to conspecifics while minimizing the signals to potential predators (fig. 2), then there are certain characteristic color-pattern designs that should evolve repeatedly in order to allow the same body-reflectance pattern to send different signals at different times and under different conditions.

One way to vary signals using the same color pattern is to take advantage of the relation between brightness matching and contrast. Brightness matching of the ambient light and transmission spectra can increase contrast, but this depends on the spectra of the animal's color-pattern patches. For example, as mentioned earlier, in bluish light, a blue patch would be bright whereas a yellow or red patch would be dark, and a green patch would be intermediate, if one assumes the same total reflectance. The relative radiance of the three patches would shift markedly under green, yellow, or red light and, consequently, so too would the color pattern's brightness and color contrast (Endler 1986, 1991). The effect can be stronger if the color pattern consists of both saturated and unsaturated colors. The radiance of unsaturated colors changes with ambient light more rapidly than that of saturated colors (fig. 4). This allows the degree of conspicuousness to vary with light conditions. The transmission properties of colored water or foggy or dusty air may also be taken advantage of in order to vary the conspicuousness of a single color pattern. Displaying at short distances to conspecifics while being seen at longer distances by predators and using combinations of colors such that

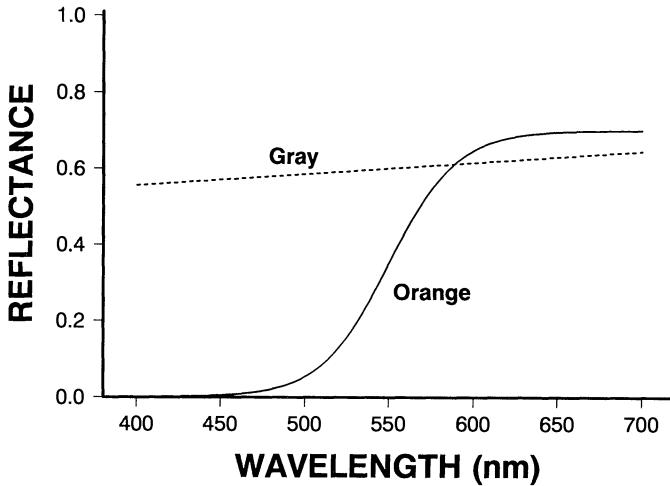


FIG. 4.—An example of how the color of ambient light affects the contrast between two different patches, in this case, a brownish gray and an orange patch. If both patches were illuminated by white light (same intensity at all wavelengths), the gray patch would be brighter because it reflects 1.71 times as much light as the orange patch; the orange patch reflects very little light below 550 nm. If both patches were illuminated by orange light (no light at 400–550 nm, flat spectrum at 550–700 nm), the relative brightness of the two patches would be very similar (0.98:1.00), and an orange patch would disappear on the gray background (everything would appear orange to an animal with color vision). This is simply because the reflectances of the two patches are similar in the available light. However, if both patches were illuminated in greenish light (flat spectrum at 400–550 nm; no light at 550–700 nm), there would be very high brightness and color contrast because the gray patch would reflect 8.74 times as much of the available light as would the orange patch. The orange patch is most efficient in reflecting the available light if the available light is orange or red. Similar effects are found for other colors; patches are most efficient as signals if they match the ambient light spectrum.

the pattern has lower contrast at longer distances also allow behavioral manipulation of the appearance of color patterns, as in guppies (Endler 1991).

Another way in which conspicuousness may vary is if the color pattern consists of colors easily seen by mates but not seen or relatively poorly seen by predators. For example, blue patches of guppies can be seen by other guppies but are probably not as conspicuous to *Crenicichla*, and orange patches can be seen by guppies but are probably not as conspicuous to prawns (Endler 1978, 1991). Because there is so much variation in spectral sensitivity among fish species (Levine and MacNichol 1979; Lythgoe 1979) and among other vertebrates and invertebrates (Jacobs 1981; Laughlin 1981; Goldsmith 1990), there may be ample opportunity for private wavelengths throughout the animal kingdom. As mentioned earlier, the conspicuousness of complementary colors may also vary with the predator's vision.

As in the case of conspicuousness, these methods are probably used by a wide variety of species, but comparative studies have not yet been made. The predictions about visual signals reveal only the "tip of the iceberg" regarding the

TABLE 1
RULES FOR SIGNALING WITH SOUND

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1. Use lower frequencies (<2 kHz) in order to minimize reverberation, attenuation, and scattering by the atmosphere, objects, and "shadows" resulting from temperature gradients. Do not use frequencies that are too low (>0.5–1 kHz) to minimize destructive interference and to avoid energetically costly coupling between low-frequency sound generation and the atmosphere.
 2. Send signals from a position that is greater than 1 m above the ground and preferably upwind of the receiver, in order to minimize destructive interference from ground reflection and temperature-gradient effects.
 3. Avoid rapid syllable repetition rates in places (such as forests) with strong reverberation.
 4. Use frequency modulation rather than amplitude modulation because reverberation and turbulence modify sound amplitude more than frequency.
 - *5. Use redundant signal structure in order to average out background noise.
 - *6. Use greater amplitude and/or physical structures to beam the signal more effectively.
 - *7. Use higher frequencies if much information must be transmitted in a short time because receptors have a faster frequency response at higher frequencies, and there will be less degradation by turbulence.
 - *8. Use species-specific frequency bands and tuned receptors in order to minimize noise at other frequencies.
 - *9. Choose frequency bands, places, seasons, and times of day that minimize turbulence and/or background noise.
 - *10. Avoid signaling at the same time as immediate neighbors (unless jamming their signals is desired).
 - *11. Use rapidly degrading signals for short-distance communication and slowly degrading signals for long-distance communication.
 - *12. Use simpler, more effective alerting signals to attract the receiver's attention before sending the main signal.
-

NOTE.—Rules marked with an asterisk also apply to other sensory systems. The table is modified from Wiley and Richards 1982; Capranica and Moffat 1983; Brenowitz 1986; Okanoya and Dooling 1988; and Ryan 1988*b*.

effects of sensory drive on systems related to visual signaling and would repay much further research. Additional predictions about color patterns are discussed in Endler (1978, 1984, 1986).

SOME GENERAL PREDICTIONS FOR ALL SENSORY SYSTEMS

Introduction: Sensory Drive for Sound

Sensory drive (fig. 2) should apply to all sensory systems and signals, not only to vision and color patterns. For example, there is enough known about sound and hearing to make some general rules about the optimum design and timing of (terrestrial) auditory signals; these are summarized in table 1. There is good evidence for the operation of these rules in crickets (Jones 1966; Greenfield 1988; Simmons 1988), frogs (Capranica and Moffat 1983; Ryan 1988*a*, 1990; Brush and Narins 1989; Ryan and Rand 1990; Narins 1992; Ryan and Keddy-Hector 1992), birds (Henwood and Fabrick 1979; Richards and Wiley 1980; Dooling 1982; Wiley and Richards 1982; Brenowitz 1986; Okanoya and Dooling 1988), mole rats (Heth et al. 1986), and primates (Waser and Waser 1977; Waser and Brown 1984). For detailed discussions, see Wiley and Richards (1982), Brenowitz (1986), and Okanoya and Dooling (1988). From this research, it is easy to envision sensory drive for sound: the auditory system favors particular traits in male songs and

calls that are best used under particular conditions, times of day, and seasons. These traits then favor specialization of the auditory system for use in those microhabitats, which in turn affects mate choice and male sounds. A similar process should work in chemosensory and electrosensory systems as well, and, indeed, many of the rules in table 1 (marked with an asterisk) apply to other sensory modes.

If sensory drive works in all sensory modes, then it should be possible to make some general predictions about the evolution of signals, sensory systems, and behavior by using the clues gained by a study of visual and auditory signals. The following are some of the ways in which sensory drive should affect the direction of evolution of these suites of traits. Once again, these are tentative and purely qualitative predictions; detailed and quantitative predictions require detailed knowledge of sensory biology, environmental biophysics, signal structure, and behavior.

Increasing Signal Intensity

Signals should evolve to maximize the signal-noise ratio for the receiver under the conditions in which they are sent and received. One of the simplest ways of accomplishing this is to increase the intensity or amplitude of the signal (Capranica and Moffat 1983). There is much evidence for this in a variety of organisms and sensory modes; females usually prefer males with brighter, more contrasting colors, faster motion or flashing during visual display, louder sounds, stronger chemical or electrical signals, and so on (see especially Ryan and Keddy-Hector 1992). Larger body size and tail length are also frequently favored. Although other explanations for these preferences are often given, larger tails or bodies give a stronger visual signal, especially if the display is accompanied by movement. It is probably safe to predict that signals should evolve to become stronger, with constraints set by the genetics and energetics of signal production (for a discussion of constraints in sound, see Ryan 1988*a*, 1988*b*; for a general discussion of signal-intensity limits in any sensory mode, see Cohen 1984). However, if the signal is given against intense background noise, natural selection may favor a weak signal, and the "hole" in the background noise, which contrasts the signal and the noise, is the real signal. Black or dark animals against white or bright backgrounds are a good example, and this kind of signal may be used by crows, ravens, and vultures. The difference between the pattern of light sent by an animal and the resulting visual contrast between the animal and the background illustrates that one needs to be careful about what is meant by "signal"; signals are context-dependent (Endler 1978, 1984, 1986, 1990).

The signal-noise ratio can also increase through the evolution of signal design. This is affected by the physics of the environment through which the signal must travel, the biophysics of signal reception and processing, and the problem of not signaling to predators at the same time.

Reducing Signal Degradation

Natural selection to reduce signal degradation and the physics of the environment favors particular kinds of signals with particular properties. At the most

basic level, the sensory mode that evolves to predominate in signaling will be the one with the greatest efficiency of transmission in the local environment (Wiley and Richards 1982; Capranica and Moffat 1983). For example, signaling is most efficient for vision by day in places where an unobstructed view is possible, for hearing in dense vegetation or at night, for electroreception in streams with cloudy water or nocturnal species, and for chemical communication in burrows. Because signals in all sensory modes are degraded by the environment and during detection, if all else is equal, the sensory mode with the greatest potential for information-transmission rate should be used in preference to modes with narrower bandwidth. For example, visual signals contain temporal and spatial components, and the spatial component (at any one instant in time) varies in intensity and spectral composition. Thus, the added spatial component may mean that visual signals are able to transmit more information than sound or electrical signals, which contain only temporally varying information. Chemical and some tactile signals may be able to transmit much information, but they cannot be frequency or amplitude modulated as rapidly as visual, auditory, or electrical signals. The choice of sensory mode or modes used in signals depends on both environmental degradation and potential information-transfer rate. Using many sensory modes is always better than using a few or one, but environmental conditions, energetics, and developmental constraints may limit how much each mode is actually used. Because these conditions may vary from place to place and among species, the use of multiple-mode signaling should also vary. The relative importance of different sensory modes can vary among species within a genus; for example, different *Drosophila* species use different combinations of visual, auditory, and chemical cues during courtship (Ewing 1983). It should be possible to predict which mode (or modes) is most useful and, therefore, which mode is most commonly used, if one knows the physics of the environment and the design of the signals.

Within a sensory mode it should be possible to predict many of the details of the signals as well as the microhabitat, time, and season of transmission, if we know the environmental physics. The design should be one that attenuates and degrades as slowly as possible, and it should be sent in the microhabitat and at the time and season in which degradation is minimized. Many details were given earlier in this article for vision and hearing, and similar logic could be used in other sensory modes. For example, in turbulent air or streams in which water of different salinities or light transmission spectra are mixing turbulently, frequency-modulated signals are better than amplitude-modulated signals (for electric and sound signals, see Brenowitz 1986), and the signal sender should choose places and times with minimum turbulence. Electric signals are affected by water salinity, so breeding electric fish should avoid the wet season or particularly rainy days, when salinity is reduced (Brenowitz 1986). For any sensory system, signaling behavior and microhabitat choice can be used to maximize the signal-noise ratio.

If there is geographical variation in degradation within the range of a species, then its signals should vary accordingly. There are several examples. In sticklebacks (*Gasterosteus aculeatus*) the red nuptial color is much rarer in places where

the water strongly absorbs red (Reimchen 1989). The geographical variation for orange preference in guppies (Houde and Endler 1990) may also relate to water color. A frog species and several bird species show the predicted song variation with habitat among populations within species (Bowman 1979; Hunter and Krebs 1979; Gish and Morton 1981; Anderson and Conner 1985; Ryan et al. 1990), and an apparent exception may be explained by air turbulence (Wiley and Richards 1982). Two different populations of *Drosophila mojavensis* show different combinations of epicuticular dienes, which are used as pheromones and affect mate choice (Markow and Toolson 1990). This is a particularly interesting example because the volatility of these hydrocarbons is temperature-dependent and the mean temperature of the two sites is different; both factors affect signal efficiency. In addition, the dienes affect water balance, so the direct effect of signal efficiency and natural selection for water regulation may jointly bias the direction of the evolution of pheromones in different populations (Markow and Toolson 1990). It would be interesting to know how common geographical variation in signals is within species. There should also be a correlation between signals and habitat among species; this is reasonably well known for color patterns in fish (Levine and MacNichol 1979; Lythgoe 1979) and for sound, as mentioned earlier, and it would be interesting to know whether it is true for other sensory modes.

Reduction of Noise

The signal-noise ratio can be increased by reducing background noise. Behavior should evolve so that signals are sent and received at places, times, and seasons with low ambient noise, which would otherwise mask or degrade the signal. As mentioned earlier, male guppies signal to females at a time when they will reflect the most light and show the greatest visual contrast within the color pattern (Endler 1991). An *Anolis* lizard must move its head and dewlap at a frequency different from that of the moving vegetation background (Fleishman 1988, 1992). The same considerations apply to predators: the *Anolis*-eating vine snake (*Oxybelis aeneus*) vibrates its body at approximately the same frequency as the oscillations of the vegetation background in order to minimize detection by *Anolis* and, perhaps, the snake's own predators (Fleishman 1986, 1992). Noise can come from other species, which is a problem particularly when they are closely related (Brush and Narins 1989; Narins 1992). Because the conspecific signaling time is also adjusted to a time of minimum environmental noise, the presence of conspecifics may cause a trade-off between reducing random environmental noise at certain times and reducing conspecific noise at other times (Capranica and Moffat 1983). *Neoconocephalus* katydids are a good example. In the absence of congeners, four species of katydids sing at night. However, *Neoconocephalus spiza* sings by day wherever it is sympatric with one or more of the other three species (Greenfield 1988).

At very low signal intensities the choice of when and where to signal becomes even more important. For example, vertebrate rods can react to single absorbed photons (Lythgoe 1979) but will fire spontaneously even in the dark, because of molecular noise. At very low light levels, when rods are responding to the occasional single photons striking them, random noise can significantly degrade the

image (see photographs in Lythgoe 1979) because the spontaneous firing rate may be similar to the signal (signal-noise ratio near 1.0). As the temperature of the retina increases, the molecular noise increases, which makes detection of weaker signals increasingly difficult. As a result, toads and frogs are actually more sensitive when they are cold than when they are warm (Aho et al. 1988). Because the chemistry of visual pigments is very similar among vertebrates and invertebrates (Goldsmith 1990), visual signals involving the lowest light intensities might also occur at the lowest temperatures, such as at night (fireflies) and in the deep sea. The temperature-dependent signal-noise ratio applies to all sensory systems, so we might also expect the weakest signals in any mode to be most common at night and cooler seasons. Of course there are other possible reasons for these patterns. For example, signaling can occur at night as a result of stronger diurnal predation. Weaker signals could occur at night because there is less environmental (rather than thermal) noise at that time; therefore, weaker and energetically cheaper signals are required to yield a given minimum signal-noise ratio.

The properties of visual signals generated by the animal (bioluminescence) can be quite different from those redirected from the environment (color patterns). Most nocturnal fireflies send a green signal similar in spectral composition to the vegetation background (Seliger et al. 1982). This spectral matching causes a larger fraction of the emitted light to be reflected off the vegetation than if the flashes were white with the same photon flux. If the flashes were white, then longer and shorter wavelengths would be differentially absorbed by the vegetation, which would yield a weaker signal. Fireflies that flash at dusk have a different problem, because there is significant ambient light that can interfere with their signals. However, at dusk the light is purplish (deficient in middle wavelengths; fig. 3). Fireflies that flash at dusk minimize the interference of ambient light by flashing with a yellowish rather than a greenish light (Seliger et al. 1982). Their yellow flashes are rich in intermediate wavelengths, precisely the wavelengths that are least intense at dusk, making the signal-noise ratio much higher than it would be if they flashed green (Seliger et al. 1982; Endler 1991). Note the difference between the yellow flashes of dusk-signaling fireflies and the rarity of yellow in guppies signaling at the same time. Unlike fireflies, the signal from a male guppy originates in the ambient light, so its color patterns must match the ambient light in order to reflect a high proportion of it, which thus keeps a relatively high signal-noise ratio.

Signal Receiver Design

A larger signal-noise ratio can also be achieved by specialized design of the signal receptors and how the signals are processed after reception. A common way to reduce noise is to adjust the characteristics of the signal receptors to match the characteristics of the signal (Capranica and Moffat 1983). This is most efficient if the noise exists over a broad band of frequencies (light, sound, or electric signals) or chemicals. If a signal consists primarily of only a limited range of frequencies, then a tuned receptor attains a higher signal-noise ratio than one that has a broad sensitivity. For example, fireflies that flash yellow light at dusk are particularly sensitive to yellow light and not very sensitive to other wave-

lengths (Seliger et al. 1982). If these fireflies were sensitive to green light, as are their night-flashing congeners, then they would receive much irrelevant background light (noise) and proportionally less signal from their flashes. This signal matching is quite common in virtually all sensory modes in which it has been examined, which yields a good correlation among species between signal characteristics and receptor properties. For example, receptor signal matching is found in color patterns and vision in fishes (Levine and MacNichol 1979; Lythgoe 1979) and *Lycaena* butterflies (Bernard and Remington 1991), in motion detection in lizards (Fleishman 1986, 1988, 1992) and insects (Alexander 1962; Seliger et al. 1982), and in hearing in birds (Wiley and Richards 1982; Okanoya and Dooling 1988) and frogs (Ryan 1990). A correlation between signals and signal receptors should exist within the limits of energetic and phylogenetic constraints (Ryan and Brenowitz 1985; Ryan 1988a, 1988b, 1990), and the correlation should be tighter for those environments and those senses that are associated with greater environmental noise. The signal tuning may be set to minimize the noise in the environment, but it automatically favors those individuals who send signals best matching the receptors: this is Ryan's (Ryan 1990; Ryan and Rand 1990) "sensory exploitation" model (fig. 1, *shaded areas*). The evolutionary result is that signals are tuned to match the characteristics of the receptors. Of course, the receptors can also evolve (fig. 2).

Noise reduction by tuning need not be restricted to frequency bands but may involve nearly any aspect of signal structure; the only criterion is reduction of background noise. This is most apparent in visual signals, which are very multidimensional. A variety of vertebrate and invertebrate visual systems have various kinds of edge detectors and neural "units" that preferentially respond to particular shape and size elements of images and to motion in particular directions and speeds (Ewert et al. 1983; Guthrie 1983; Stone 1983; Blakemore 1990). Thus, any signals other than those that fit the receptor characteristics in great detail are automatically filtered out. For example, fiddler crabs and other semiterrestrial decapod crustaceans are very sensitive to vertically oriented objects, and a vertical tower at the burrow of *Uca beebei* is a significant component of female choice (Christy 1988). Of course the pillars also allow fiddler crabs to find their beach burrows in a hurry when they are chased by predators. This "template matching" between specific signal structure and neural units in the brain has also been suggested for sound but so far has only been demonstrated in foraging bats (Carranica and Moffat 1983). It is possible that these signal-specific properties of the sensory system can predispose the evolution of female choice and male traits in particular directions (Basolo 1990; Ryan 1990; Ryan and Rand 1990; Ryan and Keddy-Hector 1992).

Pattern-specific visual properties may also have profound implications for habitat selection. For example, Morton (1990) found that male hooded warblers (*Wilsonia citrina*) preferentially orient themselves toward vertical stripes and prefer artificial habitats with tall stems rather than those with low, dense stems. Females orient themselves preferentially toward diagonal stripes and have no significant preferences for different artificial habitat structures. These differences are associated in the field with males' spending more time in the forest and females' spend-

ing more time in shrub or open habitats in the overwintering grounds (Morton 1990). These differences are also associated with differences in the mean and variance of male and female color patterns, which one would expect from the radically different light environments of the two habitats (fig. 3). For poikilotherms, particularly small ones, such as insects, strong microhabitat preferences are associated with a host of biological consequences that tend to be associated with different microenvironments (Willmer 1982), which further encourages differentiation. These are the kinds of differences that could easily cause and maintain species differences and could suggest ways in which sensory systems, signals, and behavior can coevolve (fig. 2).

Signal Processing

Special mechanisms of signal processing can also increase the efficiency of a signal. One way to circumvent problems of both background and sensor noise, especially at low signal intensities, is by averaging a signal over time. If noise from the environment or the receptors is random, then averaging a signal causes the random noise fluctuations in the received signal to cancel out; thus, a greater frequency of signals with redundant and repetitive structure should evolve in sensory modes and environments with greater noise. Certainly many signals are repetitive, but there are not yet enough data on environmental noise to test this prediction.

Another factor is sensory adaptation or habituation—the phenomenon, common to all senses, of ignoring constant signals. This may allow unpredictable and complex, yet monotonous, background noise to be filtered out. The commonness of sensory adaptation suggests that temporally varying signals should be more common than constant ones. This is true even in complex visual signals; visual displays are usually associated with motion. But sensory adaptation may require the use of alerting signals. Alerting signals are special simple signals designed to attract the receiver's attention before the main signal is sent; examples of alerting signals are found for both vision (Fleishman 1988) and hearing (Wiley and Richards 1982).

Signal-processing mechanisms may set limits to signal reception and, hence, bias the direction of the evolution of signals and signal receptors. Response rate is a good example. In vision, if a flicker or motion is too rapid, then the signal is degraded or missed entirely (Lythgoe 1979); this is called flicker fusion. Flicker fusion can set an upper limit to the rate of displays, although this limit may not be reached in some species (e.g., butterflies; Magnus 1958). In fish there is a wide range in the maximum frequency at which flicker is no longer resolved, from 14 to 67 Hz (Lythgoe 1979). In general, faster-moving species have higher flicker-fusion frequencies, which are needed in order to track and visually investigate more rapidly moving objects (and backgrounds): another example of the correlation between sensory properties and behavior. Flicker-fusion frequency decreases with light intensity (Lythgoe 1979), so one can predict that motion associated with visual displays at low light levels should, on the average, be slower than that of visual displays at higher light intensities. Flicker-fusion frequency is also wavelength-dependent, at least in vertebrates; blue-sensitive cones tend to have

lower flicker-fusion rates than middle- or long-wavelength cones. Thus, blue and green should be used in rapid visual displays less often than yellow and red, especially at lower light intensities. However, if the *rate* of motion is an important part of motion, then interference colors, which change total reflectance and color as a function of visual angle, are superior to other colors, particularly at short wavelengths. In hearing, the temporal response is faster at higher frequencies, leading to a trade-off between spectral and temporal information in bird songs (Okanoya and Dooling 1988). If environmental conditions favor songs with particular frequencies, then these conditions will affect what kinds of information can be transmitted and how rapidly. Another example is visual acuity, the smallest visual angle that can be resolved (Goldsmith 1990). Because visual acuity decreases with decreasing light intensity, color patterns with larger spots and patches are predicted to be more common in signals sent at lower light intensities. Visual acuity also sets the lower limit to spot size that is used in signaling at any light intensity.

Avoiding Predation

All of the foregoing factors can be used to predict the direction of the joint evolution of signal properties, receptor properties, behavior, and microhabitats of species. But this ignores the fact that signals between conspecifics can be used by predators, so many signals may reflect an evolutionary compromise between signaling to conspecifics and avoidance of signaling to potential predators (Endler 1978, 1983, 1986, 1988, 1991; Tuttle and Ryan 1982; Ryan 1985, 1988*a*). Predicting where the compromise should fall is much more difficult than simply predicting the best signal. However, there are at least five ways to reduce the need for a compromised signal.

First, choose times and places that serve to increase the distance at which predators detect and recognize prey while at the same time not degrading the signal to conspecifics. For example, signalers that signal from shade can perceive other animals (including predators) at a greater distance than those that signal in the sun (Helfman 1981). There are two possible reasons for this: (1) the sunlit viewer (predator) has a raised contrast-perception threshold, which makes it more difficult to detect contrast at the relatively low light levels in the shade, and (2) veiling light is greater in sunlit water (or foggy or dusty air) than in shaded water (or air). Shade signaling probably works in fish (Helfman 1981) and could work in other aquatic or terrestrial animals. In aquatic environments the distance at which predators first detect prey can also be decreased by prey's choosing to signal adjacent conspecifics in water that attenuates the signal rapidly. In water or on land there is an additional advantage for aposematic animals to signal from a greater distance. This allows more time for an approaching predator to remember the noxious properties of the signaler and to decide correctly not to attack (Guilford 1986, 1990).

Second, aggregate with other conspecifics. Aggregation makes any single signaler less vulnerable to predation (Endler 1986), but it leads to a trade-off with interference among adjacent signalers (Brush and Narins 1989; Narins 1992). For aposematic prey, aggregation may also serve to enhance the signal or its rein-

forcement in the predator's brain (Guilford 1990). Third, display intermittently in order to reduce the probability that a predator will be present to detect or locate the signal. Displaying intermittently also reduces the probability that a conspecific will receive the signal, unless calling and activity times are synchronized or at least cued by specific environmental factors. Fourth, use signals that degrade or attenuate rapidly with distance so that they will be detectable only over short distances. In this way, predators are less likely to sense the signals than the conspecifics (Wiley and Richards 1982). Fifth, use different sensory modes than predators (private channels), or use the same channels differently by using different "tuning" properties, as in guppies. Because guppy vision differs from that of their predators, their color and brightness contrast can be greater to other guppies than to the predators (Endler 1991). All of these methods reduce the need for a given signal to be a compromise between conspecific signals and predator avoidance, but most of these possibilities are virtually unexplored.

CONCLUSIONS

Sensory systems, the signals that they receive, signaling behavior, and microhabitat selection should evolve together because each induces natural selection (including sexual selection; Endler 1986) acting on the other (fig. 2). The physics of the environment and the general biophysical properties of signals and receivers can be used to predict the direction of evolution of these suites of traits. There should often be conflicting requirements for different functions of the same signal and sensory system, as between predation and sexual selection. We must be very careful not to assume that only one function or one process affects a trait or our predictions may fail. Willson and Whelan's (1990) even-handed approach to a discussion of fruit color is an excellent example of a careful consideration of multiple functions and constraints. Conflicts arising from multiple functions and constraints can be at least partially resolved by the use of different senses, different sensory characteristics, appropriate behavior, and appropriate microhabitat choice (Endler 1978, 1983, 1991; Alberts 1989, 1992) or even different vision in different parts of the same eye (Bernard and Remington 1991). Multiple functions and constraints have not been explored in any detail in any system.

From the foregoing discussion, it is clear that behavior is intimately related to successful communication; it is not sufficient to say that communication merely depends on signals' being successfully transmitted through the environment and received by the receptors. Specific behavior is required in order to choose the times, seasons, and microhabitats that transmit the signal most efficiently with the least degradation and attenuation, have the least ambient noise, and have minimal risk of predation. Thus, both breeding behavior and microhabitat choice are likely to coevolve with sensory systems and signals (fig. 2). The result should be a correlation between sensory systems, signals, signaling behavior, and microhabitat choice. Because the sensory system is under direct selection from functions not directly related to mate choice, such as food finding and predator escape, the direction of evolution of mate choice and other behavior can be affected by sensory biology.

The evolutionary bias of sensory drive is unlikely to be geographically uniform, a fact that has strong implications for geographical differentiation and speciation. Female choice criteria may be geographically variable (Houde and Endler 1990) and can evolve, sometimes rapidly, under sexual selection (Fisher 1930; Lande 1981; Kirkpatrick 1982; Pomiankowski 1988). Even if female choice were unimportant, microhabitats, times, and seasons of communication would vary among populations and species. Because signal transmission conditions and background noise also vary with microhabitats, times, and seasons, divergence of behavior and signal and receptor properties among populations and species is likely. Variation in intraspecific signals may not only maintain but also cause differences among populations. Speciation and further divergence can result if populations and species evolve in different directions (Lande 1981, 1982; Kirkpatrick 1982; Lande and Kirkpatrick 1988). Further divergence is enhanced through divergence in microhabitat choice. For example, for poikilotherms, especially small ones, such as insects, variation in microhabitat is associated with strong differences in temperature, humidity, thermal balance, posture, and other thermally related behavior, favoring differences in size and shape. Microhabitat variation is also associated with differences in water balance, parasites and parasitoids, success and duration of egg and larval development, fecundity, reproduction, orientation, and orientation cues (Willmer 1982). This should result in suites of apparently unrelated traits as disparate as senses, signals, behavior, and physiology evolving in concert, thus producing populations and, eventually, species that differ in multiple characteristic ways. In principle, these sets of apparently unrelated traits should be predictable, but only if one suite of traits is considered in the context of the microenvironment and the other suites. Thus a consideration of the joint evolution of signals, sensory systems, and their associated behavior may yield new insights into the mechanisms of the evolution and divergence of species.

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