

# Ultra-violet photoreceptors in the animal kingdom: their distribution and function

Martin J. Tovée

**M**ost invertebrate and vertebrate species can see much shorter wavelengths than can humans, and many can see longer wavelengths too. These species perceive a different set of visual cues to the world that influences their behaviour in activities as diverse as navigation, intraspecific communication and foraging, and even their circadian rhythms. Without an adequate understanding of the perceptual cues to which an animal is responding, it is impossible even to start to explain its behaviour<sup>1,2</sup>.

Humans can perceive light of wavelengths between 400 and 700 nm. Light just below this range (300–400 nm) is called ultra-violet (UV). The human lens and cornea absorb strongly in this region, preventing UV light from reaching the retina<sup>3,4</sup>. However, the human short-wavelength (or blue) photopigment's absorption spectrum extends into the UV range (see Fig. 1e), and if the lens is removed, such as in cataract surgery, a subject can perceive UV light. A good reason for preventing UV light reaching the retina is that it is absorbed by many organic molecules, including DNA. Thus, UV light, even of comparatively long wavelengths such as 380 nm, can cause retinal damage and cancer<sup>5</sup>. However, a wide variety of animal species shows sensitivity to UV light, ranging from insects to mammals. Some have developed specific UV-sensitive photoreceptors to detect UV light, whereas others have combined a clear ocular medium with short-wavelength receptors whose spectral absorbance extends into the UV range (Fig. 1). Recent research is clarifying the adaptive significance of these differences.

## Species distribution

Many invertebrates seem to have UV receptors. The insect and crustaceans have been studied in the most detail. The colour vision of insects varies from dichromacy in Blattoptera, through trichomacy in Diptera, Hemiptera and Orthoptera, to tetrachromacy in Lepidoptera and Odontata<sup>6,7</sup>. Although the number of pigments varies, most insects seem to have a UV receptor with an average peak spectral absorbance of around 336 nm (Ref. 6). The existence of the UV pigments in the retina does not prove that they are used in a colour discriminating system. However, the ability of some insect species to discriminate colour in this region has been shown behaviourally. The most intensively studied system is that of the honeybee (*Apis mellifera*). It has three receptor classes that absorb maximally in the UV (at around 340 nm), short-wavelength (around 430 nm) and middle-wavelength (around 535 nm) light (Ref. 6). Behaviourally, the honeybee shows good wavelength discrimination throughout this spectral range, indicating that the UV receptors are fully integrated within its visual system<sup>7</sup>.

**Until very recently, the role of ultra-violet (UV) colour perception in vertebrate and invertebrate vision has largely been ignored. However, in the past few years, a host of detailed information has become available on the widespread distribution of UV receptors in different species – from insects to mammals – and the important functions they seem to play in navigation, foraging, intraspecific communication and the control of circadian rhythms.**

Martin Tovée is at the Dept of Psychology, Ridley Building, University of Newcastle, Newcastle Upon Tyne, UK NE1 7RU.

Most of the crustaceans have a less-elaborate colour vision system, often with no more than two pigments<sup>8</sup>, although these pigments may absorb in the UV. For example, the spiny lobster (*Panulirus argus*) has a 370 nm photoreceptor class and the crayfish (*Procambarus clarkii*), a 440 nm class. The water flea (*Daphnia magna*) has four visual pigments in its eye, including a UV receptor with a spectral peak at 348 nm (Ref. 8). The real superstars of the crustacean colour world are the mantis shrimps, which have around 10 to 11 visual pigments<sup>9–11</sup>; through a system of

at least six filters, this quantity is magnified to produce at least 16 different receptor types, with six absorbing maximally in the 300–400 nm region and some of them sensitive to polarization<sup>10–12</sup>, suggesting a potential for exceptional wavelength discrimination in the UV region.

UV receptors have been reported in many species of fish, including freshwater species, such as goldfish (*Carassius auratus*) (Fig. 1b) and guppies (*Poecilia reticulata*)<sup>13,14</sup>, euryhaline species, such as juvenile trout and salmon, and marine fish, such as tropical coral reef fish<sup>15,16</sup>. The UV pigment is located in distinctive short single cones, which in salmonids are located at the corners of a square retinal mosaic. Microspectrophotometry (MSP) studies have suggested a maximum absorbance of the UV cone pigment in fish of about 360–365 nm<sup>14,15,17</sup>. For colour discrimination, different cone classes in the vertebrate retina have to be organized into a colour opponent system. In this system, the differences in the responses of the different cone classes are compared, so that changes in wavelength can be differentiated from changes in light intensity. Behaviourally, this can be demonstrated in the peaks and troughs of the spectral sensitivity function<sup>18</sup>. Such functions obtained from fish suggest that the UV cone class is integrated into a colour opponent system that would allow their use in wavelength discrimination, rather than just for the detection of UV light for a specific physiological purpose<sup>19</sup>. For example, the goldfish has four cone pigments, including a UV receptor absorbing maximally at 360 nm (Ref. 13), and the shape of its spectral sensitivity function in behavioural experiments clearly shows the peaks and dips associated with colour-opponent interactions<sup>20</sup>.

The retinas of comparatively few species of amphibians and reptiles have been examined for UV receptors. Suction electrode recordings from cones in the tiger salamander (*Ambystoma tigrinum*) retina suggest the presence of a UV-sensitive pigment<sup>21</sup>, but this is the only evidence within the amphibians. In the reptiles, UV receptors have been found in eight species so far; a turtle (*Pseudemys scripta elegans*), two species of gecko (*Gonatodes albogularis* and *Gecko gecko*) (see Fig. 1b) and five species of anoline lizards<sup>22–24</sup>. These UV cone receptors seem to be comparatively rare in the retina,

making up only a few percent of the total cone population, rather like the short-wavelength cones in the primate retina. Behavioural experiments suggest that the turtle at least can use these UV pigments in a colour opponent system for wavelength discrimination<sup>22</sup>.

A combination of MSP, electrophysiology and behavioural methods suggests that UV sensitivity is present in at least 31 species of bird<sup>25</sup>. Birds seem to have particularly good colour vision, and most species possess four or even five cone pigments in their retina. Of these cone pigments, it seems that one will either absorb maximally in the UV region of the spectrum (as in the red-billed leiothrix, *Leiothrix lutea*, Fig. 1d<sup>26</sup>), or have a short-wavelength sensitive cone whose absorption spectrum extends into the UV region (as in the mallard duck, *Anas platyrhynchos*<sup>27</sup>). These UV sensitive receptors seem to be fully integrated into the birds' colour vision system, as suggested by the spectral sensitivity function of several species (including the red-billed leiothrix<sup>28</sup>; see Box 1) and the ability of many species to make wavelength discriminations within the UV spectral range<sup>30</sup>.

Mammals, with the exception of primates, are mainly dichromats, with one cone class having a peak spectral absorbance in the middle- to long-wavelength region (530–560 nm) and another cone class absorbing in the short-wavelength region (420–440 nm) (Ref. 31). In some crepuscular rodents, it seems that both pigments are shifted towards shorter wavelengths. For example, in the pigmented house mouse (*Mus musculus*) and in the mongolian gerbil (*Meriones unguiculatus*) the peak sensitivity of the long-wavelength pigment is shifted down to 500–510 nm and the short-wavelength pigment has a peak spectral absorbance of 360–370 nm (Ref. 32). This is combined with a lens that is UV-transparent. Behavioural experiments suggest that at least one of these species is able to use the UV receptor in a colour opponent system, the way other mammals use the short-wave cone class. These are so far the only mammals that have been shown to possess a UV pigment, although the visual pigments of a very wide range of species has been examined<sup>31,33</sup>. However, other

mammals may be able to perceive UV light if they possess a UV-transparent lens, as the absorbance spectrum of the short-wave pigment extends into the UV range. A possible example of this is the rat, whose lens still has 50% transmission at 350 nm (Ref. 5).

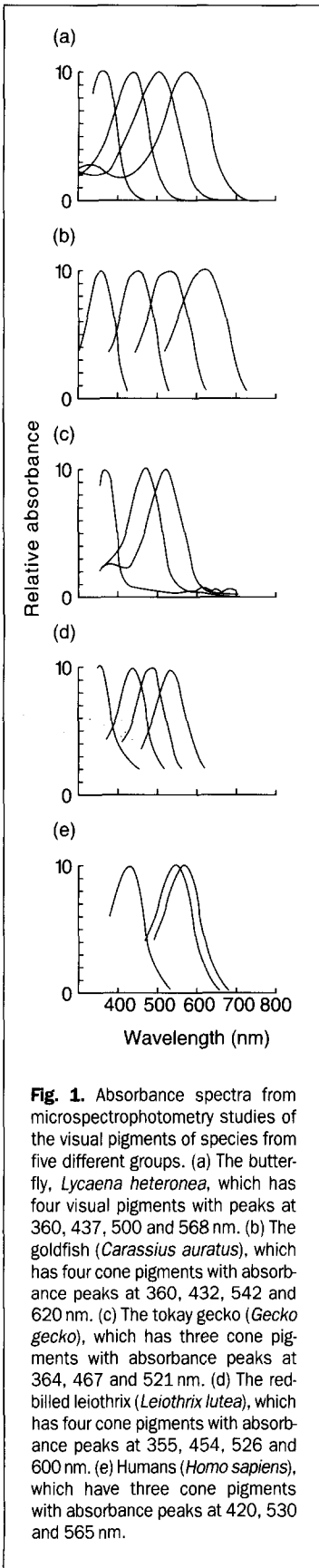
**Navigation**

Light passing through a medium is scattered and plane-polarized by any particles it encounters. If the particles are small relative to the wavelength of the light (e.g. dust particles, oxygen or nitrogen molecules) the degree of scattering and polarization is proportional to the inverse of the fourth power of the wavelength (primary Rayleigh scattering). So shorter wavelengths, such as UV light, are scattered and polarized more than longer wavelengths. Plane polarization due to scatter occurs orthogonally to the angle of the incident light, so there are concentric rings of plane-polarized light around the sun<sup>34</sup>. If an animal can detect these rings (*e*-vectors), it can determine the position of the sun when the sun is obscured. It seems that at least some insects can detect the position of the sun in this way.

The navigational abilities of two insect species have been studied in detail; the honeybee and the desert ant (*Cataglyphis bicolor*)<sup>34</sup>. The most important population of UV receptors seems to be located on the dorsal rim of the eye, comprising a small percentage of all the photoreceptors<sup>34</sup>. These UV receptors are sensitive to UV polarization and are used in navigation. It is believed that these insects do not carry out any complex celestial trigonometry or have a chart of the polarization patterns in all their detail, but possess only a simplified map of the *e*-vector distribution in the sky, based on the spatial distribution of UV receptors on the dorsal rim<sup>34</sup>. Each UV receptor is maximally sensitive to an *e*-vector of a particular direction. The preferred *e*-vector direction of a receptor changes in a step-wise manner, so that there is a gradual rotation in the preferred direction of receptors, moving from the front to the back of the eye. To use its map, the insect simply turns until the retinal map is in register with the *e*-vectors in the sky<sup>34</sup>. At this point, the photoreceptors generate a maximal signal that tells the insect it is pointing directly away from the sun. The insect's map is invariant, and corresponds only to the actual *e*-vector distribution at dawn and dusk, but the errors induced in the left and right eyes are believed to be opposite in sign and so will cancel each other out. Many other insect species, such as hymenopterans, crickets and lepidopterans, have similar arrays of polarization-sensitive photoreceptors in their dorsal eye regions, and there is some evidence that these are used for navigation in the same way<sup>34</sup>.

Fish may also use polarized light in a navigational system. The goldfish has four cone pigments<sup>13</sup>. Both the long-wavelength cone classes and the UV cone class are very sensitive to *e*-vector orientation, although the preferred plane orientation of the UV cones is orthogonal to that of the other two cone classes<sup>35</sup>. The input from the UV cones and the longer wavelength cone classes may form the sensory basis of a mechanism to allow discrimination of the plane of polarization in the absence of any consistent visual cues, such as brightness or colour. The trout (*Salmo spp.*) can discriminate *e*-vector orientation as indexed by changes in their spatial orientation – behaviour that can be maintained even in partially polarized light<sup>36,37</sup>. This information may allow the fish to orient itself and determine its vertical position within the water column.

It is not clear how UV polarization is detected in fish. To detect plane-polarized light of a particular orientation, the double bond of the visual pigment chromophore must be



**Fig. 1.** Absorbance spectra from microspectrophotometry studies of the visual pigments of species from five different groups. (a) The butterfly, *Lycaena heteronea*, which has four visual pigments with peaks at 360, 437, 500 and 568 nm. (b) The goldfish (*Carassius auratus*), which has four cone pigments with absorbance peaks at 360, 432, 542 and 620 nm. (c) The tokay gecko (*Gecko gecko*), which has three cone pigments with absorbance peaks at 364, 467 and 521 nm. (d) The red-billed leiothrix (*Leiothrix lutea*), which has four cone pigments with absorbance peaks at 355, 454, 526 and 600 nm. (e) Humans (*Homo sapiens*), which have three cone pigments with absorbance peaks at 420, 530 and 565 nm.

aligned in the same orientation<sup>38</sup>. If all the molecules in a receptor are aligned in the same orientation then the cell will respond to polarized light of that orientation and not of any other. If another cell has its pigment molecules arranged in another orientation, say at right-angles to those molecules in the first receptor, then between the two receptors, a signal can be generated that resolves the angle of polarization<sup>38</sup>. In invertebrates most of the visual pigment molecules are aligned along the axis of the microvilli, automatically ensuring sensitivity to light of a particular polarization. However, in vertebrate receptors, there is no systematic arrangement of the pigment within a receptor. In some fish, birds and reptiles, some of the receptors are twinned to form double cones<sup>27</sup>. It has been suggested that the inner segment of the double cone acts as a birefringent polarization-sensitive waveguide, and that the double cone mosaic produces a 'polarization-contrast' neural image<sup>39</sup>. As UV cones have

not been reported as part of a double-cone system, there is no obvious neural basis for the behaviourally demonstrated ability.

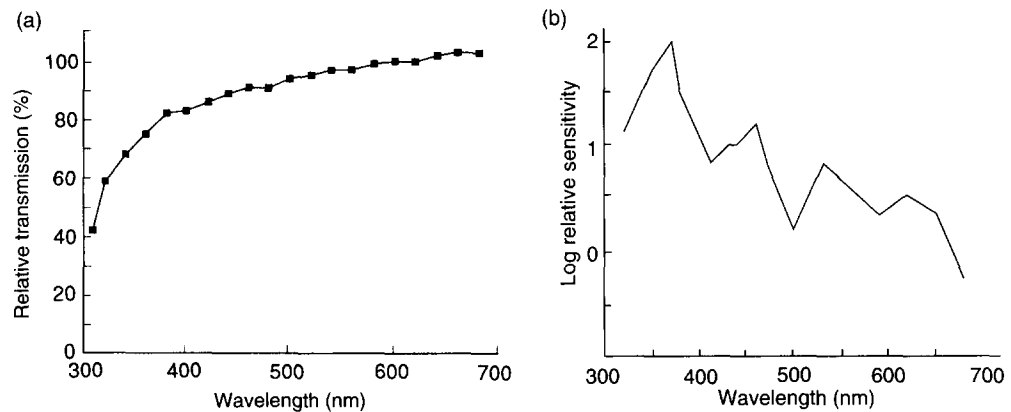
It seems that birds cannot detect differences in the angle of polarization<sup>40</sup>, and therefore do not use this mechanism for navigation. However, the position of the sun can also be determined from intensity and wavelength gradients across the sky<sup>40</sup>. As short wavelengths are more prone to scatter than longer wavelengths, the short wavelengths have a more even distribution of intensities across the sky. Also, the intensity of longer wavelength light increases strongly towards the horizon (horizon brightening). Thus, the intensity ratio of any two wavelengths will vary with the angular distance to the sun<sup>40</sup>. Therefore, analysis of the spectral composition of part of the sky, by comparison of long wavelengths against a comparatively uniform UV background, could provide an animal with a sensitive estimate of the sun's position, even when the sun itself is obscured<sup>40</sup>. It seems, therefore, that these could be important cues for birds in navigation.

### Foraging

UV pigments are used in a colour discrimination system by some insects, fish, reptiles, birds and mammals. UV receptors may also play a role in spatial discrimination, a question that is important for the possible functions of the UV pigments. The finer the discrimination the system can perform, the better it will be able to detect potential food or intraspecific communication. Pigeons have been able to make shape discriminations under UV illumination<sup>41</sup>, which has been taken as evidence for good spatial vision using UV

### Box 1. The red-billed leiothrix

A particularly well-studied example of bird vision is the red-billed leiothrix or Peking robin (*Leiothrix lutea*). The spectral transmission of its ocular medium is very transparent down to 400 nm (Ref. 28). Below 400 nm, there is some absorbance and at below 330 nm it starts to absorb strongly (a). In birds, the cones contain brightly coloured oil droplets in the ellipsoid region of the outer segment. They are located between the cone visual pigment and the incoming light, and can act as filters. These oil droplets can be either bright red, orange, yellow or transparent. Behavioural experiments on the red-billed leiothrix<sup>29</sup> suggested four peaks in its spectral sensitivity function, at 370, 460, 530 and 620 nm, separated by significant dips in the sensitivity at about 590, 500 and 400 nm (b).



The four maxima suggest the existence of four separate cone mechanisms underlying the sensitivity, and the dips between the peaks are indicative of opponent processes between receptor types. Four spectrally different cone classes were identified with typical combinations of photopigments and oil droplets: (1) a long-wavelength sensitive cone containing a photopigment with a peak spectral absorbance at 568 nm and a droplet with a cut off at 564 nm; (2) a middle-wavelength cone containing a 499 nm pigment and a droplet with a 506 nm cut off; (3) a short-wavelength cone containing a 454 nm pigment and a droplet with maximum absorbance below 410 nm; and (4) a UV cone containing a 355 nm pigment and a transparent droplet that only absorbs significantly below 300 nm (Ref. 26). The effect of the lens absorbance is to shift the effective spectral absorbance of the short-wavelength and UV cones towards slightly longer wavelengths. Many birds possess double cones with morphologically distinct primary and accessory members<sup>27</sup>, in the case of the red-billed leiothrix these are filled with the 568 nm pigment. The UV pigment has been found only in single cones in all the species studied so far. These single cones are much smaller than the other types of single cone and are very rare in the retina. Figures redrawn from Ref. 29.

cones<sup>25</sup>. However, the discriminations made by the birds were not particularly fine, and the broad-band UV light used would stimulate both the shorter wavelength mechanisms. In the more difficult spatial discrimination task of detecting seeds under UV illumination, the pigeons performed poorly<sup>42</sup>.

It is unlikely that UV receptors would be used in a system that mediates high spatial resolution. The proportion of UV cones in the retina of most vertebrate species is very low (around 5–10%), and such a receptor mosaic could not support a high spatial resolution system on its own. The responses of UV receptors would have to be pooled with the responses of some, or all, of the other cone types. However, there are good reasons why this may not happen. UV light is easily scattered by particles in air or water, a phenomenon that would lead to distant objects appearing blurred and indistinct when using UV light. Also, UV and short-wavelength light is particularly sensitive to scatter by any imperfections in the optical media. In addition, there is also the problem of chromatic aberration, which is the difference in focal length that a lens will have for different wavelengths. For example, in the human lens, the difference in focal length between short- and long-wavelength refracted light is 0.5 mm. Thus, when an image is in focus on the retina for long-wavelength light, it will be out of focus for short-wavelength or UV light. Therefore, inclusion of the responses from receptors sensitive to a wide range of wavelengths in a high spatial acuity system would degrade the image. It then makes sense to base a high spatial acuity system on the responses of the more numerous, longer wavelength receptors that detect wavelengths less prone to wavelength-dependent scatter. The function of

**Box 2. Age-dependent effects in fish**

One-year-old brown trout (*Salmo trutta*) are tetrachromatic, with pigments absorbing maximally at 355, 441, 535 and 600 nm (Ref. 15). However, over the next year, the UV-sensitive pigment is lost and so are the short single cones that contained them. The loss of UV receptors during the development is also seen in at least four other species, the Atlantic salmon (*Salmo salar*), the rainbow trout (*Oncorhynchus mykiss*), the rudd (*Scardinius erythrophthalmus*) and the yellow perch (*Perca flavescens*)<sup>27,44,45</sup>. The change seems to be associated with major changes in the fish's development (e.g. in salmon with the parr-smolt transformation) and is a size- rather than an age-dependent phenomenon<sup>46</sup>.

The loss of UV receptors seems to be under the control of the thyroid hormone, thyroxine<sup>47</sup>. Manipulation of its levels can increase or reduce the rate of UV receptor loss and can stimulate production of the UV pigment in an older fish that has lost its UV pigment. The change in the proportion of UV receptors in the retina is concomitant with changes in the absorbance of the lens, which starts to increase its short-wavelength absorbance and so significantly reduces the amount of UV light reaching the retina. This change in lens absorbance is widespread among fish species. It has been suggested that UV sensitivity is generally much reduced in older individuals and may even only occur in young fish<sup>48</sup>. There are some exceptions to the proposed rule. For example, the juvenile form of the blacksmith (*Chromis punctipinnis*) does not have a UV pigment, but the adult form does<sup>16</sup>.

the UV receptors may be analogous to that of the short-wavelength receptors in human visual perception (where they play a role in wavelength discrimination) and coarse spatial discrimination, but not in fine discrimination, which is mediated by the more-numerous, longer wavelength receptors.

UV wavelengths may be used to detect food that either absorbs, scatters or reflects strongly in the UV region of the spectrum relative to the background. In fish, UV receptors tend to be found in juvenile forms, which live close to the surface and feed on small planktonic organisms. Such planktonic food particles will preferentially scatter short wavelengths, and UV perception has been shown to play a role in plankton predation<sup>43</sup> – the loss of UV sensitivity as a fish becomes larger and changes its feeding patterns is not surprising (see Box 2)<sup>15</sup>. UV light may also be used by mantis shrimps to detect both prey and predators<sup>11,12</sup>. Water scatters short-wavelength light, including UV light, and at short range this scatter can be used to silhouette an object that might otherwise be difficult to perceive. Many fish have a silvery surface that reflects light in such a way as to minimize the difference in the amount and wavelength composition of light reflected from themselves relative to the underwater light field. This type of camouflage does not work against a scattering background. Also, as the silvery reflectance is produced by constructive interference, it is even less effective in the UV. So such a fish would be very visible against a bright UV background<sup>11,12</sup>. Thus, the UV system may potentially allow the mantis shrimp an enhanced window on the world, and give it the maximum information on whether to emerge from its burrow to feed or to stay hidden<sup>12</sup>.

Many fruits and seeds eaten by birds reflect in the UV, while most leaves do not. Also, many insects, such as moths and butterflies, which are potential prey for many species of bird, also reflect in the UV<sup>49,50</sup>. The colour of flowers is an important source of information for foraging pollinators<sup>51</sup>, although shape also has a strong role to play<sup>52</sup>. Many flowers reflect in the UV, and this is an important cue in the foraging behaviour of many species of pollinating insect<sup>53,54</sup>, as well as for avian pollinators such as the hummingbird<sup>55</sup>.

A particularly intriguing method of foraging is that of the Eurasian kestrel (*Falco tinnunculus*), which feeds primarily on small mammals, such as the vole (*Microtus agrestis*). The voles mark their runways with urine and faeces, which strongly absorb UV light in comparison with the surrounding vegetation. In behavioural studies, both in the wild and in the laboratory, the kestrels spent far more time hunting in

areas treated with artificial urine runways than in non-treated areas<sup>56</sup>. The experimenters suggest that the kestrels flying over a wide area can use the runways to quickly screen and identify areas of high vole population density where hunting is likely to be more productive.

**Intra- and interspecies communication**

UV vision may be involved in intraspecies communication, particularly in sexual displays. Elaborate plumage in birds has long been cited as an example of a secondary characteristic, with colour used for impressing females and intimidating rivals, and many bird species have UV-reflecting plumage and fleshy ornaments. One type of feather seems to be especially good at producing UV patterns. Its structure consists of a spongelike network of seemingly randomly orientated keratin granules that, because of their size, scatter UV light<sup>57</sup>. Multi-layer interference also seems to play a role, as alteration of the refractive indices of the substances filling the cavities changed the reflectance in the UV. Evidence for the importance of UV patterns in communication comes from an experiment where birds (the red-billed leothrix) preferred a partner viewed through UV-transparent Plexiglas over a partner viewed through a UV-opaque glass. Although birds are probably the most striking example of body colour display, UV perception may also play a role in the enhancement of intraspecific visual signals on the body of fish, for example, the guppy<sup>14</sup>.

Another good example of UV body-patterning is found in five closely related anoline lizards studied in Puerto Rico by Leo Fleishman<sup>24</sup>. Each of these five species has four visual pigments in its retina, with absorption maxima at 365, 450, 495 and 565 nm. Visual signalling is a very important medium of communication in these species, and they have a highly coloured, expandable throat-fan called a dewlap. These dewlaps are used almost exclusively in communication and are hidden at other times. Two of the lizard species (*Anolis cristellus* and *A. krugi*) have dewlaps with a high UV reflectance and a third species (*A. pulchellus*) has a UV pattern on its dewlap<sup>24</sup>. The other two species (*A. evermanni* and *A. gundlachi*) have low UV reflectance from the dewlap. In addition, in all five species there is a bright UV spot at the corner at the mouth. This spot is visible only when the mouth is open, a typical anoline threat gesture<sup>24</sup>. These differences in UV absorbance can be correlated with the visual environment of the different species. The former three species come from environments that are often exposed to bright sunlight and blue sky, and so receive a comparatively high level of UV radiation. Under these conditions, the UV-reflective dewlaps will appear bright and contrast against the background vegetation, which reflects very little UV light. The other two species live in a heavily shaded, forest environment, where UV light levels are low, and so UV patterns would be of little use in visual communication. The evidence suggests that UV patterns play an important role in anoline communication where the light levels are high enough to support good contrast. This importance is emphasized in that UV patterns are found only on the dewlaps (which are specialized for communication through display), and not on the rest of the body.

In butterflies, UV colouration and patterning on the wings and body may also play an important role in both inter- and intraspecies communication<sup>49,50</sup>. It may be important in avoiding hybridization, which can occur when closely related species occupy the same range. For many species, the visual pigment spectra and the distribution of the pigment in the receptor mosaic seem to be well matched to wing and reflectance spectra to allow the effective discrimination of

conspecific males of other species<sup>49,50,57</sup>. However, a recent report on a number of sympatric *Colias* and *Gonepteryx* species suggests that the variation in intraspecific UV wing-patterning is so great that they are unlikely to play a role in species identification and the prevention of hybridization<sup>58</sup>. Instead, it has been suggested that their primary role is in intraspecific communication.

In these species of butterfly, the male's only contribution to the production of offspring seems to be the spermatophore, containing sperm- and accessory-gland secretions (containing nutrients that are absorbed by the female). The amount of this material produced by recently mated males is seriously reduced, and females that mate with such males have a significantly lower reproductive output and longevity than females that had mated with previously unmated males. The time taken for the act of copulation is also increased, with a concomitant rise in the risk of predation. It is therefore to a female's advantage to mate with an unmated male. If one assumes an unmated male is also likely to be a younger male, then it would be to a female's advantage to determine the age of potential mates. It has been suggested that this might be accomplished by observation of a male's UV wing-patterns. These patterns are based on optical interference in the microscopic lamellae system associated with the ridges on the outer-wing scales, which makes them potentially susceptible to becoming worn and damaged over time. Therefore, the condition of UV wing-patterns could be an index of male age, and be the subject of sexual selection by female choice<sup>58</sup>.

Alternatively, the patterns may be involved in intraspecific competition between males<sup>58</sup>. Female butterflies tend to be solitary, but males interact with each other in the defence of territory, or in fighting over potential mates. This suggests that long-distance visual signalling will be important for males, but less so for females. Consistent with this hypothesis, UV patterns are generally found only in males<sup>58</sup>.

Thus, UV patterns in butterflies seem to be important for communication, although whether they are used in inter- or intraspecific communication is a matter of debate. UV patterning also seems to play an important role in communication in other insect and invertebrate species<sup>1,2,12</sup>.

### Circadian rhythms

Daily fluctuations in UV light provide information on the time of day, and may be used as a way of calibrating circadian rhythms<sup>59</sup>. It has long been known that UV light plays a role in invertebrate circadian rhythms, but more recently it has been shown that it is important for vertebrates too. For example, the addition of UV light was used to entrain the circadian rhythms of canaries (*Serinus canaria*) and UV wavelengths can regulate neuroendocrine and circadian responses in some rodent species, such as the golden hamster (*Mesocricetus auratus*) and the rat (*Rattus norvegicus*)<sup>60</sup>. In these rodents, UV exposure can (1) block the short-photoperiod-induced collapse of the reproductive system, (2) cause a rapid suppression of nocturnal melatonin synthesis, (3) regulate melatonin rhythms, and (4) phase-shift wheel-running rhythms.

### The origin of vertebrate UV receptors

Studies using the techniques of molecular genetics have shown that, within vertebrates, the spectral absorbance of pigments can be a reasonably good guide to their evolutionary relationships<sup>19,61,62</sup>. This suggests that UV opsins should be most closely related to the short-wavelength cone opsins. This is consistent with the finding that rodents have either UV receptors or short-wave receptors but not both<sup>31</sup>, suggesting that the two genes that code for these pigments

may be alternatives in mammals<sup>19</sup>. Moreover, in histological studies of the retinas of rats and pigeons, both the UV and short-wavelength receptors are found by the same monoclonal antibody<sup>63,64</sup>. However, the gene for the UV cone pigment of zebrafish (*Brachydanio rerio*) shows closer affinities to rhodopsin than to other opsins, including the short-wavelength pigment<sup>65</sup>. It is therefore possible that UV pigments have evolved more than once in vertebrates<sup>19</sup>.

### Summary

Sensitivity to UV light seems to be present in all major animal groups. It is an important cue for the navigation and spatial orientation of an individual within its environment, for foraging, intraspecific communication and biological rhythms. However, more work still needs to be done. For example, what is the function of the UV receptors in the mantis shrimp? Are they integrated into some kind of wavelength-discrimination system? Is there a division of the world into spectral 'windows' of particularly fine discrimination? Or do they mediate specific behaviours<sup>12</sup>? There is some evidence of the latter for the UV receptors in the water flea<sup>8</sup>. A similar problem of interpretation exists in most species where the presence of UV receptors has been demonstrated. Very little evidence exists as to how they are used. Equally, comparatively little is known of the UV patterning on the bodies of animals and the UV reflectance of the environment in which these species exist, and even recent studies seem to have overlooked this<sup>66,67</sup>. To ignore this dimension is to introduce fatal flaws into an experiment, as without an accurate representation of the sensory environment of an animal, its behaviour cannot be accurately interpreted<sup>1,2</sup>.

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## Statistical power of methods of meta-analysis

The review of meta-analysis (MA) by Arnqvist and Wooster<sup>1</sup> was informative and useful. It highlighted how MA can derive conclusions from a set of research studies, even if the individual studies have low statistical power (probability of correctly rejecting the null hypothesis<sup>2</sup>). Ironically, they appear to have overlooked a major point concerning the statistical power of the conclusions from their own example of MA. They applied MA to a hypothetical example of 15 different studies of the effect of a factor *x* on a response variable *y*. As well as stating other conclusions, they noted in Box 2 that:

We then test for heterogeneity across studies by performing a diffuse test of homogeneity, but the null hypothesis that all studies share a common effect size [ $\chi^2_{(14)} = 13.43, P > 0.5$ ] cannot be rejected...To conclude, this simple MA has...indicated that the outcome of the 15 studies are statistically indistinguishable and thus, in that sense, indeed 'consistent'.

However, the authors fail to state the statistical power of the MA method itself in their example! If power is low, then there is a high probability of committing a Type II error, that is, failing to reject the null hypothesis when the null is false. In the above quotes, the authors thus apparently committed the far-too-common error of failing to reject some null hypothesis and then concluding that the null must therefore be true, without asking what the statistical power was of the method of inference, given the data<sup>3–6</sup>. Because the authors failed to state anything about the power of the MA

in this case, they are not justified in automatically concluding that the 15 studies are consistent. It is possible that they are indeed consistent, but it is also possible that they are not and that the MA method simply did not have a high probability of detecting inconsistency (i.e. rejecting the null hypothesis of homogeneity).

While the authors stated in Box 4 that the probability of making Type II errors is 'drastically reduced' with MA methods, the readers of *TREE* would benefit greatly if the authors could inform us of the statistical power of their particular example of MA, especially for different effect sizes (degrees of homogeneity among studies). As well, there are undoubtedly general factors that affect statistical power of MA methods. In classical statistical methods, for instance, power is affected by  $\alpha$ , sample size, sample variance, and the true effect size<sup>2</sup>. What affects the power of MA methods? What guidelines can the authors provide for drawing conclusions from MA when a researcher fails to reject some null hypothesis?

### Randall M. Peterman

School of Resource and Environmental Management, Simon Fraser University, Burnaby, B.C., Canada V5A 1S6

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## Reply from G. Arnqvist and D. Wooster

Peterman raises the issue of statistical power in meta-analysis (MA). Indeed, the basic principles for formulating and rejecting null hypotheses are shared between MA and conventional inferential statistics. A failure to reject a null hypothesis cannot, in itself, validate acceptance of the null. With regard to the quote from Box 2 in our review<sup>1</sup>, we concluded only that the results of the studies were statistically indistinguishable (as evaluated by a simple test of homogeneity). The phrase 'consistent' in Box 2 relates to the phrase 'inconsistent' in Box 1, and was used to contrast the conclusions from a narrative review with our meta-analytic synthesis. In other words, we wanted to illustrate and make it clear that there are no objective grounds for claiming that the studies in our example are 'inconsistent' (i.e. the null cannot be rejected), a subjective conclusion often found in narrative reviews of sets of studies such as this.

However, we wish to make two points. First, statements such as 'inconsistent' are, for the most part, meaningless when multiple studies are compared, unless accompanied by quantitative statistical evaluations. Second, diffuse tests, used for illustration in our simple example, are often relatively blunt instruments for hypothesis testing. A wide variety of more-complex and focused tests for comparing subgroups of studies are available, and should be employed in concert with diffuse tests of homogeneity in more extensive MAs<sup>2</sup>.