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ULTRAVIOLET REFLECTANCE OF COLOR PATCHES IN *Gallotia galloti* LIZARDS FROM TENERIFE, CANARY ISLANDS

Font, E.[1] & Molina-Borja, M.[2]

Abstract: Bright colors and conspicuous visual displays have been described in many lacertid species. However, previous studies of lacertid coloration and behavior have largely ignored differences between the lizards' and our own visual perception, including the possibility that the visual range of lacertids extends into the near ultraviolet (UV) region of the spectrum. In this study we use UV photography and reflectance spectrophotometry to document the presence and distribution of UV reflectance in color patches of *Gallotia* lizards from the Canary Islands. We found considerable reflection of UV light in blue, yellow, and green color patches of different *Gallotia* species. For example, the lateral and ventro-lateral blue patches of *G. galloti* from Tenerife show a single peak of reflectance with a maximum in the near UV waveband, close to the peak sensitivity of UV retinal cones in lizards with known UV vision. The blue, UV-reflecting patches are present in lizards of either sex. However, there are differences in the spectral shape of blue patches from male and female lizards, particularly in the UV range. We conclude that *G. galloti* are sexually dichromatic in their own visual world. Furthermore, we found large interindividual differences in the reflectance of blue patches in lizards from the same sex and population. These differences are again most marked in the UV region of the spectrum. We discuss possible functions of UV-reflecting patches in sex recognition, male-male contests, and mutual mate choice.

Key words: ultraviolet, lizard, coloration, signaling, sexual dichromatism, spectrophotometry, UV photography

Resumen: Reflectancia ultravioleta de las manchas de color en *Gallotia galloti* de Tenerife, Islas Canarias.-Coloraciones brillantes y exhibiciones visuales llamativas han sido descritas en muchas especies de lacértidos. Sin embargo, la mayoría de los estudios previos sobre la coloración y el comportamiento de los lacértidos no han tenido en cuenta diferencias entre nuestra percepción visual y la de los lagartos, incluyendo la posibilidad de que el rango de visión de los lagartos se extienda a la región del ultravioleta (UV) cercano del espectro. En este estudio utilizamos fotografía en el UV y espectrofotometría de reflectancia para documentar la presencia y distribución de reflectancia UV en las manchas de color de lagartos del género *Gallotia* de las Islas Canarias. Los resultados indican que distintas especies de *Gallotia* presentan

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[1] Instituto Cavanilles de Biodiversidad y Biología Evolutiva,Universidad de Valencia. Apdo. 22085, 46071 Valencia *enrique.font@uv.es*

[2] Departamento de Biología Animal, Facultad de Biología, Universidad de La Laguna, Tenerife, Canary Islands.

manchas azules, amarillas y verdes que reflejan en el UV. Por ejemplo, las manchas azules laterales y ventro-laterales de *G. galloti* de Tenerife exhiben un único pico de reflectancia en el UV cercano, próximo al pico de sensibilidad de los conos sensibles al UV de lagartos con visión en el UV. Las manchas azules están presentes en lagartos de ambos sexos. Sin embargo, existen diferencias en los espectros de las manchas azules de machos y de hembras, especialmente en la región del UV. A partir de esta evidencia concluimos que los lagartos de la especie *G. galloti* son sexualmente dicromáticos en su propio mundo visual. Además, encontramos grandes diferencias en la reflectancia de las manchas azules de lagartos del mismo sexo y población. Estas diferencias son más pronunciadas en el UV que en otras regiones del espectro. Por último, discutimos el posible significado funcional de las manchas que reflejan en el UV en relación al reconocimiento del sexo, la competencia entre machos y la elección de pareja.

Palabras clave: ultravioleta, lagarto, coloración, señalización, dicromatismo sexual, espectrofotometría, fotografía ultravioleta.

Resum: Reflectància ultraviolada de les clapes de color en *Gallotia galloti* de Tenerife, Illes Canàries.- Les coloracions brillants i exhibicions visuals sorprenents han estat descrites en moltes espècies de lacèrtids. No obstant això, la majoria dels estudis previs sobre la coloració i el comportament dels lacèrtids no han tingut en compte diferències entre la nostra percepció visual i la dels llangardaixos, incloent la possibilitat que el rang de visió dels llangardaixos s'estengui a la regió de l'ultraviolat (UV) proper de l'espectre. En aquest estudi hem utilitzat fotografia en l'UV i espectrofotometria de reflectància per documentar la presència i distribució de reflectància UV en les clapes de color de llangardaixos del gènere *Gallotia* de les Illes Canàries. Els resultats indiquen que diferents espècies de *Gallotia* presenten clapes blaves, grogues i verdes que reflecteixen en l'UV. Per exemple, les clapes blaves laterals i ventro-laterals de *G. galloti* de Tenerife exhibeixen un únic pic de reflectància en l'UV proper al pic de sensibilitat dels cons sensibles a l'UV de llangardaixos amb visió en l'UV. Les clapes blaves estan presents en llangardaixos d'ambdós sexes. Malgrat això, existeixen diferències en els espectres de les clapes blaves de mascles i femelles, especialment en la regió de l'UV. A partir d'aquesta evidència concloem que els llangardaixos de l'espècie *G. galloti* són sexualment dicromàtics en el seu propi món visual. A més, trobem grans diferències en la reflectància de les clapes blaves de llangardaixos del mateix sexe i població. Aquestes diferències són més pronunciades en l'UV que en altres regions de l'espectre. Finalment, discutim el possible significat funcional de les clapes que reflecteixen en l'UV en relació al reconeixement del sexe, la competència entre mascles i l'elecció de parella.

Paraules clau: ultraviolat, llangardaix, coloració, senyalització, dicromatisme sexual, espectrofotometria, fotografia ultraviolada.

INTRODUCTION

Bright colors, often emphasized during stereotyped behavioral displays, are an important element of visual communication in many vertebrate groups (Hailman, 1977; Burtt, 1979; Zahavi & Zahavi, 1997; Bradbury & Vehrencamp, 1998). Traditionally, assessments of animal coloration and its role in behavior have relied on human visual perception or standards and instrumentation based thereon, largely ignoring differences between our color vision and that of other vertebrates (BENNETT *et al.*, 1994). One such major difference concerns the range of wavelengths perceived as visible light. While humans cannot normally see light below 400 nm, vision in the ultraviolet (UV) range of wavelengths (300-400 nm) is well documented for many species of vertebrates (JACOBS, 1992; TOVÉE, 1995; LOSEY *et al.*, 1999; HART, 2001; HUNT, *et al.*, 2001). In fact, it has been suggested that UV vision may be the plesiomorphic condition for vertebrates and has probably been retained in many extant taxa (GOLDSMITH, 1994; ROBINSON, 1994; YOKOHAMA & SHI, 2000; EBREY & KOUTALOS, 2001). Thus, contrary to common wisdom, our inability to perceive UV light is probably the exception, rather than the rule, as far as vertebrates are concerned. Furthermore, recent research has revealed the presence of UV reflectance patterns, invisible to humans, in many vertebrates capable of UV vision. It has been suggested that UV vision and UV reflectance patterns may play a role in navigation, foraging, crypsis, intraspecific signaling, or in mate choice (e.g., CUTHILL & BENNETT, 1993; BENNETT & CUTHILL, 1994; TOVÉE, 1995; CHURCH *et al.*, 1998; CUTHILL *et al.*, 2000a, b; HONKAVAARA *et al.*, 2002; SIITARI *et al.*, 2002).

Behavioral and physiological studies have provided evidence that many lizards are capable of UV vision (ALBERTS, 1989; FLEISHMAN *et al.*, 1993, 1997; LOEW, 1994; ELLINGSON *et al.*, 1995; LOEW *et al.*, 1996, 2002; KAWAMURA & YOKOYAMA, 1998). UV vision in lizards is subserved by specialized cone receptors in the retina that contain a UV-sensitive photopigment. The wavelength of peak absorption of the UV-sensitive photopigments of lizards, as determined by microspectrophotometry, lies in the 362-367 nm range (FLEISHMAN *et al.*, 1993, 1997; LOEW, 1994; ELLINGSON *et al.*, 1995; LOEW *et al.*, 1996, 2002). UV reflectance patterns have also been described in several lizard species (see Table 1). The dewlaps of some *Anolis* lizards, for example, show reflectance peaks in the UV range that may function as hidden UV signals (FLEISHMAN *et al.*, 1993). In the agamid *Ctenophorus ornatus*, throat reflectance extends into the UV range and variation in female throat reflectance is involved in male choice of females (LEBAS & MARSHALL, 2000). However, the available studies encompass only a small percentage of lizard species, and further studies are critical to evaluate the generality of these observations.

Lacertids are a particularly interesting group in this respect, as a lot of recent research has focused on their coloration (e.g., DÍAZ, 1993; OLSSON, 1993, 1994a, b; SALVADOR *et al.*, 1996; MOLINA-BORJA *et al.*, 1997, 1998; MARTÍN & FORSMAN, 1999; GALÁN, 2000; LÓPEZ & MARTÍN, 2001; LÓPEZ *et al.*, 2002). Lacertids are diurnally active lizards with a well developed visual system that includes the capacity for color discrimination (SWIEZAWSKA, 1950; ANH, 1968; UNDERWOOD, 1970). Many inhabit exposed, full sunlight environments and are highly dependent on visual cues for foraging, sexual, and agonistic behaviors (e.g., VERBEEK, 1972; DESFILIS *et al.*, 2003). Sexual differences in coloration (i.e., sexual

species	body region showing UV reflectance	source
Anolis spp. (Puerto Rico)	dewlaps of five species examined show reflectance peaks in the UV (>35% at 360 nm in *A. krugi* and *A. cristatellus*)	Fleishman *et al.*, 1993 Fleishman & Persons, 2001
Anolis spp. (Jamaica and Grand Cayman)	dewlaps of 11 species and subspecies studied reflect in the UV. Dewlap reflectance of three *A. conspersus* color morphs peaks at around 340 nm (>40%); individuals of the brown morph exhibit strong short wavelength reflectance that extends well into the ultraviolet on the head, legs and tail	Macedonia, 1999, 2001; Macedonia *et al.*, 2000
Anolis carolinensis	dewlap presents two reflectance peaks, one in the UV and one in the visible part of the spectrum	Stoehr & McGraw, 2001
Anolis trinitatis, A. roquet	in some populations, the dewlap and other body areas show strong UV reflection	Thorpe, 2002 Thorpe & Stenson, 2003
Carlia pectoralis	gray-blue gular region of a breeding male has a reflectance peak at 338 nm	Blomberg *et al.*, 2001
Ctenophorus ornatus	the throat (both sexes) and the chest patch (females only) reflect in the UV; sexual dichromatism extends into the UV region and throat reflectance spectra differ greatly among same-sex individuals	LeBas & Marshall, 2000, 2001
Gallotia galloti	males of the two subspecies present in Tenerife have lateral and ventro-lateral blue patches with reflectance peaks in the UV (360 ± 20 nm)	Thorpe & Richard, 2001

Table 1. Studies showing UV reflectance in lizards

dichromatism) are widespread in lacertids and members of one sex, typically the males, often show bright colors that may be sexually selected (Cooper & Greenberg, 1992; Olsson & Madsen, 1998). However, almost without exception, previous analyses of lacertid coloration have relied on human perception and are thus implicitly based on the assumption that lizards perceive colors in the same way that we do.

In this study we use UV photography and spectrophotometry to describe reflectance patterns, including the UV range of wavelengths, of color patches in *Gallotia galloti* lizards from Tenerife (Canary Islands). Because *G. galloti* lives in open habitats exposed to sunlight and appears to rely heavily on color in social interactions (e.g., Molina-Borja *et al.*, 1997, 1998), we hypothesized that some of their bright color patches may be reflective in the UV. Background coloration in adult male *G. galloti* is gray or brown in the dorsal trunk, tail and limbs, and black in the head. Throughout the island, males exhibit conspicuous lateral, ventro-lateral, and cheek patches that appear different shades of blue to humans (Figure 1). These blue patches are sometimes surrounded by a light gray rim and contrast sharply with the dark background of the head and body. Geographic variation in color pattern, possibly linked to different latitudinal biotopes, affects mostly the size and distribution of blue patches (Thorpe & Brown, 1989). Males in the northern part of the island (hereafter referred to by the subspecific name *G. g. eisentrauti*) have large cheek patches and small lateral and ventro-lateral patches. In contrast, males in the central and southern parts of the island (hereafter *G. g. galloti*) have large lateral and ventro-lateral patches and small cheek patches (Figure 1). Occasionally, the rostralmost lateral patches of adult male *G. g. galloti* may fuse giving raise to conspicuous shoulder patches. A further difference between the two populations is the presence of yellow dorsal cross bars in males from the northern part of the island (*G. g. eisentrauti*).

Recently, Thorpe and Richard (2001) reported that the blue patches of northern and southern *G. galloti* reflect maximally in the UV range of wavelengths, with a peak around 360 nm. However, these authors presented reflectance spectra for only three body regions of modal northern and southern male lizards. Our aim in the present work is to further document the presence and variation of UV reflectance patterns in *G. galloti*, including spectral reflectance data from a larger sample of individuals of either sex. Our primary focus is on *G. galloti* from Tenerife, but we also present preliminary data on UV reflectance patterns of other *Gallotia* species for comparative purposes.

MATERIAL AND METHODS

UV photography and spectrophotometry were used to characterize the reflectance patterns of lizards. Both techniques have extensively been used to reveal UV reflectance patterns of vertebrate and invertebrate animals and yield complementary information (Knüttel & Fiedler, 2000). UV photography permits rapid visualization of UV reflectance patterns and their spatial distribution, whereas spectrophotometry provides accurate quantitative data regarding the spectral reflectance patterns of selected color patches (Endler, 1990).

Lizards were collected from ravines in Bajamar and Tejina (*G. g. eisentrauti*) and in Igueste de Candelaria (*G. g.

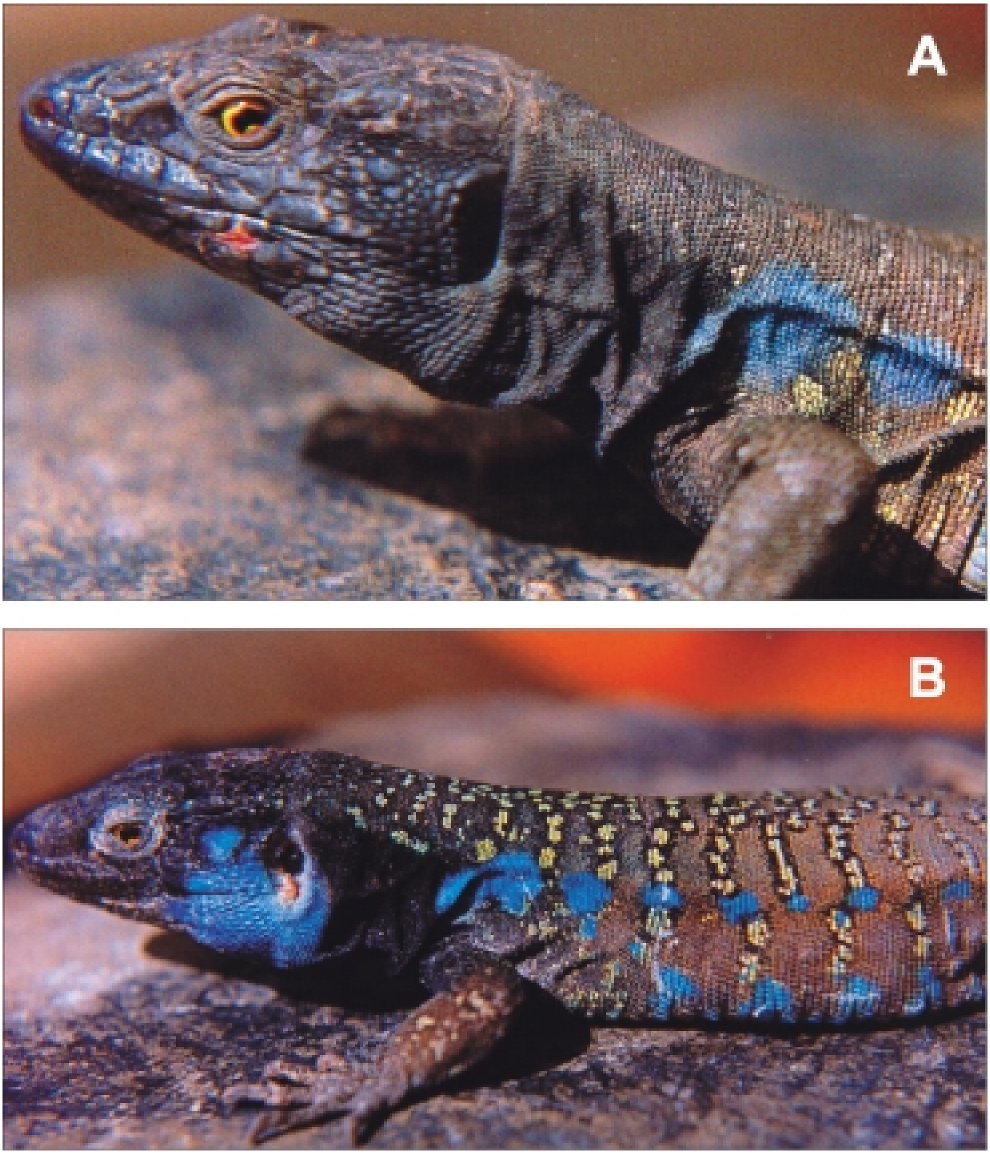

Figure 1. Color photographs of the anterior part of the body of representative male *G. g . galloti* (**A**) and *G. g. eisentrauti* (**B**). Note the presence of well developed blue cheek, lateral, and ventro-lateral patches and yellow dorsal cross bars in *G. g. eisentrauti*. Male *G. g. galloti* typically lack the yellow dorsal cross bars and have reduced cheek patches, but their lateral patches are larger than those of male *G. g. eisentrauti*

galloti) using tomato-baited traps, and were transported to the laboratory at the Universidad de La Laguna. Sixteen lizards of both sexes were transported to the Universidad de Valencia for further analyses (under permit EIC-132/2000 from the Cabildo Insular de Tenerife). In the laboratory, the lizards were housed singly or in small groups in terraria placed inside a temperature-controlled room. Light was provided by fluorescent bulbs with day light spectrum (Reptistar, F18W 6500 K, Sylvania). Food was supplied every 2-3 days in the form of mealworm larvae (*Tenebrio molitor*), cat food, and pieces of tomato. Water was available continuously. At the completion of the experiments, all the lizards were released unharmed at their original capture sites.

A total of 22 *G. g. eisentrauti* (10 males, 12 females) and 19 *G. g. galloti* (12 males, 7 females) were used for UV photography. Of these, 14 *G. g. eisentrauti* (7 males, 7 females) and 13 *G. g. galloti* (9 males, 4 females) were also used for reflectance spectrophotometry. Though there is no indication of short-term color changes in this species, in most cases photographs and spectral measurements were taken within two days of original capture. To facilitate handling, lizards were held in a cold room (4°C) for 10 min prior to the experimental manipulations. Additionally, some lizards were lightly anesthetized with an intramuscular injection of ketamine hydrochloride (250 mg/kg b.w.).

For UV photography, lizards were positioned on a light stand and photographed through a 100 mm macro lens mounted on a Yashica FX-103 camera against a UV reflective background. Each lizard was photographed through a UV-blocking filter (Skylight 1A) that transmits only wavelengths above 400 nm, and again through a UV-transmitting filter with peak transmittance at 360 nm (Hoya U-360 or Tiffen 18A), using UV-sensitive black and white film (Kodak T-MAX P3200; for additional details see Silberglied, 1976). Illumination was provided by a standard flash light for photography within the human visible range. For photographs in the UV range, the standard flash light was coupled to a second flash light modified for UV output. The two flash lights were set in manual mode so that the same amount of light was available for every exposure. Photographic processing and development of film material was standardized as much as possible. Most lizards were photographed in dorsal, ventral, and lateral views. To provide a photographic record of color in the human visual range, we also took color photographs of all the lizards using a high-resolution digital camera (Sony DSC-F707).

The spectral composition of light reflected off the skin of lizards was determined using a USB2000 portable diode-array spectrometer optimized for ultraviolet detection and a PX-2 Xenon strobe light source, both from Ocean Optics. Spectra were recorded in 0.37 nm steps from 200 to 850 nm and expressed as percent of light reflected relative to a Spectralon WS-1 white diffuse reflectance standard (> 95% reflectance from 250-2000 nm). Measurements were taken using a bifurcated fiber optic probe with six 200 μ illuminating fibers surrounding a 200 μ measuring fiber. The probe was held at a 90° angle to the lizard's skin. As relative reflectance of spectra varies with distance to the target, we attached a fixed length pointer (made from an insect pin) to the probe to maintain a constant 5 mm distance between the end of the probe and the lizard's skin, resulting in a reading spot of ca. 2 mm in diameter. A dark current and white standard reference spectrum were taken at approximately every 10 min during measurements of lizard coloration. Data integration time was set at 55 ms using data smoothing level 10. For most lizards, spectral data were acquired from the following body regions: head (dorsal, anterior to parietal eye), gular area (center), cheek, lateral and ventro-lateral patches, dorsum (midpoint along vertebral column), dorsal cross bars, ventrum (center), leg (outer, upper thigh), and tail (dorsal, slightly distal to base). For each body region, 20 spectra were measured, averaged and graphed using OOIBase32 software from Ocean Optics. All measurements were taken in a darkened room to minimize interference from external light sources. Analyses were confined to the 300-700 nm range, which spans visible and near ultraviolet wavelengths. Variation in spectral shape was determined by visual inspection of the reflectance curves. Total reflectance of the first (i.e., rostralmost) lateral blue patch of male and female lizards was calculated by summing the percent reflectance across the 300-700 nm range of wavelengths.

Previous studies have used sunblock chemicals to alter the spectral reflectance of UV-reflecting patches of flowers and birds (e.g., Andersson & Amundsen, 1997; Johnsen *et al.*, 1998; Sheldon *et al.*, 1999; Johnson & Andersson, 2002; Siitari *et al.*, 2002). In order to evaluate the usefulness of this technique for selective manipulation of specific colored patches in lizards, we applied UV-absorbing sunscreen (Sun Protection Factor 60+) to the blue, UV-reflecting patches of selected lizards. A thin layer of sunscreen was smeared onto the blue patches using cotton-tipped applicators, after which the lizards were photographed and their reflectance spectra recorded as described above.

RESULTS

The comparison of photographs in the visible and UV range reveals that the blue lateral, ventro-lateral and cheek patches of male *G. g. galloti* and *G. g. eisentrauti* reflect strongly in the UV. The blue patches are relatively inconspicuous in black and white photographs covering the visible range of wavelengths, yet they stand out markedly in photographs in the UV range (Figure 2). The blue patches are usually bordered by areas of dark skin that are nonreflective in the UV range, thus providing a sharp contrast between the UV-reflecting spots and their background. Although generally smaller than those of males, blue patches are also present in females from the two populations, and they too reflect in the UV (Figures 3 and 4). In addition, lizards of both sexes occasionally present one or more rows of yellow-cream patches interspersed between the lateral and ventro-lateral blue patches. These yellow patches are also UV-reflecting, although they do not appear as bright as the blue patches in UV photographs (Figure 3). Other color markings, such as the yellow dorsal cross bars, are relatively inconspicuous in the UV range. When UV-absorbing sunscreen was applied to the blue patches, no UV reflectance was present in the photographs.

Spectrograms confirm the presence of UV reflectance in the blue patches of *G. g. galloti* and *G. g. eisentrauti*. The lateral and ventro-lateral patches of lizards of either sex exhibit a single peak of reflectance with a maximum in the near ultraviolet range. The human-perceived blue is generated by the tail of the spectral curve, while the maximum is close to the peak sensitivity of UV retinal cones in other lizards. Figure 5 shows reflectance spectra for the first (i.e., rostralmost) lateral patch in a sample of males and females from the two populations. Cheek patches also have reflectance maxima in the UV but tend to yield flatter reflectance curves compared with the lateral and ventro-lateral patches (Figures 6A, 6C). In contrast, the head, gular area, dorsum, legs, and tail have extremely low reflectance across the entire spectrum (Figure 6). Other body regions, such as the ventrum and the dorsal cross bars, reflect in the human visible range but not in the UV (Figures 6D, 6E). Yellow patches reflect both in the visible and in the UV range, with reflectance dropping off sharply below 330-340 nm (Figures 6B, 6F). In agreement with the results of UV photography, the spectra of blue patches smeared with UV-absorbing sunscreen show a marked reduction in reflectance below 400-420 nm. Interestingly, this effect is still detectable two weeks after application of the sunscreen chemicals.

A comparison of the reflectance spectra of male and female lizards reveals striking sex differences in color patches that appear monomorphic to humans (Figure 5). Peak reflectance (i.e., hue) of the first lateral patch differs between the sexes, with males having reflectance maxima at 383 ± 16 nm (mean ± SD, $n = 16$) and females at 363 ± 9 nm ($n = 11$), and the difference is statistically significant (Mann-Whitney test, two-tailed, $U = 152$, $p < 0.05$). In addition, the first lateral patch of *G. g. eisentrauti* is brighter in males (mean reflectance ± SD = 30580 ± 8218, $n = 7$) than in females (17671 ± 5545, $n = 7$). The sex difference in brightness is statistically significant ($U = 43$, $p < 0.05$) and greater in the UV than in other regions of the spectrum. No sex differences in brightness are evident in the first lateral patch of *G. g. galloti* (Figures 5A, 5B), although given the small sample size this result should be taken only as tentative. In addition to these sex differences, lizards of the same sex and population show interindividual variation in spectral shape of the UV-reflecting blue patches. This variation is again most marked in the UV region of the spectrum (Figure 5).

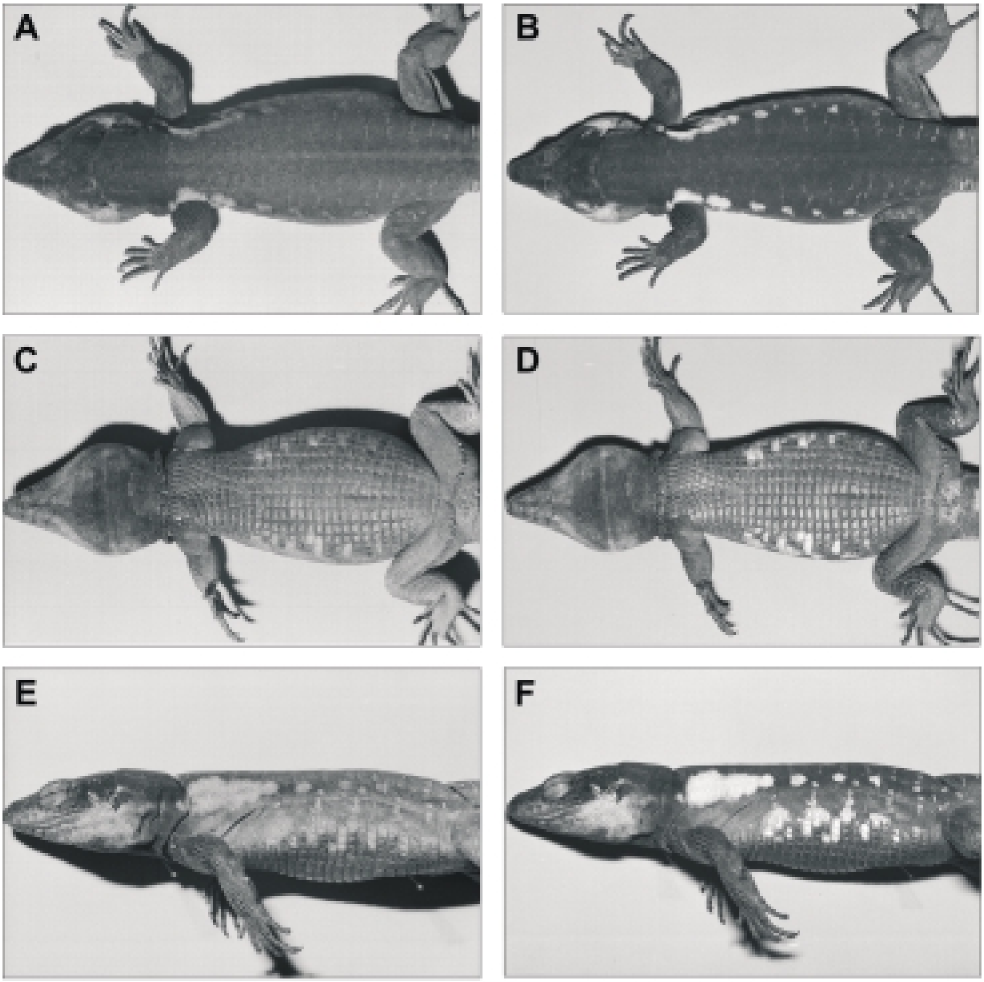

Figure 2. Male *G. g. galloti* photographed in dorsal (**A**, **B**), ventral (**C**, **D**), and lateral (**E**, **F**) views. The three photographs on the left side of the figure were taken through a UV-blocking filter, while those on the right were taken through a UV-transmitting filter with peak transmittance at 360 nm. The white areas in **B**, **D**, and **F** correspond to areas of enhanced UV reflection. The UV-reflecting cheek, lateral, and ventro-lateral patches are particularly conspicuous in lateral view

UV-reflecting color patches are not only found in *Gallotia galloti* from Tenerife. Preliminary results of work with other Canarian lacertids reveal the presence of areas of UV reflectance in *G. g. palmae* from La Palma, *G. simonyi* from El Hierro, and in two subspecies of *G. atlantica*: *G. a. atlantica* from Lanzarote and *G. a. mahoratae* from Fuerteventura (Figure 5D). In *G. g.*

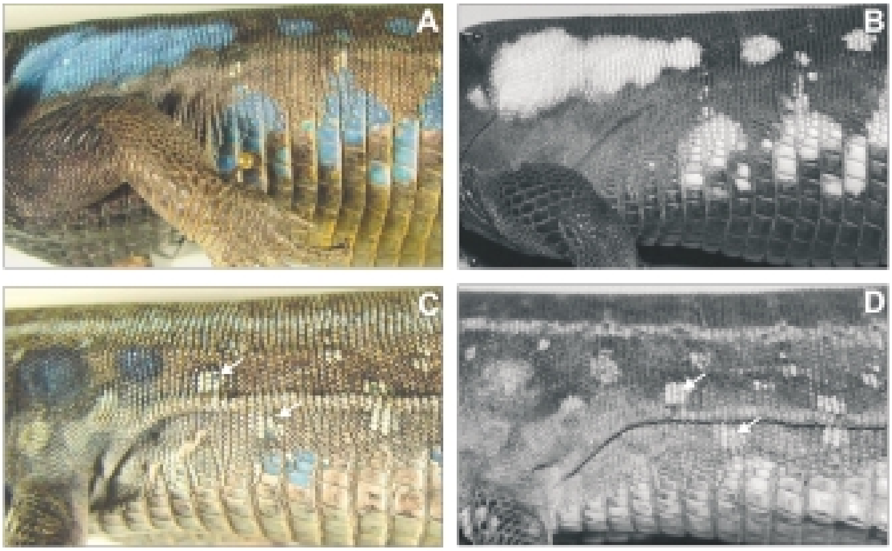

Figure 3. Photographs of the anterior part of the trunk of male (**A**, **B**) and female (**C**, **D**) *G. g. galloti* (anterior is to the left). The photographs on the right were taken using a high-resolution digital camera and show the coloration of this area in the human visible range. The same area was photographed in **B** and **D** through a UV-transmitting filter to reveal areas of enhanced UV reflection. Note the presence of UV-reflecting blue and yellow patches in lizards of both sexes. The arrows in **C** and **D** point to UV-reflecting yellow patches in the female

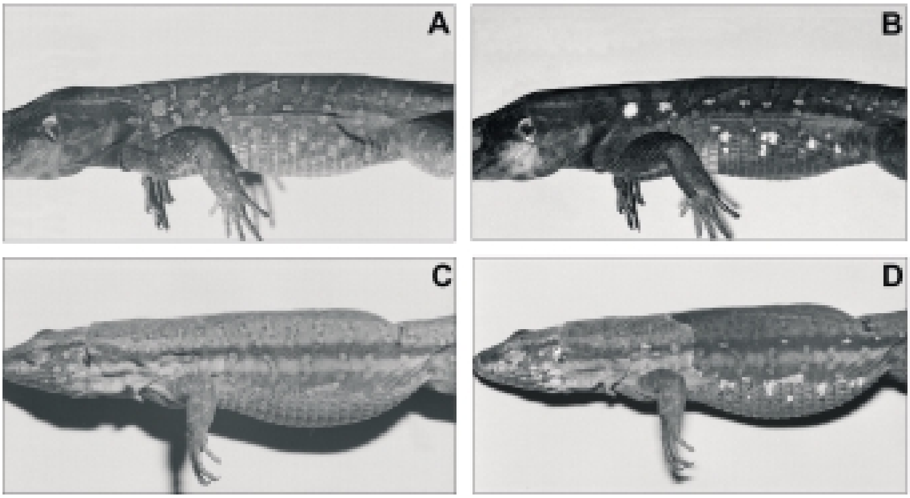

Figure 4. Photographs of male (**A**, **B**) and female (**C**, **D**) *G. g. eisentrauti* in lateral view. The two photographs on the left were taken through a UV-blocking filter, while those on the right were taken through a UV-transmitting filter. Note the presence of UV-reflecting patches in the two sexes. The first lateral patches of the female are clearly visible through a piece of loose skin (**D**)

palmae and *G. a. atlantica*, the UV-reflecting patches correspond to areas of blue skin similar to the blue patches of *G. galloti* from Tenerife. The UV-reflecting patches look yellow in *G. simonyi* and green in *G. a. mahoratae*. However, not all *Gallotia* species display UV-reflecting patches; males of at least one species, *G. stehlini* from Gran Canaria, are relatively drab when viewed in the UV and show no specific areas with enhanced UV reflection.

DISCUSSION

Our results document the presence of UV reflectance in some of the bright color patches of *Gallotia* lizards from the Canary Islands. As UV reflectance patterns are invisible to human observers, these results underscore the need for assessments of animal coloration that are truly independent of human color vision (BENNETT *et al.*, 1994). It has been suggested that UV

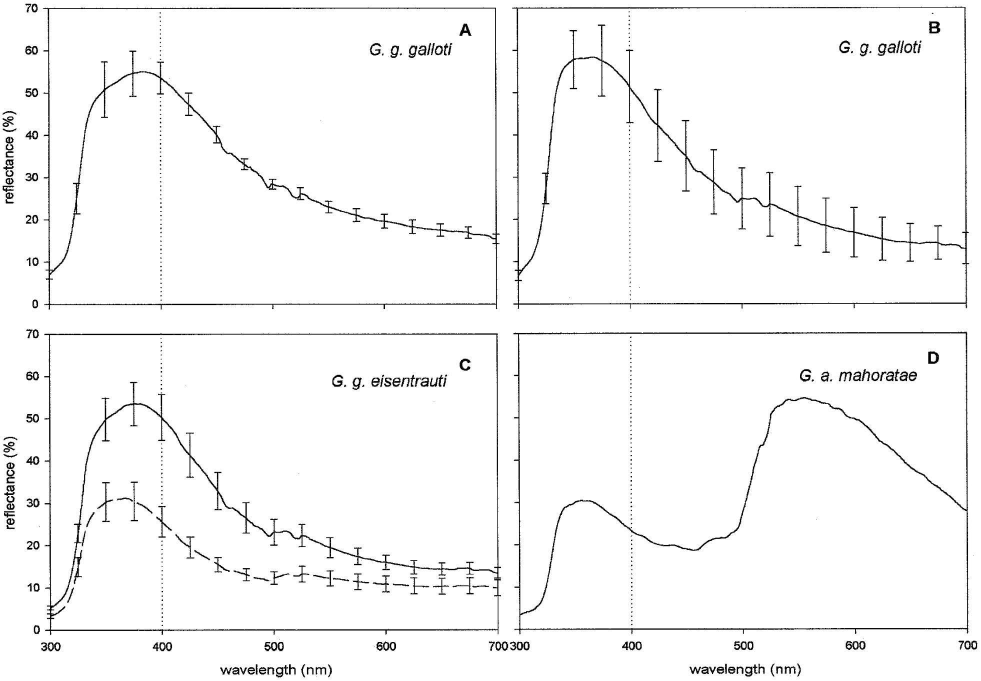

Figure 5. Percentage reflectance relative to a Spectralon white diffuse reflection standard of the first lateral patch (right side of the body) of *Gallotia* lizards. Values shown are the mean (± SEM) of the lizard means (20 spectra for each lizard). **A**) Blue patches of male *Gallotia galloti galloti* (n = 9). **B**) Blue patches of female *G. g. galloti* (n = 4). **C**) Blue patches of male (solid line, n = 7) and female (broken line, n = 7) *G. g. eisentrauti*. **D**) Green patch of a male *Gallotia atlantica mahoratae*. Note the presence of a single reflectance peak in the near UV for the blue patches of *G. galloti* and two reflectance peaks for the green patch of *G. atlantica*. Also note the sexual dichromatism in the blue patches of *G. g. eisentrauti*. Vertical dotted lines on each figure indicate the lower end of human visual sensitivity (400 nm)

reflectance patterns may, at least in birds, be particularly suited for a signaling role (HAUSMANN *et al.*, 2002; but see HUNT, *et al.*, 2001). That the UV-reflecting patches of *Gallotia* are located in a lateral or ventro-lateral position and are maximally exposed during interactions with conspecifics likewise suggests a potential role in intraspecific signaling. However, the presence of UV-reflecting patches cannot by itself be taken as evidence for a signal function. A fundamental premise of studies of the role of UV in intraspecific communication is that the UV reflectance patterns are visible to the animals producing them. Among lizards, UV vision has so far been confirmed in 19 iguanid and 5 geckonid species (ALBERTS, 1989; FLEISHMAN *et al.*, 1993, 1997; LOEW, 1994; ELLINGSON *et al.*, 1995; LOEW *et al.*, 1996, 2002). In fact, evidence for UV vision has been found in every lizard

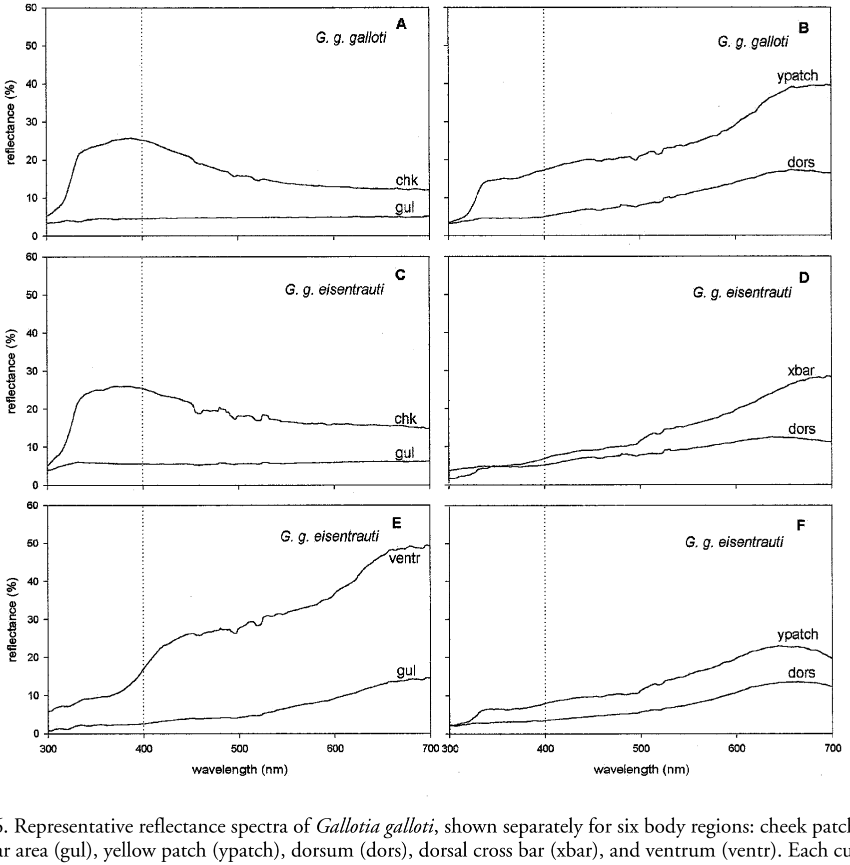

Figure 6. Representative reflectance spectra of *Gallotia galloti*, shown separately for six body regions: cheek patch (chk), gular area (gul), yellow patch (ypatch), dorsum (dors), dorsal cross bar (xbar), and ventrum (ventr). Each curve represents the average of 20 spectra taken from the same lizard. **A**, **B**) Male *G. g. galloti*. **C**, **D**) Male *G. g. eisentrauti*. **E**, **F**) Female *G. g. eisentrauti*

species in which it has been sought with appropriate experimental techniques, including nocturnal lizards and those lacking UV-reflecting color patches (LOEW, 1994; LOEW *et al.*, 1996; MACEDONIA, 1999). Although no studies of visual pigments or spectral sensitivity have been conducted with any lacertid, the ubiquity of UV vision among squamate reptiles suggests that lacertids may have UV-sensitive vision. In fact, preliminary evidence obtained using electroretinography, which provides information about the range of wavelengths that can effectively stimulate the retina, indicates that the eyes of *G. galloti* are sensitive to light in the near UV waveband, very likely by means of an independent photopigment similar to the UV-sensitive photopigment found in other lizards (PALACIOS, HERRERA, DESFILIS & FONT, unpublished results).The peak reflectance of the blue patches of *Gallotia* lizards is in the near UV region, very close to the wavelength of peak absorption of the UV receptors of lizards with known UV vision (FLEISHMAN *et al.*, 1993; LOEW, 1994; ELLINGSON *et al.*, 1995; LOEW *et al.*, 1996, 2002; KAWAMURA & YOKOYAMA, 1998), and agrees with data on UV reflectance in other lizards (see Table 1). Short wavelength reflectance in lizards is produced structurally by dermal iridophores. Iridophores contain arrays of reflecting platelets and generate colors by the optical phenomenon of thin-layer interference. The structural colors interact with pigments in the chromatophores to produce a diversity of human visible colors (e.g., MORRISON *et al.*, 1995, 1996; MACEDONIA *et al.*, 2000). In birds, plumage peak blue reflectance often includes a UV color component (ANDERSSON, 1996; ANDERSSON & AMUNDSEN, 1997; HUNT *et al.*, 1998; KEYSER & HILL, 1999). Similarly, blue patches in the skin of some lizards reflect strongly in the UV (e.g., *Anolis conspersus*, MACEDONIA, 1999, 2001; *Carlia pectoralis*, BLOMBERG *et al.*, 2001; *Gallotia galloti*, THORPE & RICHARD, 2001, this study). In contrast, blue patches of other lizards do not show enhanced reflection in the UV range. For example, male *Sceloporus undulatus* posses striking blue throat and belly patches that do not reflect in the UV (STOEHR & MCGRAW, 2001). UV reflectance in *Gallotia* is not limited to areas of blue skin, as we also found strong short wavelength reflectance in yellow (*G. galloti*, *G. simonyi*) and green (*G. atlantica mahoratae*) color patches. Interestingly, not all yellow skin in *Gallotia* shows UV reflectance. The yellow dorsal cross bars of *G. g. eisentrauti* are a case in point. The cross bars are very conspicuous in the human visible range yet they show almost no reflectance in the UV range. Thus, it appears that the human visible coloration of lizard skin does not offer a reliable criterion for distinguishing between UV-reflecting and non UV-reflecting color patches (see also CUTHILL *et al.*, 2000a). These results emphasize anew the need to objectively assess color patterns of lizards, as color patches that look similar to us may look different to the lizards.

Assuming that UV reflectance patterns are visible to the lizards, the question arises as to the function(s) of UV-reflecting patches in *Gallotia galloti*. One possibility is that color patterns, including those in the UV range, are important for subspecies recognition and reproductive isolation. Thorpe and Richard (2001) argued that differences in the size and distribution of UV-reflecting patches could function to reduce interbreeding between northern and southern population lizards. According to this scenario, UV reflectance patterns could provide a mechanism for assortative mating via female choice, allowing females to mate preferentially with males from their own population. Thorpe and Richard (2001) showed that differences in the size and distribution of the UV-reflecting patches are associated with patterns of gene flow in *G. galloti* from Tenerife. This association is congruent with the notion that variation in UV reflectance patterns promotes reproductive isolation between the two populations. However, as the UV-reflecting patches are visible to us as blue patches, a comparison of northern and southern males in the human visible range should yield identical results. Thus, the presence of UV reflectance in the blue patches seems irrelevant to Thorpe and Richard's main conclusion (see also Thorpe, 2002). Moreover, Thorpe and Richard (2001) restricted their analyses to a sample of sexually mature males. As UV-reflecting patches are also present in females from both populations, reproductive isolation between northern and southern lizards of the sort envisioned by Thorpe and Richard cannot be the (only) agent selecting for UV reflectance in *G. galloti*.

An alternative interpretation is suggested by our finding of sex differences in the UV reflectance of blue patches. Reflectance spectrophotometry reveals that the peak reflectances of the blue patches of males are shifted ca. 20 nm above those of females. In addition, the blue patches of male *G. g. eisentrauti* are brighter than those of females, particularly in the near UV range. Although adult male *G. galloti* are usually larger and have larger blue patches than females (Molina-Borja *et al.* 1997), smaller lizards are often monomorphic in size and coloration. Sexual dichromatism in the UV-reflecting patches could thus facilitate recognition of the sex of conspecifics, particularly during interactions at close range. Sexual dichromatism in the UV range has been previously reported in birds (Andersson *et al.*, 1998; Hunt *et al.*, 1998; Cuthill *et al.*, 1999), but this is the first lizard species shown to be sexually dichromatic in the UV but relatively monomorphic in the human visible spectrum.

Additionally, there is the possibility that lizards from the same population use variation in UV reflectance patterns as a cue in contest competition, mutual mate choice, or both (Andersson, 1994). Our results show large amounts of spectral shape variation in blue patches from individuals of the same sex and population. As with the sex differences, this interindividual variation is most marked in the UV region of the spectrum. Previous studies have shown that color patches in male lizards may signal status (Thompson & Moore, 1991; Zucker, 1994), are related to fighting ability (Olsson, 1994a), or affect dominance relationships (Rand, 1991; Carpenter, 1995). Molina-Borja *et al.* (1998) reported slight differences in the human visible color of the first lateral blue patch of winners and losers in staged encounters between male *G. g. galloti*. Although no UV status signals have been described in lizards, it is conceivable that the color differences between winners and losers could extend to (or even be more pronounced in) the UV. If so, UV-reflecting patches could act as cues to male fighting ability in *G. galloti* and perhaps in other species as well.

Among vertebrates, assortative mating with respect to UV reflectance has been studied most extensively in birds (Bennett *et al.*, 1996, 1997; Hunt *et al.*, 1997, 1998, 1999; Andersson *et al.*, 1998; Johnsen *et al.*, 1998; Siitari & Huhta, 2002; Siitari *et al.*, 2002) and fish (Kodric-Brown & Johnson, 2002; Macías-Garcia & Burt de Perera, 2002; Smith *et al.*, 2002). Only a single study has demonstrated an effect of UV reflectance on patterns of mate choice in lizards. In the agamid *Ctenophorus ornatus*, males tend to associate with females with a high throat chroma (i.e., saturation) between 370 and 400 nm (LeBas & Marshall, 2000). Female throat coloration seems unrelated to female quality, but may indicate female receptivity. Interestingly, in this species the two sexes show variation in the UV reflectance of throat patches. However, variation in male throat reflectance does not affect female mate choice (LeBas & Marshall, 2001). Experiments are currently underway to test the role of UV reflectance patterns on mutual mate choice in *G. galloti*.

The role of UV-reflectance patterns in intraspecific signaling and mate choice has often been investigated using UV-blocking or UV-transmitting filters (e.g., Bennett *et al.*, 1996, 1997; LeBas & Marshall, 2000, 2001; Hunt *et al.*, 1997, 1999, 2001; Kodric-Brown & Johnson, 2002; Macías-Garcia & Burt de Perera, 2002). However, changing the light environment by completely filtering out one waveband may result in target objects that appear unnatural to the receiving animals. Alternatively one could alter the color of the target objects themselves. Our results suggest that UV-blocking sunscreen chemicals could be used to effectively remove the UV reflectance from the blue patches of *G. galloti* and perhaps other lizards.

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REFERENCES

Alberts, A.C. (1989): Ultraviolet visual sensitivity in desert iguanas: Implications for pheromone detection. *Anim. Behav.*, 38: 129-137.

Andersson, M. (1994): *Sexual Selection*. Princeton University Press, Princeton, New Jersey.

Andersson, S. (1996): Bright ultraviolet coloration in the Asian whistling-thrushes (*Myiophonus* spp.). *Proc. R. Soc. Lond. B*, 263: 843-848.

Andersson, S. & Amundsen, T. (1997): Ultraviolet colour vision and ornamentation in bluethroats. *Proc. R. Soc. Lond. B*, 264: 1587-1591.

Andersson, S., Örnborg, J. & Andersson, M. (1998): Ultraviolet sexual dimorphism and assortative mating in blue tits. *Proc. R. Soc. Lond. B*, 265: 445-450.

Anh, J.N.H. (1968): Ultrastructure des récepteurs visuels de la retine de *Lacerta viridis*. *Bull. Assoc. Anat.*, 53: 1247-1259.

Bennett, A.T.D. & Cuthill, I.C. (1994): Ultraviolet vision in birds: What is its function? *Vision Res.*, 34: 1471-1478.

Bennett, A.T.D., Cuthill, I.C. & Norris, K.J. (1994): Sexual selection and the mismeasure of color. *Am. Nat.*, 144: 848-860.

Bennett, A.T.D., Cuthill, I.C., Partridge, J.C. & Maier, E.J. (1996): Ultraviolet vision and mate choice in zebra finches. *Nature*, 380: 433-435.

Bennett, A.T.D., Cuthill, I.C., Partridge, J.C. & Lunau,K. (1997): Ultraviolet plumage colors predict mate preferences in starlings. *Proc. Natl. Acad. Sci. USA*, 94: 8618-8621.

Blomberg, S.P., Owens, I.P.F. & Stuart-Fox, D. (2001): Ultraviolet reflectance in the small skink *Carlia pectoralis*. *Herp. Review*, 32: 16-17.

Bradbury, J.W. & Vehrencamp, S.L. (1998): *Principles of Animal Communication*. Sinauer Assoc. Press, Sunderland, Massachusetts.

Burtt, E.H. (ed.) (1979): *The Behavioral Significance of Color*. Garland STPM Press, New York.

Carpenter, G.C. (1995): Modeling dominance: The influence of size, coloration, and experience on dominance relations in tree lizards (*Urosaurus ornatus*). *Herpetol. Monogr.*, 9: 88-101.

Church, S.C., Bennett, A.T.D., Cuthill, I.C. & Partridge, J.C. (1998): Ultraviolet cues affect the foraging behaviour of blue tits. *Proc. R. Soc. Lond. B*, 265: 1509-1514.

Cooper, W.E. & Greenberg, N. (1992): Reptilian coloration and behavior. pp. 298-422, *in*: Gans, C. & Crews, D. (eds.), *Biology of the Reptilia, Vol. 18, Physiology E, Hormones, Brain and Behavior*. University of Chicago Press, Chicago.

Cuthill, I.C. & Bennett, A.T.D. (1993): Mimicry and the eye of the beholder. *Proc. R. Soc. Lond. B*, 253: 203-204.

Cuthill, I.C., Bennett, A.T.D., Partridge, J.C. & Maier, E.J. (1999): Plumage reflectance and the objective assessment of avian sexual dichromatism. *Am. Nat.*, 160: 183-200.

Cuthill, I.C., Partridge, J.C., Bennett, A.T.D., Church, S.C., Hart, N.S. & Hunt, S. (2000a): Ultraviolet vision in birds. *Adv. Study Behav.*, 29: 159-214.

Cuthill, I.C., Partridge, J.C. & Bennett, A.T.D. (2000b): Avian UV vision and sexual selection. pp. 61-82, *in*: Espmark, Y., Amundsen, T. & Rosenqvist, G. (eds.), *Animal Signals:*

Signalling and Signal Design in Animal Communication. Tapir Academic Press, Trondheim, Norway.

Desfilis, E., Font, E. & Guillén-Salazar, F. (2003): Stimulus control of predatory behavior by the Iberian wall lizard, *Podarcis hispanica* (Sauria, Lacertidae): Effects of familiarity with prey. *J. Comp. Psychol.*, 117: 309-316.

Díaz, J.A. (1993): Breeding coloration, mating opportunities, activity, and survival in the lacertid lizard *Psammodromus algirus*. *Can. J. Zool.*, 71: 1104-1110.

Ebrey, T. & Koutalos, Y. (2001): Vertebrate photoreceptors. *Prog. Ret. Eye Res.*, 20: 49-94.

Ellingson, J.M., Fleishman, L.J. & Loew, E.R. (1995): Visual pigments and spectral sensitivity of the diurnal gecko *Gonatodes albogularis*. *J. Comp. Physiol. A*, 177: 559-567.

Endler, J.A. (1990): On the measurement and classification of colour in studies of animal colour patterns. *Biol. J. Linn. Soc.*, 41: 315-352.

Fleishman, L.J. & Persons, M. (2001): The influence of stimulus and background colour on signal visibility in the lizard *Anolis cristatellus*. *J. Exp. Biol.*, 204: 1559-1575.

Fleishman, L.J., Loew, E.R. & Leal, M. (1993): Ultraviolet vision in lizards. *Nature*, 365: 397.

Fleishman, L.J., Bowman, M., Saunders, D., Miller, W.E., Rury, M.J. & Loew, E.R. (1997): The visual ecology of Puerto Rican anoline lizards: Habitat light and spectral sensitivity. *J. Comp. Physiol. A*, 181: 446-460.

Galán, P. (2000): Females that imitate males: Dorsal coloration varies with reproductive stage in female *Podarcis bocagei* (Lacertidae). *Copeia*, 2000: 819-825.

Goldsmith, T.H. (1994): Ultraviolet receptors and color vision: Evolutionary implications and a dissonance of paradigms. *Vision Res.*, 34: 1479-1487.

Hailman, J.P. (1977): *Optical Signals: Animal Communication and Light*. Indiana University Press, Bloomington.

Hart, N.S. (2001): The visual ecology of avian photoreceptors. *Prog. Retinal Eye Res.*, 20: 675-703.

Hausmann, F., Arnold, K.E., Marshall, N.J. & Owens, I.P.F. (2002): Ultraviolet signals in birds are special. *Proc. R. Soc. Lond. B*, 270: 61-67.

Honkavaara, J., Koivula, M., Korpimäki, E., Siitari, H. & Viitala, J. (2002): Ultraviolet vision and foraging in terrestrial vertebrates. *Oikos*, 98: 504-510.

Hunt, D.M., Wilkie, S.E., Bowmaker, J.K. & Poopalasundaram, S. (2001): Vision in the ultraviolet. *Cell. Mol. Life Sci.*, 58: 1583-1598.

Hunt, S., Cuthill, I.C., Swaddle, J.P. & Bennett, A.T.D. (1997): Ultraviolet vision and band-colour preferences in female zebra finches, *Taeniopygia guttata*. *Anim. Behav.*, 54: 1383-1392.

Hunt, S., Bennett, A.T.D., Cuthill, I.C. & Griffiths, R. (1998): Blue tits are ultraviolet tits. *Proc. R. Soc. Lond. B*, 265: 451-455.

Hunt, S., Cuthill, I.C., Bennett, A.T.D. & Griffiths, R. (1999): Preferences for ultraviolet partners in the blue tit. *Anim. Behav.*, 58: 809-815.

Hunt, S., Cuthill, I.C., Bennett, A.T.D., Church, S.C. & Partridge, J.C. (2001): Is the ultraviolet waveband a special communication channel in avian mate choice? *J. Exp. Biol.*, 204: 2499-2507.

Jacobs, G.H. (1992): Ultraviolet vision in vertebrates. *Am. Zool.*, 32: 544-554.

Johnsen, A., Andersson, S., Örnborg, J. & Lifjeld, J.T. (1998): Ultraviolet plumage ornamentation affects social mate choice and sperm competition in bluethroats (Aves: *Luscinia s. svecica*): A field experiment. *Proc. R. Soc. Lond. B*, 265: 1313-1318.

Johnson, S.D. & Andersson, S. (2002): A simple field method for manipulating ultraviolet reflectance of flowers. *Can. J. Bot.*, 80: 1325-1328.

Kawamura, S. & Yokoyama, S. (1998): Functional characterization of visual and nonvisual pigments of American chameleon (*Anolis carolinensis*). *Vision Res.*, 38: 37-44.

Keyser, A.J. & Hill, G.E. (1999): Condition-dependent variation in the blue-ultraviolet coloration of a structurally based plumage ornament. *Proc. R. Soc. Lond. B*, 266: 771-777.

Knüttel, H. & Fiedler, K. (2000): On the use of ultraviolet photography and ultraviolet wing patterns in butterfly morphology and taxonomy. *J. Lepid. Soc.*, 54: 137-144.

Kodric-Brown, A. & Johnson, S.C. (2002): Ultraviolet reflectance patterns of male guppies enhance their attractiveness to females. *Anim. Behav.*, 63: 391-396.

LeBas, N.R. & Marshall, N.J. (2000): The role of colour in signalling and male choice in the agamid lizard *Ctenophorus ornatus*. *Proc. R. Soc. Lond. B*, 267: 445-452.

LeBas, N.R. & Marshall, N.J. (2001): No evidence of female choice for a condition-dependent trait in the agamid lizard, *Ctenophorus ornatus*. *Behaviour*, 138: 965-980.

Loew, E.R. (1994): A third, ultraviolet-sensitive, visual pigment in the Tokay gecko (*Gekko gecko*). *Vision Res.*, 34: 1427-1431.

Loew, E.R., Govardovskii, V.I., Rohlich, P. & Szel, A. (1996): Microspectrophotometric and immunocytochemical identification of ultraviolet photoreceptors in geckos. *Visual Neurosci.*, 13: 247-256.

Loew, E.R., Fleishman, L.J., Foster, R.G. & Provencio, I. (2002): Visual pigments and oil droplets in diurnal lizards: A comparative study of Caribbean anoles. *J. Exp. Biol.*, 205: 927-938.

López, P. & Martín, J. (2001): Pheromonal recognition of females takes precedence over the chromatic cue in male Iberian wall lizards *Podarcis hispanica*. *Ethology*, 107: 901-912.

López, P., Martín, J. & Cuadrado, M. (2002): Pheromone-mediated intrasexual aggression in male lizards, *Podarcis hispanicus*. *Aggr. Behav.*, 28: 154-163.

Losey, G.S., Cronin, T.W., Goldsmith, T.H., Hyde, D., Marshall, N.J. & McFarland, W.N. (1999): The UV visual world of fishes: A review. *J. Fish Biol.*, 54: 921-943.

Macedonia, J.M. (1999): Color signal evolution in an ancestor-descendant species pair of Caribbean anoles. *Anolis Newsletter*, V: 67-80.

Macedonia, J.M. (2001): Habitat light, colour variation, and ultraviolet reflectance in the Grand Cayman anole, *Anolis conspersus*. *Biol. J. Linn. Soc.*, 73: 299-320.

Macedonia, J.M., James, S., Wittle, L.W. & Clark, D.L. (2000): Skin pigments and coloration in the Jamaican radiation of *Anolis* lizards. *J. Herpetol.*, 34: 99-109.

Macías Garcia, C. & Burt de Perera, T. (2002): Ultraviolet-based female preferences in a viviparous fish. *Behav. Ecol. Sociobiol.*, 52: 1-6.

MARTÍN, J. & FORSMAN, A. (1999): Social costs and development of nuptial coloration in male *Psammodromus algirus* lizards: An experiment. *Behav. Ecol.*, 10: 396-400.

MOLINA-BORJA, M., PADRÓN-FUMERO, M. & ALFONSO-MARTÍN, M.T. (1997): Intrapopulation variability in morphology, coloration, and body size in two races of the lacertid lizard, *Gallotia galloti*. *J. Herpetol.*, 31: 499-507.

MOLINA-BORJA, M., PADRÓN-FUMERO, M. & ALFONSO-MARTIN, T. (1998): Morphological and behavioural traits affecting the intensity and outcome of male contests in *Gallotia galloti galloti* (Family Lacertidae). *Ethology*, 104: 314-322.

MORRISON, R.L., RAND, M.S. & FROST-MASON, S.K. (1995): Cellular basis of color differences in three morphs of the lizard *Sceloporus undulatus erythrocheilus*. *Copeia*, 1995: 397-408.

MORRISON, R.L., SHERBROOKE, W.C. & FROST-MASON, S.K. (1996): Temperature-sensitive, physiologically active iridophores in the lizard *Urosaurus ornatus*: An ultrastructural analysis of color change. *Copeia*, 1996: 804-812.

OLSSON, M. (1993): Nuptial coloration and predation risk in model sand lizards, *Lacerta agilis*. *Anim. Behav.*, 46: 410-412.

OLSSON, M. (1994a): Nuptial coloration in the sand lizard, *Lacerta agilis*: An intrasexually-selected cue to fighting ability. *Anim. Behav.*, 48: 386-388.

OLSSON, M. (1994b): Why are sand lizard males (*Lacerta agilis*) not equally green? *Behav. Ecol. Sociobiol.*, 35: 169-173.

OLSSON, M. & MADSEN, T. (1998): Sexual selection and sperm competition in reptiles. pp. 503-577, *in*: Birkhead, T.R. & Moller, A.P. (eds.), *Sperm Competition and Sexual Selection*. Academic Press, London.

RAND, M.S. (1991): Behavioral function and hormonal control of polymorphic sexual coloration in the lizard *Sceloporus undulatus erythrocheilus*. Ph.D. Diss. Univ. of Colorado, Boulder.

ROBINSON, S.R. (1994): Early vertebrate colour vision. *Nature*, 367: 121.

SALVADOR, A., VEIGA, J.P., MARTÍN, J., LÓPEZ, P., ABELENDA, M. & PUERTA, M. (1996): The cost of producing a sexual signal: Testosterone increases the susceptibility of male lizards to ectoparasitic infestation. *Behav. Ecol.*, 7: 145-150.

SHELDON, B.C., ANDERSSON, S., GRIFFITH, S., ÖRNBORG, J. & SENDECKA, J. (1999): Ultraviolet colour variation influences blue tit sex ratios. *Nature*, 402: 874-877.

SIITARI, H. & HUHTA, E. (2002): Individual color variation and male quality in pied flycatchers (*Ficedula hypoleuca*): A role of ultraviolet reflectance. *Behav. Ecol.*, 13: 737–741.

SIITARI, H., HONKAVAARA, J., HUHTA, E. & VIITALA, J. (2002): Ultraviolet reflection and female mate choice in the pied flycatcher, *Ficedula hypoleuca*. *Anim. Behav.*, 63: 97-102.

SILBERGLIED, R.E. (1976): Visualization and recording of longwave ultraviolet reflection from natural objects. *Func. Photogr. (Photogr. Appl. Sci. Tech. Med.)*, 11: 20-33.

SMITH, E.J., PARTRIDGE, J.C., PARSONS, K.N., WHITE, E.M., CUTHILL, I.C., BENNETT, A.T.D. & CHURCH, S.C. (2002): Ultraviolet vision and mate choice in the guppy (*Poecilia reticulata*). *Behav. Ecol.*, 13: 11-19.

Stoehr, A.M. & McGraw, K.J. (2001): Ultraviolet reflectance of color patches in male *Sceloporus undulatus* and *Anolis carolinensis*. *J. Herpetol.*, 35: 168-171.

Swiezawska, K. (1950): Colour discrimination of the sand lizard, *Lacerta agilis* L. *Bull. Int. Acad. Pol. Sci. Lett. Ser. B*, 569: 1-20.

Thompson, C.W. & Moore, M.C. (1991): Throat colour reliably signals status in male tree lizards, *Urosaurus ornatus*. *Anim. Behav.*, 42: 745-753.

Thorpe, R.S. (2002): Analysis of color spectra in comparative evolutionary studies: Molecular phylogeny and habitat adaptation in the St. Vincent anole (*Anolis trinitatis*). *Syst. Biol.*, 51: 554-569.

Thorpe, R.S. & Brown, R.P. (1989): Microgeographic variation in the colour pattern of the lizard *Gallotia galloti* within the island of Tenerife: Distribution, pattern and hypothesis testing. *Biol. J. Linn. Soc.*, 38: 303-322

Thorpe, R.S. & Richard, M. (2001): Evidence that ultraviolet markings are associated with patterns of molecular gene flow. *Proc. Natl. Acad. Sci. USA*, 98: 3929-3934.

Thorpe, R.S. & Stenson, G. (2003): Phylogeny, paraphyly and ecological adaptation of the colour and pattern in the *Anolis roquet* complex on Martinique. *Mol. Ecol.*, 12: 117-132.

Tovée, M.J. (1995): Ultra-violet photoreceptors in the animal kingdom: Their distribution and function. *Trends Ecol. Evol.*, 10: 455-460.

Underwood, G. (1970): The eye. pp. 1-97, *in*: Gans, C. & Parsons, T.S. (eds.), *Biology of the Reptilia, Vol. 2*. Academic Press, New York.

Verbeek, B. (1972): Ethologische Untersuchungen an einigen europaischen Eidechsen. *Bonn. Zool. Beitr.*, 23: 122-151.

Yokoyama, S. & Shi, Y. (2000): Genetics and evolution of ultraviolet vision in vertebrates. *FEBS Lett.*, 486: 167-172.

Zahavi, A. & Zahavi, A. (1997): *The Handicap Principle: A Missing Piece of Darwin's Puzzle*. Oxford University Press, Oxford.

Zucker, N. (1994): Social influence on the use of a modifiable status signal. *Anim. Behav.*, 48: 1317-1324.