Although the unaided human eye cannot see ultraviolet (UV) radiation, it has been known since at least 1882 that some nonhuman animals are sensitive to UV light (Lubbock 1882), and it is now appreciated that UV sensitivity is widespread in the animal kingdom (Tové 1995). The role of UV sensitivity in avian vision has received significant attention in the last 15 years, in part because the technology for studying it has become more affordable, but sustained no doubt by the mystery attached to a form of visual perception that is unavailable to humans. With the growing body of evidence that birds use UV signals in a variety of tasks (reviewed by Cuthill et al. 2000), speculation persists as to whether UV signals represent hidden channels of communication in mate choice (Guilford and Harvey 1998)—that is, channels facilitating within-species signaling while preventing eavesdropping by unintended receivers of other species (particularly potential predators). Mammalian predators of birds are probably not sensitive to this part of the spectrum (Jacobs 1993), and so UV signals could go undetected by these predators. This could be a good way of evading the well-known trade-off between sexually selected ornamentation and predation risk (Endler 1988).

Certainly, many birds use UV signals in mate selection (Cuthill et al. 1999, 2000), and some species, such as blue tits (Cyanistes [Parus] caeruleus, a species of European chickadee), are more sexually dimorphic in the UV than in other parts of the visible spectrum (Andersson et al. 1998, Hunt et al. 1998), with males’ plumage patches reflecting UV light more strongly than the analogous patches in females. However, the primary predators of songbirds are often birds of prey, which can see UV light (Viitala et al. 1995), shedding doubt on the idea of these hidden messages. Recently, several studies have revived the idea that UV signals are special, including models of avian visual processing and comparative analyses. These studies apparently provide evidence for the importance of UV signals in mate choice, and indicate that songbirds are less visible to avian predators than they are to each other. Other studies, in contrast, have indicated the opposite: that the UV component of visual signals in birds is no more important in mate choice than other parts of the visual spectrum. Here we review the evidence for and against the idea that UV signals are special, and make some suggestions as to how the issue can be resolved.

Martin Stevens (e-mail: ms726@cam.ac.uk) is a postdoctoral research fellow of Girton College, based in the Department of Zoology, University of Cambridge, Cambridge CB2 3EJ, United Kingdom. He studies avian vision, brood parasitism, and adaptive coloration. Innes C. Cuthill (e-mail: I.Cuthill@bristol.ac.uk) is a professor of behavioral ecology at the School of Biological Sciences, University of Bristol, Bristol BS8 1UG, United Kingdom. His research interests span sensory and behavioral ecology. © 2007 American Institute of Biological Sciences.
Receiver psychology and color vision

It has long been known that light rays are not colored, but rather the visual pathway and brain interpret the wavelengths of light entering the eye as possessing different colors (Endler 1990). Signals are often aimed at specific receivers, and so should be considered from the perspective of the receivers’ sensory experience (Endler 1978, 1990, Guilford and Dawkins 1991).

Color vision in humans is based on opponent processing ("neural comparison") of the output from three types of photosensitive cells in the retina: short-, medium-, and long-wave–sensitive cones. By contrast, behavioral, physiological, and molecular genetic evidence indicates that all diurnal bird species have color vision based on four cone types, one of which confers sensitivity to the UV (reviewed by Cuthill 2006). This means that birds are potentially able to perceive a greater range of colors and to discriminate between hues that appear identical to humans, and indeed to other mammals.

Generally, birds can be divided into two main groups on the basis of the wavelength of maximum sensitivity (\(\lambda_{\text{max}}\)) of the visual pigment in their ultra-shortwave-sensitive cone type. In the “UV group,” the ultra-shortwave cone type is maximally sensitive in the UV part of the spectrum (a UV-sensitive, or UVS, cone). This group includes the songbirds (Passerida), whose cone pigment \(\lambda_{\text{max}}\) lies between 355 and 380 nanometers (nm) (Hart 2001). The “violet group” (with a violet-sensitive, or VS, cone) includes most, but not all, nonpasserines, with a \(\lambda_{\text{max}}\) of 402 to 463 nm (figure 1; Hart 2001, Ödeen and Håstad 2003). While both groups are sensitive to UV light, the VS group has reduced sensitivity, compared with the UVS group. There are also significant differences in the spectral positioning of the shortwave-sensitive cone types in the two groups (Hart 2001, Hart and Vorobyev 2005). This probably leads to differences in the perception of colors in the shortwave part of the spectrum, although both groups have some ability to detect UV radiation (Vorobyev et al. 1998, Hästad et al. 2005).

The significance of ultraviolet in mate choice

UV vision in birds appears to have a range of functions (reviewed by Cuthill et al. 2000), but two are particularly relevant to the issue of private communication channels: mate choice and foraging. A role for UV vision in avian mate choice has been demonstrated repeatedly (Cuthill et al. 2000). Indeed, the UV component of sexually selected signals may be an important component of divergent selection leading to reproductive isolation, and potentially to speciation (Bleilweiss 2004). A range of hypotheses suggests that UV signals may have a special function in avian communication. For example, because UV light is more scattered in air than are longer wavelengths (Lythgoe 1979), it may be advantageous in short-range communication (e.g., in mate choice), with less risk of attracting more distant predators or eavesdroppers because the signal degrades quickly over longer distances (Burkhardt 1989, Bennett et al. 1994, Cuthill et al. 2000, Hausmann et al. 2003). In addition, more backscattered light is plane polarized toward shorter wavelengths, and this polarization may be useful for assessing structural details in mate choice (if birds can in fact see polarized light; Martin 1991, Vos Hzn et al. 1995, Greenwood et al. 2003). Polarization aside, as many UV signals originate from precisely arranged nanostructural (very fine-scale) feather elements, they may be reliable signals of age and condition (Andersson 1999, Hausmann et al. 2003). UV signals may also be particularly effective because they may contrast strongly with background vegetation, since chlorophyll absorbs UV (Hausmann et al. 2003), although glossy leaves reflect UV light. Finally, it has been suggested that UV mate-choice signals may be useful for signaling to conspecifics without attracting predators, regardless of the relative spatial distances involved, because of difference in receiver physiology; we return to this hypothesis later.

In experiments with zebra finches (Táeniopygia guttata), Bennett and colleagues (1996) showed that females preferred males with UV light present over males in the absence of UV light. Furthermore, Siitari and colleagues (2002) showed that female pied flycatchers (Ficedula hypoleuca) chose males that possessed enhanced UV-reflecting plumage over those with reduced UV reflectance. The significance of UV in mate choice is also illustrated in blue tits, which are sexually dimorphic with respect to UV, with males showing higher UV
fluorescent plumage, which selectively absorbs UV light and birds are of special significance in mate choice. Hausmann and A recent comparative analysis suggests that UV signals in Comparative analyses by the removal of shorter wavelengths than of longer wave- 
shortwave reflectance, such as blue tits, may be more affected 
ments is not surprising. The highest contrast between the seeds 
and background in the study by Maddocks and colleagues 
Both raptors (birds of prey, such as hawks or falcons) and 
ors or corvids, especially in the UV range of the spectrum. (Ödeen and Håstad 2002). That said, because birds 
use for foraging. For example, Viitala and colleagues (1995) showed that kestrels (Falco tinnunculus) hunt using UV 
cues stemming from the urine and feces with which voles (Microtus agrestis) mark their runways. The use of UV cues in for- 
aging, when these are available, should not be surprising, and has been demonstrated in several other contexts (Church et al. 1998, Honkavaara et al. 2002). Thus, in mate-choice experiments such as those described here, viewing males under the entire avian visible spectrum may simply provide more information about quality (and make them look more natural) than viewing them with any part of the spectrum removed (Banks 2001). The 
relative importance of the different parts of the visual spectrum is likely to relate to the predominant colors used in communica- 
tion, such that species with plumage of relatively high shortwave reflectance, such as blue tits, may be more affected by the removal of shorter wavelengths than of longer wave- 
lengths. This has yet to be tested.

**Comparative analyses**

A recent comparative analysis suggests that UV signals in birds are of special significance in mate choice. Hausmann and colleagues (2003) argue that many species of parrots have fluorescent plumage, which selectively absorbs UV light and reemits it at longer wavelengths, and that these patches are often found adjacent to regions of high UV reflectance, enhancing the visual contrast of plumage patches. Measurements of 108 species of birds showed a significant association between UV plumage colors and body regions involved in courtship displays (Hausmann et al. 2003). In addition, the presence of UV-reflecting plumage at regions of the body not involved in sexually selected displays was far lower. Among the parrots measured, there was also an association between flu- orescent colors and courtship displays (Hausmann et al. 2003).

Hausmann and colleagues (2003) posit that these results are not just an artifact of the plumage used in courtship displays being more colorful in general, because they found no association between displays and colors lacking UV or fluorescence. The results remained unchanged when controlling for phylogeny (i.e., the fact that closely related species may share common features because of recent shared ancestry rather than common adaptation). In addition, in parrots, UV-reflective patches were usually found next to fluorescent patches, and this can lead to a 25-fold increase in chromatic contrast (Hausmann et al. 2003). However, despite these convincing results, fluorescent plumage is apparently confined to parrots, as was Hausmann and colleagues’ (2003) study; it is therefore unclear how widespread the results are across birds as a group. In fact, evidence indicates that the UV component of sexual dimorphism is not of any greater importance than other parts of the spectrum when a range of families are considered (Eaton 2005; see below).

The proposal that the widespread use of UV by birds is a private channel, because birds can see UV and mammalian predators cannot, is tempered by the fact that birds of prey can also see UV (Viitala et al. 1995, Ödeen and Håstad 2003) and use it for foraging. For example, Viitala and colleagues (1995) showed that kestrels (Falco tinnunculus) hunt using UV cues stemming from the urine and feces with which voles (Microtus agrestis) mark their runways. The use of UV cues in foraging, when these are available, should not be surprising, and has been demonstrated in several other contexts (Church et al. 1998, Honkavaara et al. 2002). That said, because birds of prey have VS rather than UVS cones, they may not be as adept as their passerine prey in using UV information, and thus passerines’ UV signals may be less detectable to birds of prey than to other songbirds.

This proposal has received recent support from a study by Håstad and colleagues (2005), who modeled the conspicuousness, to the eyes of raptors or corvids and songbirds, of several northern European songbirds against typical backgrounds. Both raptors (birds of prey, such as hawks or falcons) and corvids (e.g., crows, ravens, jays) are important predators of forest birds, which they capture while the prey birds are flying or perching on branches, or when they are chicks still in nests. Spectral sensitivity differs between songbirds and rap- tors or corvids, especially in the UV range of the spectrum (Ödeen and Håstad 2003). Håstad and colleagues (2005) predicted that the color signals of male songbirds would be more conspicuous to other songbirds, against the background

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of deciduous or coniferous woodland, than they would be to a hawk or corvid predator. Using the most sophisticated available model of avian color discrimination (Vorobyev and Osorio 1998, Vorobyev et al. 1998), they calculated the degree of color difference between the plumage patterns of 18 species of songbirds and the background environment, assuming that the chance of a plumage patch being mistaken for part of the background environment was proportional to the “color distance” between them (figure 1). The cone sensitivities of blue tits (Hart et al. 2000) represented the UV group, and those of the peafowl Pavo cristatus (Hart 2002), the violet group (figure 2). The crypsis of the patch in its environment is described by the average distance from the plumage patch to all patches in the background, in proportion to the average distance between all the background patches. Thus, relative discriminability describes the average distance of the badge from the background in standard deviations of the background.

Håstad and colleagues’ (2005) study showed that the colors of songbirds were more visible to conspecifics than they were to potential predators. They concluded that songbirds use color signals that are more visible to birds with a similar visual system than to predators, utilizing a communication channel for displaying male quality that modulates any rise in the risk of predation associated with signaling.

Although Håstad and colleagues’ (2005) study has provided an excellent and overdue test of the hypothesis that birds may use signals that are more conspicuous to conspecifics than to avian predators, there are a number of caveats that must be addressed. First, how good is the peafowl as a model for raptor vision? The peafowl was used in the model because its visual pigments are similar to those of raptors and corvids (fig-ure 2). The sensitivity of each cone; in particular, the ratios of the different cone types could differ. There is considerable variation between species in the abundance (and intraretinal distribution) of cone types, and this relates to the ecology of the species, such as the light characteristics of the foraging environment (Hart 2001). It is possible that a hawk will differ from a peafowl in this respect. The proportions of the different cone types are parameters in the model, and so they do matter for the calculations of discriminability. Håstad and colleagues (2005) assumed that the birds were perching in sun-exposed trees, but, as they acknowledge, the peafowl forages mainly in shaded environments, and such differences in ecology may have selected for different visual perception.

In Håstad and colleagues’ (2005) study, even though the songbirds were generally more visible to the songbird than to the predator used as a model, many of the birds measured were still at least two standard deviations from the background in color distance, and so would be easily detectable. Håstad and colleagues assumed that the chance of a plumage badge being mistaken for part of the background was proportional to the color distance between them, but prey detection may become much easier once some discrimination threshold is reached. Indeed, the data actually indicate that songbirds are probably still visible to raptors against the background.

Furthermore, the model used in the study disregards the achromatic information present in a signal, so that a white bird on a black background would be considered cryptic. This may not matter for the species and environments considered, and Håstad and colleagues state that the achromatic signal of a songbird does not differ between the songbird and raptor receivers. However, if achromatic information is used in detection, as it most likely is if detection is from a distance or through movement (Osorio et al. 1999), then it is potentially misleading to ignore this information. Color is unlikely to be the sole, or even the primary, cue facilitating detection. The lack of a difference between the bird groups may mean that the songbirds will be just as visible to a bird of prey as they will be to conspecifics. This is something that needs to be included in future models, since differences in color perception may be less important than has been realized, if achromatic information is one of the main features used in prey detection.

In contrast to the studies by Hausmann and colleagues (2003) and Håstad and colleagues (2005), a recent carefully designed study of sexual dichromatism in passerine birds has provided evidence that UV signals in birds are not special (Eaton 2005). By using versions of the Vorobyev–Osorio model of color discrimination, described above, for humans and birds, Eaton (2005) showed that more than 90% of 139 species

![Figure 2. Normalized absorptance of the ultraviolet-sensitive and violet-sensitive cone types of the blue tit (Cyanistes [Parus] caeruleus) and the peafowl Pavo cristatus, respectively (data from Hart et al. 2000, Hart 2002).](https://academic.oup.com/bioscience/article-abstract/57/6/501/236174/21/02/14?/full)
analyzed were sexually dimorphic to an avian visual system but could not be distinguished by the human model. This illustrates that sexual dimorphism may be the rule in birds, even in species that to humans look monochromatic, with the differences arising as a result of discrepancies in the sensitivities and positioning of the different cone types in humans and birds. Despite this high level of dichromatism, Eaton (2005) found that differences between males and females were rarely the result of UV differences alone. Statistical analysis by logistic regression showed that only approximately 4% of the species measured had strong correlations between sex and the UV signal alone (i.e., not the shortwave, medium-wave, or long-wave part of the signal). This was in contrast to strong correlations between sex and at least one of the other cone types in about 40% of cases. Eaton’s (2005) results indicate that hidden sexual dimorphism may be found in birds even in the human-visible part of the spectrum, and do not support the idea that sexual dichromatism is frequently limited to the UV part of the spectrum. Hidden dichromatism can originate from differences in the main sensitivity of the photoreceptors between different species, even if their vision encompasses a similar spectral range.

**Conclusions**

Because of the preoccupation with UV, there has been a disappointing lack of research into the relative importance of different parts of the avian visible spectrum in communication, and what evidence we have is equivocal regarding a specialized role for particular wave bands (Hunt et al. 2001, Hausmann et al. 2003). It has been suggested that UV sensitivity in passerine birds may exceed their sensitivity to other parts of the visual spectrum (Burkhardt and Maier 1989, Maier 1992), and so UV signals may be especially detectable to these species. However, where heightened UV sensitivity has been found, this is more likely a sensory adaptation to the relatively low levels of UV light in the illuminant (Vorobyev et al. 1998, Kevan et al. 2001). Additional experiments systematically investigating the relative importance of different parts of the avian visual spectrum would be of great value in determining the relative importance of UV in signaling; to this end, further experiments similar to that of Hunt and colleagues (2001) are required.

The relative importance of different parts of the spectrum is likely to depend on the content of the signal in question; a signal reflecting relatively more light of shorter wavelengths (such as the crown on a blue tit) is more likely to be affected by the manipulation of UV light than is a signal that reflects more long wavelengths (Banks 2001). Furthermore, as Banks (2001) points out, the significance of UV, and of different parts of the avian visual spectrum, may be affected by the time of day when a specific species is active. For instance, crepuscular birds may be more affected by the removal of UV light than diurnal birds, since during crepuscular hours there is relatively less medium-wave light and more shortwave light than during the day. Further analyses comparing the abundance and distribution of signals differing in their spectral content across the birds, while considering species’ ecology, would be invaluable.

Recent evidence indicates that UV-reflecting plumage may be found in all avian families, indicating at least that UV light is an important component of the visual information utilized by birds (Eaton and Lanyon 2003). However, these estimates are often based on arbitrary assessments of what constitutes a significant level of UV reflectance (e.g., 5%; Eaton and Lanyon 2003), rather than on discrimination thresholds (but see Eaton 2005). Nevertheless, in an analysis of 142 avian families and 312 avian species, Eaton and Lanyon (2003) found just 10 potential incidences of hidden dimorphism in which the signal differed between males and females by less than 10% in the human-visible part of the spectrum, but by more than 10% in the UV region. Thus, it seems uncommon for strong sexual dimorphism to be expressed exclusively or primarily in the UV part of the spectrum.

Although the significance of Håstad and colleagues’ (2005) results is unclear in terms of hidden communication channels, it is a good example of how the perception of a particular signal is dependent on the visual system of the receiver (Guilford and Dawkins 1991, Bennett et al. 1994). Certainly, more models such as Håstad and colleagues’ (2005) would be useful, particularly if these could be combined with additional studies and data regarding predatory visual systems. It would be useful in general to have more information regarding avian visual processing, especially with respect to opponent processing; this would make it possible to develop more accurate models of color discrimination. As Kevan and colleagues (2001) point out, when inputs from more than one receptor type are present, predictions of signal conspicuousness require knowledge of neuronal connections between the receptor types. Indeed, it may be misleading to consider the UV reflectance of an object in isolation from the rest of the visual signal toward which the receiver is sensitive (Kevan et al. 2001). Further work should also incorporate more information on different visual background and light environments. The findings of Håstad and colleagues’ model are in one respect not surprising: it makes sense that the visual signals of songbirds extend into the UV, because they can see UV light—this does not mean that the reduced sensitivity of raptors to UV had any evolutionary role in this. We would expect animals’ signals aimed at conspecifics to be matched to their own visual systems.

The idea that animals, such as birds, use UV signals to exploit a private communication channel invisible to their predators holds great sway, both with the public and with professional scientists. Such arguments are not exclusive to birds, and there is some evidence that UV signals in male northern swordtail fish (Xiphophorus), which are used in mate selection by females, may be less detectable to predators than to conspecifics, as a result of reduced UV sensitivity in predators (Cummings et al. 2003). In addition, several species of deep-sea dragon fish may produce long-wave light from photophores, to which they are sensitive but other species are not (Douglas et al. 2000).
However, while some wave bands may be of special importance in specific instances, there is still little evidence that UV is any more important in animal communication than are other parts of the spectrum, especially in birds, and the importance of UV as a signal component has frequently been exaggerated (Kevan et al. 2001). Molecular phylogenetic reconstruction indicates that tetrachromacy is an ancient trait within vertebrates (Bowmaker 1998, Yokoyama 2002), with opsins maximally sensitive to UV lost and secondarily acquired in several lineages, including lineages within the birds and mammals (Shi et al. 2001, Yokoyama 2002). In fact, UV receptors are common in nature, whereas vision in the long-wave part of the spectrum appears to be more derived (Kevan et al. 2001). It is difficult to escape the human fascination with UV signals, which stems largely from the fact that we cannot see them, but the question of whether UV signals represent a special channel of communication in songbirds remains open.

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