Spectrophotometric Studies of Avian Plumage Coloration with Special Emphasis on the Ultraviolet Range

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General Introduction

Some 30 years ago, it was discovered that a bird could perceive ultraviolet light (Huth & Burkhardt 1972). This was the birth of an era of numerous studies dealing with taxon specific ultraviolet light perception, shortwave sensitive (SWS) receptor determination, and behavioral experiments conducted in order to find an answer to the question why, and for what reason UV perception has evolved (Burkhardt 1982, Jane & Bowmaker 1988, Bennett & Cuthill 1994, Viitala *et al.* 1995, Church *et al.* 1998, Koivula *et al.* 1999, Pearn *et al.* 2001, Jourdie *et al.* 2004, Penteriani *et al.* 2006). Many aspects seem much clearer today, as there is evidence that UV light perception plays a significant role in a number of tasks, in orientation, in foraging, and - most important - in courtship behavior (Wortel *et al.* 1987, Bennett & Cuthill 1994, Viitala *et al.* 1995, Johnsen *et al.* 1998, Hunt *et al.* 1998, Church *et al.* 2001). Although it is generally accepted that many birds, assumingly the majority, are able to see ultraviolet light with either VS (violet sensitive) receptors or UVS (ultraviolet sensitive) receptors, the latter having their peak excitation in the near ultraviolet range (around 370 nm), there is evidence for no more than about 60 studied bird species being able to see ultraviolet light (Koivula *et al.* 1999, Cuthill *et al.* 2000, Probst *et al.* 2002, Siitari *et al.* 2002, Ödeen & Håstad 2003, Hart & Vorobyev 2005). Microspectrophotometrical tests and opsin coding examinations as well as studies on the bird's ocular media and oil droplets do not prove that a bird can see ultraviolet light (Cuthill *et al.* 2000, Hart 2001). This is due to the limited knowledge we have about how birds process the incoming signals in their visual cortex. Only behavioral studies can provide irrevocable evidence of birds being really able to see ultraviolet light. However, behavioral studies of less than 30 bird species have been conducted to date (Cuthill *et al.* 2000). The reason for this small number of examined birds lies in difficulties in finding a setup which, when birds in captivity are used, as they preferably have to be as natural as possible. When visual signaling is used in courtship, nearly always the male's plumage is involved and judged by the female to gain information about the male's health, fitness, and quality. UV reflections in birds' plumages have been proven to be important indicators for male quality in mate choice (Keyser & Hill 1999, McGraw *et al.* 2002, Doucet & Montgomerie 2003). Therefore, studies on the bird's plumage with focus on the ultraviolet range have been the subject of a number of studies (Cuthill *et al.* 1999, Gomez & Voisin 2002, Shawkey *et al.* 2003, McGraw 2004, Eaton 2005, Tubaro *et al.* 2005). The results were analyzed in different ways, e.g., they were correlated with plumage regions displayed in courtship, with juxtaposed fluorescing plumage regions, and analyzed to expose hidden sexual dimorphic patterns (Arnold *et al.* 2002, Hausmann *et al.* 2002, Eaton & Lanyon 2003, Eaton 2005). Evidence was provided that the presence of ultraviolet light reflections in a bird's plumage is not a coincidence but actually serve as signals. Screening a larger amount of bird species in search of UV reflections was made possible by the introduction of portable reflection spectrophotometers at the beginning of the 1990s. Increased computer power allowed the researcher to follow the change of the spectra on screen in real-time (Fig. 1). To accurately judge plumage coloration, reflection spectrophotometry has become a valuable tool to qualify plumage color and has, with its ability to detect ultraviolet light reflecting patches, replaced the use of color plates (Cuthill *et al.* 2000). Astonishingly, of the approximately 9700 bird species which have been classified to date (Sibley & Monroe 1990, 1993) only three studies dealing with plumage coloration measurements via reflection spectrophotometry, included more than a hundred species. Burkhardt (1989) examined feathers of 43 bird species, Finger (1990) measured 58 species, Vorobyev *et al.* (1998) examined 61 bird species. Bennett *et al.* (1994) listed 49 UV reflecting bird species, which were measured by different authors. Bennett *et al.* (1994) examined 125 bird species, Hausmann *et al.* (2002) analyzed 108 species of birds. With the exception of Eaton & Lanyon's work (2003) in which 312 bird species of 142 families were measured, the surveys dealing with reflection spectrophotometric measurements on plumage coloration conducted previously only dealt with birds from 10 of the 23 Orders. Furthermore, the pool of examined species in the different studies often overlapped, and only a few gave detailed descriptions with regard to which feather type or color patch was measured. Moreover, in all the larger studies only one angle (90° or 45°) for measurement was used. This is an obligatory thing to do when gathering spectra for comparative analysis. The use of varying angles is recommended to find out whether a bird possesses UV reflecting plumage patches at all, independent of the onlooker's position. Furthermore, due to strongly angle dependent reflection especially in structural and iridescent colors, I used varying angles for measurements.

The overall aim of my study is to find out whether UV cues are common and discover evidence whether they are frequently used in intraspecific signaling. Therefore, I included a greater number of species than was ever dealt with before, covering all bird Orders to find whether UV reflections in birds' plumages are a widespread phenomenon or not. All investigations conducted to date, with the exception of the study from Hausmann *et al.* (2002), have simply characterized a bird being UV reflective by defining a threshold in brightness. Assuming, that UV reflections play a role in sexual signaling I defined a bird as having a distinctive UV reflection by not just adding to overall brightness with UV reflection simply being a part of broadband reflectance. I defined a bird as having distinctive UV coloration, (which I refer to as UV phenomena) when the spectrum shows a UV reflectance peak higher than 10 %. In order to include species lacking UV peaks, but with high amounts of UV reflecting plumage, I also speak of UV phenomena when any part of the UV reflectance spectrum exceeds the lowest reflection in the range of 400 to 700 nm. Spectral data is then analyzed to find possible correlations between the region of the maxima of the UV phenomena and SWS cone types found in the different bird Orders, and how the distribution of UV phenomena in species is related to their habitats and altitudinal occurrence. An emphasis lies on the hummingbirds (Trochiliformes) with their unique iridescent coloration and their enormous altitudinal distribution from sea level to 5200 m. A special focus is also placed on the parrots (Psittaciformes), the only Order (with the exception of the (Struthioniformes) in which all species studied to date possess UVS cones (Cuthill *et al.* 2000, Ödeen & Håstad 2003). Only a few birds are known to possess pure ultraviolet plumage reflectance; these birds appear black to humans (Burkhardt & Finger 1991, Andersson 1996, Burkhardt 1996, Keyser & Hill 1999, McGraw *et al.* 2002, Doucet 2002, Doucet & Montgomerie 2003). Although, they were subject to various studies dealing with different aspects of the evolution and physical structure of pure UV phenomena, none of these birds were tested if they were able to perceive ultraviolet light using behavioral studies. To test whether UV phenomena are used in signaling in species with pure UV phenomena, the Satin Bowerbird (*Ptilonorhynchos violaceus*) was chosen and a behavioral choice experiment was conducted. Furthermore, it is tested whether ultraviolet light plays a role in the complex courtship behavior of the Satin Bowerbird besides its own plumage reflecting ultraviolet light. Therefore, the males' bowers with the gathered ornaments including UV-reflecting feathers were examined. UV photography as a established special documentation technique was used to visualize UV reflective feather patches with juxtaposed non-UV reflective plumage parts.

In summary I want to investigate how UV reflections in avian species are distributed and if they are correlated to habitat and altitudinal occurrence with special focus on the parrots and hummingbirds. To test whether UV phenomena are used in signaling in species with pure UV phenomena, the Satin Bowerbird is chosen and a behavioral choice experiment is conducted.

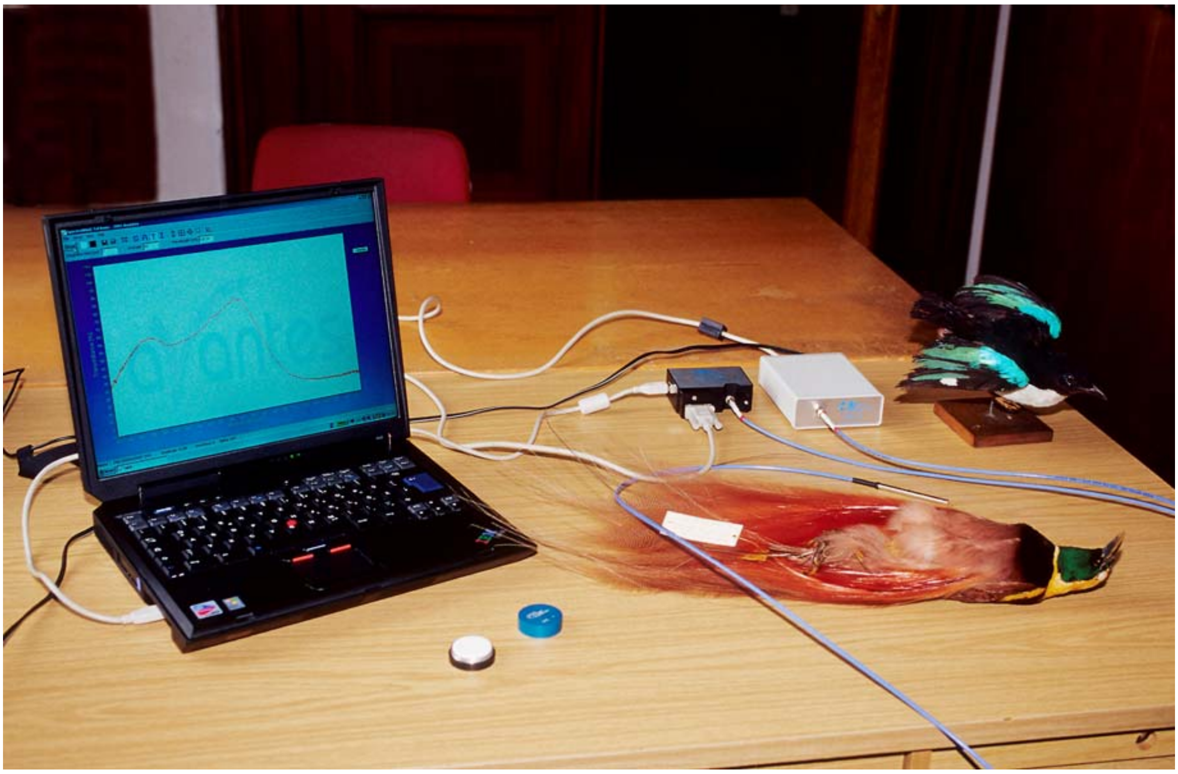

Fig. 1 Reflection spectrophotometer. Standard setup for measuring bird skins with a pulsed Xenon light source (little white box in the upper right), spectrometer (small dark box next to white box on the left), and White Standard (front).

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1. Studies on UV reflection in feathers of some 1000 bird species – are UV-peaks in feathers correlated with VS/UVS cones?

Introduction

Ultraviolet perception in a bird was reported for the first time by Huth & Burkhardt in 1972. In contrast to humans with only three cone receptors, most birds have tetrachromatic color vision and are able to perceive the UV portion of the light spectrum. Many investigations have been carried out since 1972, which further documented that near-ultraviolet light hues (300 – 400 nm) in avian plumage function in intraspecific signaling and that UV detection also influences foraging behavior (Silberglied 1979, Burkhardt 1982, Bennett & Cuthill 1994, Viitala *et al.* 1995, Church *et al.* 1998, Koivula *et al.* 1999, Pearn *et al.* 2001). Electro-physiological and behavioral experiments as well as microspectrophotometric measurements of single avian cones and a new molecular method which estimates the color sensitivities of a bird by sequencing a part of the gene coding for the ultraviolet or violet absorbing opsin in the avian retina have shown positive evidence of UV vision in at least 57 species of birds (Koivula *et al.* 1999, Cuthill *et al.* 2000, Probst *et al.* 2002, Siitari *et al.* 2002, Ödeen & Håstad 2003, Hart & Vorobyev 2005).

According to the classification system of avian taxa established by Sibley & Monroe (1990), representatives of 15 out of 23 bird Orders have been proven to see or are most likely to see UV light (Table 1). Several studies reported UV reflection in feathers to be a wide-spread phenomenon, and it is well known that all feathers, except the most deeply black, reflect UV light to some extent which contributes to their overall brightness (Cuthill *et al.* 2000, Hausmann *et al.* 2002, Eaton & Lanyon 2003). In particular, plumage regions used in courtship display exhibit high amounts of UV reflection patterns, indeed they often show a peak between 300 and 400 nm mainly due to carotenoid-based colors which have a big peak in the UV (Hausmann *et al.* 2002). My study's focus lies on this type of UV reflections. Furthermore, many behavioral experiments have demonstrated that UV waveband plays an important role in mate choice. The iridescent green feathers of the Common Starling (*Sturnus vulgaris*) (Bennett *et al.* 1997), the bright blue breast plumage of the Bluethroat (*Luscinia svecica*) (Andersson & Amundsen 1997, Johnsen *et al.* 1998), the blue crown feathers as well as the yellow breast of the Blue Tit (*Parus caeruleus*) (Andersson *et al.* 1998, Hunt *et al.* 1998), and the yellow and blue plumage of the Budgerigar (*Melopsittacus undulatus*) (Pearn *et al.* 2001) have a remarkably high peak in the UV. An exception is the Zebra Finch (*Taeniopygia guttata*) (Bennett *et al.* 1996), which does not possess plumage colors with a reflection peak in the UV. Interestingly, a recent study has reported on the overestimation of the UV waveband in mate choice in this species (Hunt *et al.* 2001).

The aim of my study is to find out if UV cues are used in intraspecific signaling. UV phenomena should then be more frequent in Orders likely to have a sensitivity to UV. If not, UV phenomena should be equally represented in all Orders. If UVS species are more sensitive than VS species to UV, then, maybe UV phenomena should be more frequent in Orders with these species and UV peaks, when present, should lie in different regions.

Methods

Similar to the proposed comparative approach introduced by Hausmann *et al.* (2002), I define a bird as having distinctive UV coloration, (which I refer to as UV phenomena) when the spectrum shows a UV reflectance peak higher than 10 %. In order to include species lacking UV peaks, but with high amounts of UV reflecting plumage, I also speak of UV phenomena when any part of the UV reflectance spectrum exceeds the lowest reflection in the range of 400 to 700 nm. On account of this definition, white and light-colored feathers are excluded, despite their ability to reflect high amounts of UV light, contributing to overall brightness. With respect to the visual abilities of the birds, continuous reflection in the whole spectrum is a basic characteristic of white (Vorobyev *et al.* 1998) and significant amounts of UV have been found in nearly all white feathers (Eaton & Lanyon 2003).

A pre-screening of species from different avian Orders revealed a lack of substantial UV reflection in most of the black, dark-grey and brown-colored feathers. These findings are supported by the results of previous work dealing with feather coloration (Burkhardt 1989, Finger *et al.* 1992, Hausmann *et al.* 2002, Eaton & Lanyon 2003). I therefore included the most colorful species in an order as they are most likely to show distinctive UV reflection (Hausmann *et al.* 2002). Orders with many colorful species and Orders lacking colorfully plumaged birds, such as the Strigiformes, the species were randomly selected. In Orders with few colored species, such as the Gruiformes, species were randomly selected, but always from a colored species pool. To evaluate whether UV amplitude distribution in feathers are more likely than expected by chance to be associated with UVS/VS cone distribution, a Fisher's Exact test was performed with a significance level of 5%.

Overall, 5362 reflectance spectra were measured, representing 968 species from approximately 65 % of all bird families and from all Orders following the taxonomic list of Sibley & Monroe (1990). One hundred percent of all species were covered in 9 Orders. All colors in all plumage patches of a species were measured. I concentrated mostly on non-passerines, in order to make possible predictions of

UV signaling in the less-studied bird Orders, since multiple studies have proven that UV plays an important role in several behavioral aspects of the passerines (Cuthill *et al.* 2000). For the purpose of this study, bird skins preserved at the Alexander Koenig Research Institute and Museum of Zoology in Bonn, Germany; The Natural History Museum in Tring, United Kingdom, and the American Museum of Natural History in New York were used for data collection. In the main, skins less than 20 years old were used to avoid failure due to possible color changes in older museum skins (Endler & Théry 1996, Hausmann *et al.* 2002, McNaught & Owens 2002). Where possible an average of 6 specimens per species of one subspecies of one geographical region were measured, all of them were adult birds. I only took specimens in a good condition which showed well-preserved colors. To find cryptic dimorphism I measured 3 males and 3 female specimens of 50 % of the chosen species, all the specimens of the other 50 % were male birds. A relatively high threshold of 15 % difference in the reflectance intensity in the UV-range was taken to distinguish a cryptic dimorphism from an artifact. Additionally, many of the spectra were based on measurements of molted bird feathers from private feather collections gathered over the last 10 years. None of these feathers had been treated with chemicals for preservation purposes and they were kept in binders, away from the light.

The reflectance spectra were measured using an Ocean Optics USB 2000 spectrometer, with a World Precision Instruments UV-VIS-NIR light source D_2H, containing both, a deuterium-halogen and a tungsten-halogen light bulb. A compressed tablet of barium sulphate (Ba SO_4) was used as a white reference standard. A black velvet cloth was used as a dark reference. Measurements were made in the ambient light of a darkened room using the bifurcated cable UV/VIS 400UM from World Precision Instruments, illuminating a field of approximately 2-3 mm^2 with a 100 ms summation time. All reflectance data were considered between the wavelengths 300 nm and 700 nm. Reflectance spectra for each distinctly colored area on a feather of each species were calculated from averages of percentage reflectance values from 10 measurements.

In many studies a non-variable measuring angle was used for spectrophotometric plumage or single feather measurements in order not to jeopardize the comparability of the resulting data. The reflection of many colors strongly depends on the angle of illumination and detection (Osorio & Ham 2002). UV reflections in birds are easily overlooked due to the lack of UV sensitivity in human sensory perception. Measurements using a standardized angle might not show UV reflections despite their existence. Therefore, in this study the angles of detection used are variable. The change in the intensity of the reflection was surveyed simultaneously at the monitor. Only the angles showing the highest amount of UV-light reflection were taken. The regions were illuminated at angles of between 35° and 90° to the long axis of the feather from a top view at a distance of approximately 7 mm. The upper side was used and in primaries and secondary feathers the outer webs were illuminated. The light was collected at the same angle. Black velvet cloth was used as a padding to avoid stray light from the colored surfaces influencing the measurements. The feathers were positioned parallel to the source of illumination and collection, and illuminated from the proximal end which was oriented to the long axis of the feather, moving only the light source and collector within the stated angles in order to obtain highest UV-reflection.

Results

With the exception of the Ciconiiformes and Passeriformes, at least 10 % of all species in each of the remaining 21 Orders were examined. According to my definition of distinctive UV reflection, 347 species of the 968 surveyed showed UV phenomena in one or more body regions (Table 1). Representatives of 16 out of 23 bird Orders exhibited UV phenomena. Bird Orders possessing VS cones according to Ödeen & Håstad (2003) showed a significant correlation to the position of UV amplitudes in birds with UV phenomena detected (Table 2). Maximum VS cone sensitivity lies at around 400 nm and species of these Orders most commonly showed highest reflections between 380 – 399 nm. Birds with UV phenomena in the Passeriformes and Psittaciformes, the two Orders where most birds were found to possess UVS cones (Ödeen & Håstad 2003), exhibited UV mainly below 380 nm. Nine Avian Orders were surveyed completely, taking into account every single species listed in Sibley & Monroe (1990).

Table 1.1

Correlation between bird Orders containing species with UV phenomena with amplitudes between 380 – 399 nm or 300 – 379 nm and bird Orders containing species with proven UV vision ability through either a VS or UVS cone type. Hyphens indicate when no data was available.The classification follows the systematic list of Sibley & Monroe (1990).

Evidence of species with UV vision abilities or lack of UV vision abilities in bird Orders are based on either microspectrophotometry of avian visual pigments: 1. Wright & Bowmaker (1998); 2. Sillmann *et al.* (1981); 3. Bowmaker *et al.* (1997); 4. Bowmaker *et al.* (1993); 5. Hart (1998); 6. Jane & Bowmaker (1988); 7. Bowmaker & Martin (1978); 8. Liebmann (1972); 9. Bowmaker & Martin (1985); 10. Maier & Bowmaker (1993); 11. Das (1997); 12. Hart *et al.* (1998); 13. Bowmaker (1979); 14. Jacobs *et al.* (1987); [for details see Cuthill *et al.* (2000)], 15. Hart (2002); 16. Hart (2004) or behavioural experiments: 15. Siitari *et al.* (2002); 16. Parrish *et al.* (1981); 17. Pearn *et al.* (2001); 18. Huth & Burkhardt (1972); 19. Goldsmith & Goldsmith 1979; 20. Goldsmith (1980); 21. Goldsmith *et al.* (1981); 22. Emmerton & Delius (1980); 23. Emmerton & Remy (1983); 24. Kreithen & Eisner (1978); 25. Viitala *et al.* (1995); 26. Koivula *et al.* (1997); 27. Koivula *et al.* (1999): 28. Bennett *et al.* (1996); 29. Bennett *et al.* (1997); 30. Andersson & Amundsen (1997); 31. Johnsen *et al.* (1998); 32. Andersson *et al.* (1998); 33. Hunt *et al.* (1998); 34. Probst *et al.* (2002); or by sequencing a part of the gene coding for the ultraviolet or violet absorbing opsin in the avian retina: 35. A. Ödeen & Håstad (2003).

Table 1.1 UV phenomena in the Class Aves.

Order	Total number of species	Total number of species measured	% of species measured	Number of species with UV phenomenon	% of species measured with UV phenomenon	% of species with UV phenomena with an amplitude between 380 – 399 nm	Species with evidence for UV vision ability detected in this Order	VS or UVS cone type according to Ödeen & Håstad (2003)	Positive association of cone type and UV amplitude
Craciformes	69	69	100	0	0	0	-	-	
Turniciformes	17	17	100	0	0	0	-	-	
Bucerotiformes	56	28	50	0	0	0	-	-	
Coliiformes	6	6	100	1	17	100	-	-	
Cuculiformes	143	24	17	5	21	80	-	-	
Apodiformes	103	103	100	0	0	0	-	-	
Musophagiformes	23	23	100	18	78	56	-	-	
Tinamiformes	47	47	100	0	0	0	No[2]	-	
Strigiformes	291	52	18	0	0	0	No[7,14,26]	VS	
Coraciiformes	152	42	28	14	33	21	Yes[16]	VS	
Piciformes	355	36	10	13	36	54	-	VS	x
Galbuliformes	51	16	100	2	12	100	-	VS	x
Upupiformes	10	10	100	8	80	100	-	VS	x
Trogoniformes	39	13	33	13	100	61	-	VS	x
Gruiformes	196	26	13	3	11	100	-	VS	x
Galliformes	214	37	17	20	54	75	Yes[3,4,5,15,17]	VS	x
Anseriformes	161	25	16	10	40	60	Yes[6]	VS	x
Columbiformes	313	40	13	11	27	54	Yes[3,22,23,24]	VS	x
Ciconiiformes	1027	65	6	11	17	72	Yes[2,3,8,9,15,16,25,27,35]	VS, (UVS)	x
Trochiliformes	319	40	13	16	40	87	Yes[18,19,20,21]	-	
Struthioniformes	10	10	100	0	0	0	Yes[1,2]	VS, UVS	
Passeriformes	5712	96	1,7	63	65	17	Yes[2,7,10,11,12,13,16, 28-35]	UVS, (VS)	x
Psittaciformes	358	143	40	140	98	8	Yes[3, 17]	UVS	x
TOTAL	9672	968		348					

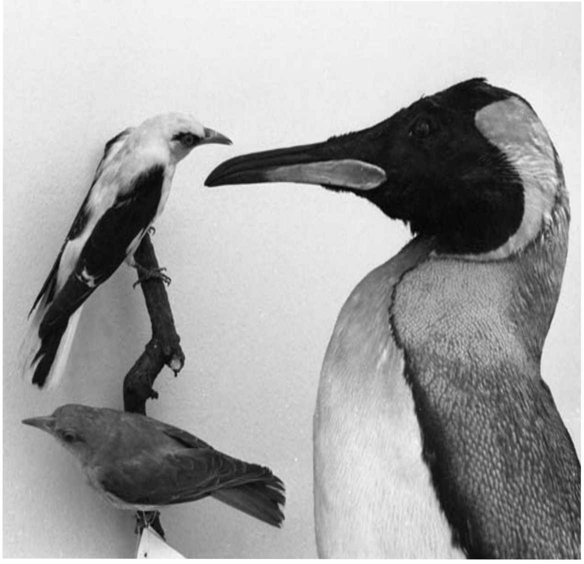

Fig. 1.1 Golden Orioles (*Oriolus oriolus*) King Penguin (*Aptenodytes patagonica*) in black & white.

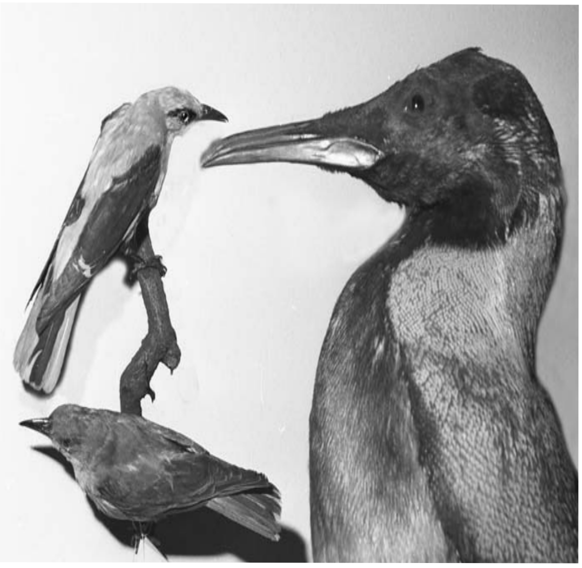

Fig. 1.2 Golden Orioles (*Oriolus oriolus*) King Penguin (*Aptenodytes patagonica*) in UV-light.

Fig. 1.3 Golden Orioles (*Oriolus oriolus*) King Penguin (*Aptenodytes patagonica*) in sunlight.

Fig. 1.4 Satin Bowerbird (*Ptilonorhynchus violaceus*), Blue Whistling-Thrush (*Myiophonus caeruleus*), Black Lory (*Chalcopsitta atra*), and Blackbird (*Turdus merula*) in sunlight.

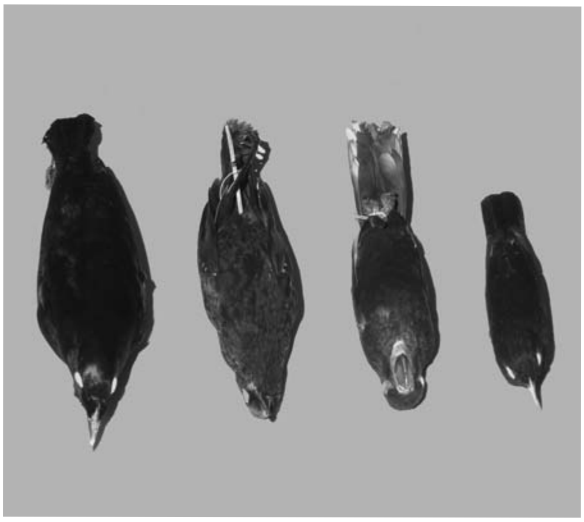

Fig. 1.5 Satin Bowerbird (*Ptilonorhynchus violaceus*), Blue Whistling-Thrush (*Myiophonus caeruleus*), Black Lory (*Chalcopsitta atra*), and Blackbird (*Turdus merula*) in black & white.

Fig. 1.6 Satin Bowerbird (*Ptilonorhynchus violaceus*), Blue Whistling-Thrush (*Myiophonus caeruleus*), Black Lory (*Chalcopsitta atra*), and Blackbird (*Turdus merula*) in UV-light.

Table 1.2 UV amplitude distribution in feathers and UVS/VS cone correlation. The Fisher's Exact test was performed on bird Orders with known UV / UVS cone types according to Ödeen & Håstad (2003) and Orders with UV phenomena assigned to their amplitude position. See last row in Table 1 for Orders taken.

	VS	UVS	p-value
Orders with > 50 % of species with UV phenomena with a max. amplitude between 380 – 399 nm	9	0	0.045
Orders with > 50 % of species with UV phenomena with a max. amplitude between 300 – 379 nm	1	2	

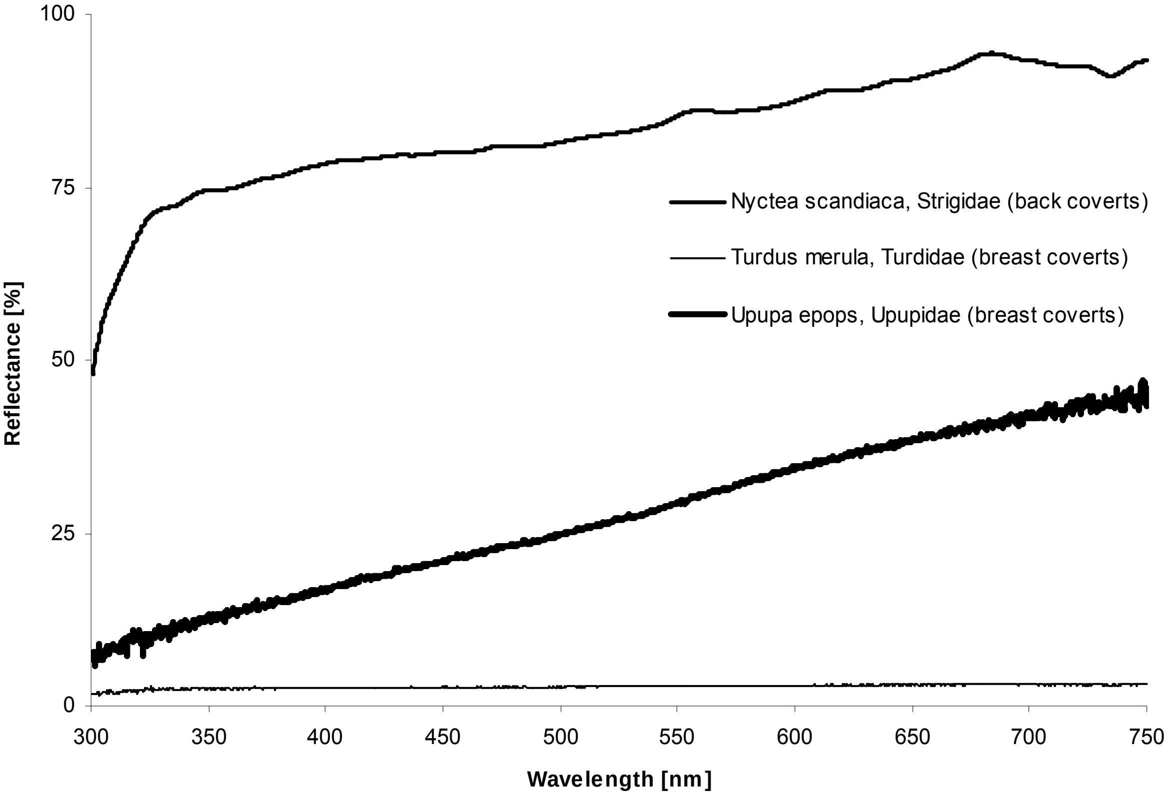

Fig. 1.7 Examples of birds lacking a UV phenomenon. I defined birds as non-UV phenomenon birds with feather patches which did not exhibit more than 10% reflectance in the UV or lacked a peak in the UV. The achromatic and brown feather patches such as a) the white breast feathers of the Snowy Owl (*Nyctea scandiaca*), b) the black breast feathers of a male Blackbird (*Turdus merula*), and c) the brown breast of the Hoopoe (*Upupa epops*) show characteristic spectra with UV reflection adding to overall brightness or simply being part of broadband reflectance.

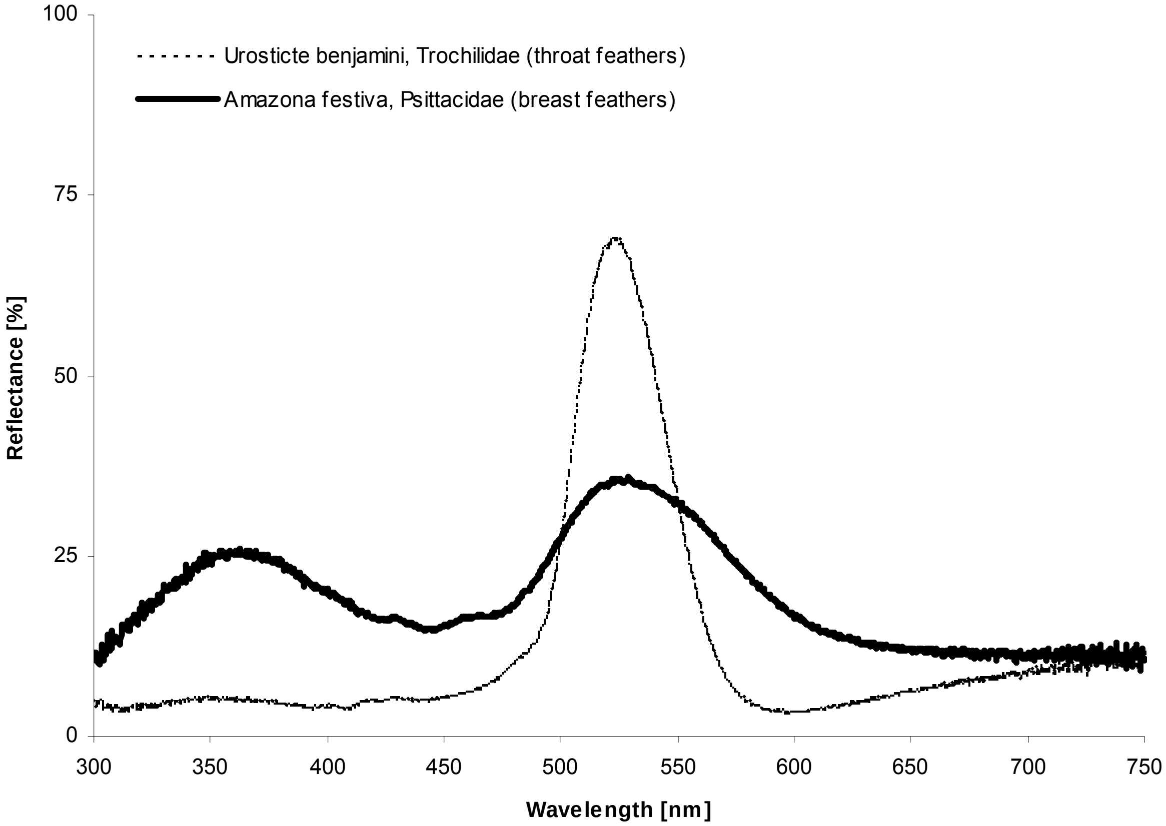

Fig. 1.8 Comparison of spectra of iridescent and n on-iridescent feather patches.

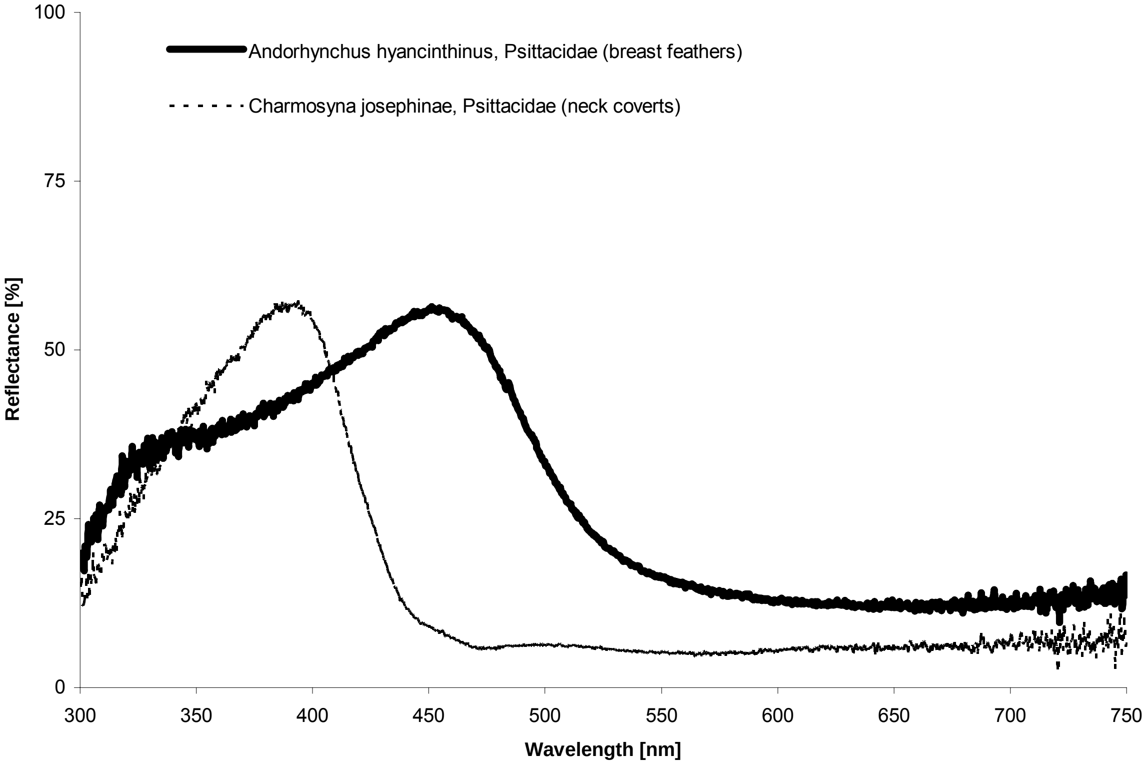

Fig. 1.9 Blue/UV-colored feather patches with different amounts of UV reflectance.

Fig. 1.8 The iridescent green throat of the hummingbird Purple-bibbed Whitetip (*Urosticte benjamini*) show a clear peak, being much narrower than peaks of non-iridescent feathers like the green breast of the Red-backed Amazon (*Amazona festiva*). The latter additionally shows a significant peak in the UV, a UV phenomenon. The spectra were taken on one specimen.

Fig. 1.9 The maximum excitation of the spectra of the blue neck feathers of Josephine's Lorikeet (*Charmosyna josefinae*) extends well into the UV, in contrast to the blue dorsal feathers of the Hyacinth Macaw (*Anodorhynchus hyancinthinus*), in which the excitation intensity in the UV decreases. Both species show clear UV phenomena: in both species reflectance in the UV spectrum exceeds the lowest reflection in the range of 400 to 700 nm. The spectra were taken on one specimen.

In five of the nine Orders UV phenomena were absent assuming that UV plays a minor role in intraspecific communication. This was the case in Struthioniformes, Tinamiformes, Craciformes, Turniciformes, Apodiformes, Strigiformes, and Bucerotiformes. In the following Orders more than 50% of the examined species exhibited UV phenomena: Passeriformes, Galliformes, Upupiformes, Musophagiformes, Trogoniformes, and Psittaciformes (Table 1). Of the 143 species studied in the Order of the Psittaciformes, a remarkable 140 species showed UV phenomena, in at least one feather patch. Most species of the Musophagiformes showed UV phenomena with the genera *Corythaixoides* and *Crinifer* as exceptions. In the genera *Tauraco* and *Musophaga* only the red patches of the primaries and secondaries exhibited UV phenomena. In the Galliformes and Anseriformes mainly the iridescent feather patches showed UV phenomena. In the Galbuliformes only the Purplish Jacamar (*Galbula chalcothorax*) and Bronzy Jacamar (*Galbula leucogastra*) showed UV phenomena, none were found in the Puffbirds (Bucconidae).

UV phenomena were primarily found in brightly colored feather patches. I divided different colored feather patches into simple color categories based on their appearance to the human visual system: violet, blue, green, yellow, red (including orange), pink, and brown. I found all the non-iridescent blue and violet-colored plumage regions to be highly, (more than 20 %) UV-reflecting. All of these color patches exhibited UV phenomena with one exception: the light blue to turquoise feather patches of several parrot species showed less than 5 % reflection in the UV and therefore lacked UV phenomena. Seventy-five percent of the green feather patches measured had UV phenomena, as did 50 % of the yellow and 40 % of the red feathers measured. Yellow plumage of the male Golden Oriole (*Oriolus oriolus*) exhibits high amounts of UV whereas the King Penguin (*Aptenodytes patagonica*) has no UV at all (Fig. 1.1 – 1.3). The brown feathers of only three species exhibited UV phenomena. The species with brown feathers having UV phenomena were the two parrots Dusky Lory (*Pseudeos fuscata)* and Brown Lory (*Chalcopsitta duivenbodei*) as well as the White-bellied Bustard (*Eupodotis senegalensis*). Black feathers exhibiting UV phenomena were rarely found. I found dark colored feathers with UV phenomena only in the Whistling Thrushes (*Myiophonus* spp.), the Black Lory (*Chalcopsitta atra*), the Dusky Lory, and in a few other parrot species and in the Satin Bowerbird (*Ptilonorhynchus violaceus*). Most dark colored birds such as the Blackbird (*Turdus merula*) have no UV reflection at all; see Figs. 1.4 – 1.6 for comparison. On the basis of my definition of a UV phenomenon, white and light colored feathers never exhibited it. However all white feathers measured showed a significant amount of UV reflection. In none of the white feather patches examined UV reflection was under 10 %, which would have indicated a non-UV/white, where the bird's UV/UVS cone would not be innervated.

I couldn't find any cryptic sexual dimorphisms. None of the measured feather patches of the species where female and male specimens were measured differed in the ultraviolet range.

Discussion

In contrast to earlier studies on UV reflection in feathers and bird skins (Burkhardt 1989, Finger 1990, Finger *et al.* 1992, Hausmann *et al.* 2002, Eaton & Lanyon 2003), the angles of detection employed in these studies were variable and, based on my definition of a UV phenomenon, all birds which did not exhibit more than 10% reflectance in the UV, or did not exhibit a peak in the UV, were considered to be non-UV phenomenon birds. Although I do not know if UV phenomena play a role in visual signaling, they might be more suggestive of a signaling role than the UV reflections which only add to the overall brightness of a bird's plumage (Fig. 1.7). However, the correlation of the position of UV maxima to Orders with VS/UVS cone location strongly indicates that UV reflections may be more associated with intraspecific signaling than alleged previously.

My results show that bird Orders in which species have been proven to perceive UV wavelengths are very likely to possess highly UV-reflecting plumage. Interestingly, no UV phenomena were found in avian Orders, which, to date, have failed to be proven to perceive UV light. It is unlikely that UV plays a role in nocturnal bird groups, e.g., owls and nightjars (Koivula 1997, Cuthill *et al.* 2000), and whether it does in the primitive palaeognathous bird Orders Struthioniformes and Tinamiformes is not clear. Behavioral experiments are the only way to prove UV vision ability confidentially. Microspectrophotometric measurements couldn't find any VS/UVS cones but opsin coding genetic studies revealed evidence for UV vision ability (Sillmann *et al.* 1981, Wright & Bowmaker 1998, Ödeen & Håstad 2003). So far no behavioral experiments have been conducted in the palaeognathous bird Orders.

The quantity of UV light at night is far less than in daylight (Endler 1993, 1995). Consequently, in this light environment it is much more important for night active birds to concentrate on perception based on contrast rather than on distinguishing colors. This is supported by the large number of rods in owls' retinas compared to the quantity of rods in birds active during daylight (Bowmaker & Martin 1978, Jacobs *et al.* 1987, Bowmaker *et al.* 1997). However, crepuscular active species as some nightjars, (e.g., the Common Nighthawk (*Chordeiles minor*)) are sexually dimorphic and show a distinctive white feather patch on the primaries, the male showing a much brighter patch than the female. Although the difference is clearly visible in normal light, differences exceed well into the UV. Whether UV light plays a role in mate choice here can only remain speculation at the moment. Yet, the proportion of UV in the spectrum is actually higher at dawn and dusk than it is at daytime. Additionally, Opsin coding genetic studies have revealed evidence for the expression of a VS cone in the European Nightjar (*Caprimulgus europaeus*) but only a behavioral test can prove UV vision ability eventually (Ödeen & Håstad 2003).

A remarkably high percentage of species in the Psittaciformes (140 out of 143 surveyed) exhibited highly UV reflective plumage patches in at least one body region. The three species lacking UV phenomena were the White Cockatoo (*Cacatua alba*), the Blue-eyed Cockatoo (*Cacatua ophthalmica*) and the Long-billed Cockatoo (*Cacatua tenuirostris*). According to my definition of UV phenomena, none of these unicolored white-plumaged birds could exhibit UV phenomena. Nevertheless, their white plumage showed a considerable amount of UV reflection, as was the case in almost all white feathers I measured. Thus I did not find a single parrot species lacking considerable amounts of UV reflective plumage, which makes this Order interesting for further investigations, especially taking into account recent studies dealing with unique feather pigments found only in parrots and the extraordinary phenomenon of fluorescence found in 52 species of parrots (Pearn *et al.* 2001, Stradi *et al.* 2001, Arnold *et al.* 2002, Masello *et al.* 2004, McGraw & Nogare 2004).

I found most of the UV phenomena in the colored feather regions. Therefore any black, brown or dull colored bird lacking brightly colored feather patches would most likely not show UV phenomena, and thus would only reflect UV to a certain extent as a contribution to overall brightness (Fig. 1.7). One of the few exceptions is the non-iridescent black feathers of the Black Lory (*Chalcopsitta atra*). The intensive UV reflection stems from light scattering by the spongy structure consisting of quasi ordered arrays of keratin separated by air vacuoles (Finger *et al.* 1992, Prum & Torres 2003). Basically UV reflection in iridescent feathers is caused by light reflected from the interfaces of regular stacks of higher and lower density material, such as rows of regularly orientated keratin rods (Cuthill *et al.* 2000).

In general, the spectra of iridescent feathers are similar to non-iridescent colored feathers. However, brightly colored iridescent feathers, such as the green breast plumage of the Purple-bibbed Whitetip Hummingbird (*Urosticte benjamini*) always exhibit a characteristic peak, being much narrower than the peaks of non-iridescent feathers like the green breast of the Red-backed Amazon (*Amazona festiva*), which also exhibits a UV peak (Fig. 1.8). Blue-colored feather patches, found in many species of different Orders, always exhibited distinctive amounts of UV. This is due to the fact that blue and violet lie next to the UV waveband and always extend into the UV to some degree. Blue and violet iridescent feather patches do not necessarily exceed into the UV, due to their much narrower peaks compared to non-iridescent colors. Blue and violet spectra either increase in the proportion of the UV waveband, with their maximum lying in the UV, as in Josephine's Lorikeet (*Charmosyna josefinae*) or decrease in intensity in the UV as is the case in the dorsal feathers of the Hyacinth Macaw (*Anodorhynchus hyancinthinus*) (Fig. 1.9). I assume that peaks in the UV and high amounts of UV reflection are more likely to play a specific role in courtship or other intraspecific behaviors than UV reflectance, as shown in Fig. 1.7.

Although in many cases both the female and the male bird were measured, I was unable to discover any cryptic sexual dimorphisms, (visible only in the UV). In brightness, the spectra show considerable variance (up to 10 % across the spectrum), so that especially with museum skins, spectra varying only in brightness have to be considered with caution due to color changes which usually are invisible for the human eye. After having examined nearly 1000 species of birds and not having found a single hidden sexual dimorphism, as has been detected in Blue Tits (Andersson *et al.* 1998, Hunt *et al.* 1998), I consider easily detectable cryptic dimorphisms as rare. If there are more cryptic dimorphisms such as found in Blue Tits they are most likely only to be discovered when dealing with totally fresh skins or live specimens and by comparing a substantial number of birds.

As suggested in earlier studies, I also believe that UV plays an important but probably not an extraordinary role than any other plumage color involved in avian courtship behavior (Cuthill *et al.* 2000, Hunt *et al.* 2001). However, UV-reflecting plumage should be treated in the same way as any colored feather patch with colors visible to humans. The high level of UV phenomena found in my study which correlated with colored feather patches throughout the Class Aves underlines the possibility of UV playing an extraordinary role in mate choice. In contrast to pigment-based plumage, structurally based ornaments such as ultraviolet colored plumage parts have been little studied, in part because they do not appear to be as variable as pigment-based ornaments. However, several recent studies indicate that structurally based ornaments serve as an honest indicator of age and quality and communicate different sets of information than pigment-based ornaments (Keyser & Hill 1997, McGraw *et al.* 2002). Furthermore, all behavioral mate choice experiments involving UV to date show a significant role for UV signaling (Bennett *et al.* 1996, Andersson & Amundsen 1997, Bennett *et al.* 1997, Andersson *et al.* 1998, Hunt *et al.* 1998, Johnsen *et al.* 1998). Due to the considerable numbers of bird species with UV phenomena in colored feather patches, I suggest more UV-related behavioral studies on birds of the following Orders might be promising: Psittaciformes, Passeriformes, Trogoniformes, Musophagiformes, Upupiformes, Trochiliformes, and Piciformes.

Summary

968 bird species covering all Orders based on Sibley & Monroe’s (1990) taxonomic list were studied in search of distinctive ultraviolet reflections. Of the following Orders all the species were completely surveyed: Struthioniformes, Tinamiformes, Craciformes, Turniciformes, Galbuliformes, Upupiformes, Coliiformes, Apodiformes, and Musophagiformes. The colored plumage regions in particular exhibited high proportions of UV reflections. A significant positive correlation was found between bird Orders with species which are believed to possess VS cone types, and Orders in which most species had their UV maxima between 380 – 399 nm. Orders with species which are assumed to have UVS cone types correlated significantly with Orders in which most species had their UV maxima between 300 – 379 nm respectively. My study supports evidence that birds of many more groups may see UV light than have been studied to date. Ecological aspects related to UV reflection and perception, as well as sexual dimorphisms visible only in the UV, are discussed.

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2. Significance of UV-vision in Courtship Behavior of the Satin Bowerbird (*Ptilonorhynchus violaceus*)

Introduction

The eighteen species of the bowerbird family Ptilonorynchidae are confined to the great island of New Guinea and the continent of Australia. The Satin Bowerbird (*Ptilonorhynchus violaceus*) shares the unique habit with other members of its family to skillfully build structures of sticks, grasses or other plant stems, which are called “bowers.” They decorate the latter with fruit, feathers, flowers, stones, and leaves or other mostly colorful objects (Frith & Frith 2004). Bowers are structures built exclusively by males to attract females for courting and, when successful, mating inside the bower. The Satin Bowerbird males build avenue bowers consisting of two parallel outwardly curving walls made of sticks. The sticks are oriented upright on a platform of sticks laid on the ground (see Figs. 2.3 and 2.8). They mainly collect blue items (ornaments) and use them to decorate their bowers. The number of decorations on a bower is an important determinant of male mating success for the Satin Bowerbird (Marshall 1954, Vellenga 1970, Borgia 1985). Preferred blue decorations include many man-made items such as blue bags, plastic bits, marbles, cloth pegs, string etc. (Chaffer 1931, 1945; Borgia & Gore 1986; Lenz 1999). Next to these human originated ornaments, satins gather items found in nature such as blue berries, blue flowers, cicada exuviae, blue butterfly wings and blue feathers (Marshall 1932, Gilbert 1939, Marshall 1954, Gilbert 1940, Chaffer 1959, Vellenga 1970, Borgia & Gore 1986). Among all ornaments Satins seem to prefer blue feathers to other material of similar color (Chaffer 1945, 1959; Borgia 1985, 1986; Borgia & Gore 1986). Bowers were found with over a hundred Crimson Rosella (*Platycercus elegans*) and Eastern Rosella (*Platycercus eximius*) retrices (Borgia & Gore 1986). Sometimes not only feathers but bodies or body parts of blue feathered birds were transported to the bower: One bower had two Crimson Rosella wings (Marshall 1934); another had a dead, blue-plumaged, male Superb Fairy-wren (*Malurus cyaneus*) among their ornaments. Male Satin Bowerbirds are known to even have killed blue captive pet birds to use their bodies as bower decorations (Murray in Chaffer 1945, Marshall

1954). All the collected feathers have in common that they are not only blue but, to at least some extent, blue and ultraviolet colored as many blue feathers from all kinds of birds reflect in the UV (Andersson & Amundsen 1997, Andersson *et al.* 1998, Cuthill *et al.* 2000, Keyser & Hill 2000, Eaton & Lanyon 2003, Hausmann *et al.* 2003). Recent studies have discovered and discussed the importance of the UV in male Satin Bowerbird plumage, the gathered ornaments and how they contrast to their environment (Doucet & Montgomerie 2003a, 2003b, 2003c; Endler *et al.* 2005; Endler & Mielke 2005). Intensive studies on feather stealing for bowers by male Satin Bowerbirds have been conducted by Borgia (1985) and Borgia & Gore (1986) for the first time. Their results suggest a male would steal more when it has a below-average number of feathers on its bower. Interestingly, the number of matings correlated positively with the number of blue feathers found at the respective bowers. Rosella feathers are hard to find in nature and it is thus suggested that females might select males with decorations that are difficult to obtain because they represented time invested in their attainment (and defense) and therefore are true indicators of fitness and dominance (Borgia & Gore 1986, Borgia *et al.* 1987, Frith 1990). Borgia's studies dealing with feather stealing were carried out at remote places where artificial ornaments were rare in contrast to a study conducted very recently (Wojcieszek *et al.* 2006). Here, the stealing behavior of bowers with natural as well as artificial ornaments was scrutinized. UV blue ornaments such as blue feathers and blue plastic bottle tops were the preferred stolen objects (Wojcieszek *et al.* 2006). Bowerbirds belong to the Ptilonorhynchidae family, a family of which no ultraviolet light studies have been conducted but bowerbirds belong to the Order of Passeriformes – a bird Order were all birds studied so far were capable of seeing UV light. They either possess a VS-type cone with maximum sensitivity at around 400 nm or a UVS-type cone with maximum sensitivity in the ultraviolet range at around 370 nm (Cuthill *et al.* 2000, Ödeen & Hastad 2003, Endler *et al.* 2005). Though likely, so far it has only been speculated that bowerbirds can perceive ultraviolet light as no behavioral test has been conducted. The purpose of my study is to find out (1) whether Satin Bowerbirds are capable of seeing ultraviolet light and (2) whether blue ultraviolet colored ornaments were found more commonly than simply blue colored ornaments at the different bower sites surveyed.

Methods

Bowerbird studies were conducted at three different locations in the wild:
The Royal National Park, New South Wales (Fig. 2.4), Australia, the Bunya Mountains National Park, Queensland, Australia and the Daintree National Park at Cape Tribulation, in Northern Queensland, Australia. Six active bowers were found, two at each location with a minimum distance of 1 km away from each other. The bowers found in Daintree NP were built by the northern subspecies *Ptilonorhynchus violaceus minor*. All other bowers were built by *Ptilonorhynchus violaceus violaceus*. The studies were carried out during three months of fieldwork from January through March. For statistical analysis I used the X^2 test, a non-parametric test. In both, the behavioral experiment and the ornament color discrimination analysis a probability level of 0,5 was assumed.

Spectrophotometry and UV photography

Feathers and ornaments were measured using reflection spectrophotometry via an Ocean Optics S2000 spectrometer and a pulsed xenon lamp (PX-2). A single fibre-optic probe was used to provide illumination from the light source and the reflected light was transferred to the spectrometer. To exclude external light from the measurement area the probe was mounted in a hard rubber cover. The feathers were checked for UV reflection by measuring at different angles. The angle with the highest UV output was finally taken. Ornaments were considered UV-reflecting when spectrophotometric measurements showed a peak intensity of at least 15 % within the range of 320 – 400 nm. The photos were taken with a Nikon D70 SLR digital body, a camera with a UV sensitive chip, the UV-Nikkor 105 mm lens using the Hoya filter U 360 to block visible light and a Heliopan BG 23 to block infrared light.

Collected Ornaments

Ornaments were gathered and measured at the six bower sites with a reflection spectrophotometer. Every ornament found was measured.

Abbreviations for bower sites used in Tables:

Bower 1: Royal National Park
Bower 2: Royal National Park
Bower 3: Bunya Mountains National Park
Bower 4: Bunya Mountains National Park
Bower 5: Daintree National Park
Bower 6: Daintree National Park

Behavioral Experiment

The behavioral studies concerning feather choice were carried out at the two bowers in Daintree National Park. At the other sites, the bowerbirds did not show any collective behavior even though their bowers were well maintained and richly decorated. Twenty tail and primary feathers of Crimson Rosellas *Platycercus elegans* were placed on the ground near each of the six bower sites to attract male Satin Bowerbirds. These feathers reflect UV-light under natural conditions (Figs. 2.1 and 2.10). 50 % of the feathers were treated with sun block lotion, a procedure already successfully tested by Andersson & Amundsen (1997) in behavioral studies with Bluethroats. Several sun lotions have been tested. Due to blocking potentials (also in the higher UV-A band) NIVEA ® Sun-Spray LSF 30 was found to be most effective in blocking UV almost instantly at 400 nm (Fig. 2.1). Spectral measurements showed no differences in brightness in the region above 400 nm in treated and untreated feathers (Fig. 2.1). These findings made an additional treatment to reduce brightness unnecessary (Andersson & Amundsen 1997). The feathers were in good shape and, from a humans eye perspective, couldn’t be distinguished from each other even after the treatment with sun block detergent. A set of 20 feathers, of which 10 were treated with UV absorbing sun blocking detergent, were placed in a well-illuminated spot on the forest floor at a distance of approximately 30 m from the bower. An equally treated number of tail and primary and secondary feathers were used in each trail. After the bird's first collection visit the feathers left over were taken away and replaced by an additional, equally treated set of 20 feathers. This procedure was repeated 3 times a day. In order not to stress the bird, I did not conduct any similar experiments the following day at this bower and moved to the second bower. At each bower, 10 days of behavioral experiment were conducted.

Results

Collected Ornaments

Altogether 276 ornaments were found, collected, and measured. To the human eye the ornaments were mainly bright blue colored, consisting of different shades of blue. The majority of ornaments (178) collected were human originated items made of plastic or plastic paper. Both bowers in Daintree National Park contained considerable amounts (33) of blue berries of one unidentified plant species, all of them were UV-reflective possibly due to the presence of a waxy bloom (Wilson 1989, Altshuler 2001). All 55 feathers found at the different bower sites showed a distinctive UV reflection at the blue patches. (See Figs. 2.9, 2.10, and 2.12 for UV reflection of a Crimson Rosella tail feather and a male Satin Bowerbird specimen). It was also the case for some artificial ornaments such as water bottle caps, hair strings and clothes pins (Figs. 2.11, 2.13, and 2.14). Some water bottle tops showed remarkable amounts of UV reflection shown in Fig. 2.2.

Table 2.1 Quantative aspects of ornaments found at the six bower sites.

Collected Bower Ornaments	Quantity
Bottle caps	46
Berries	33
Unidentified plastic objects	30
Straws	28
Blue paper	24
Clothes pins	19
Plastic teaspoons	15
Flowers	10
Shoe laces	5
Cloths	4
Hair strings	4
Ball pens	3
Feathers	
Crimson Rosella, *Platycercus elegans* Tail feathers	26
Crimson Rosella, *Platycercus elegans* Secondaries	18
Crimson Rosella, *Platycercus elegans* Primaries	8
Superb Fairywren, *Malurus cyaneus* Tail feathers	2
Eclectus Parrot, *Eclectus roratus* Primaries	1

Table 2.2 Ornaments found at bower 1.

Bower 1	# Ornaments
UV-reflecting	24
Non-UV-reflecting	11
Total	35

Chi^2 UV-reflecting ornaments: $p = 0.028$.

There is a clear preference for ornaments exhibiting UV-reflections at bower 1.

Table 2.3 Ornaments found at bower 2.

Bower 2	# Ornaments
UV-reflecting	6
Non-UV-reflecting	6
Total	12

There is no preference for ornaments exhibiting UV-reflections at bower 2.

Table 2.4 Ornaments found at bower 3.

Bower 3	# Ornaments
UV-reflecting	17
Non-UV-reflecting	8
Total	25

X^2 UV-reflecting ornaments: $p = 0.072$.

There is a clear preference for ornaments exhibiting UV-reflections at bower 3.

Table 2.5 Ornaments found at bower 4.

Bower 4	# Ornaments
UV-reflecting	44
Non-UV-reflecting	28
Total	72

X^2 UV-reflecting ornaments: $p = 0.059$.

There is a clear preference for ornaments exhibiting UV-reflections at bower 4.

Table 2.6 Ornaments found at bower 5.

Bower 5	# Ornaments
UV-reflecting	61
Non-UV-reflecting	28
Total	89

X^2 UV-reflecting ornaments: $p = 0.0005$.

There is a clear preference for ornaments exhibiting UV-reflections at bower 5.

Table 2.7 Ornaments found at bower 6.

Bower 1	# Ornaments
UV-reflecting	29
Non-UV-reflecting	14
Total	43

X^2 UV-reflecting ornaments: $p = 0.022$.

There is a clear preference for ornaments exhibiting UV-reflections at bower 6.

Table 2.8 Ornaments found at bowers 1 – 4.

Bowers 1 – 4	# Ornaments
UV-reflecting	91
Non-UV-reflecting	53
Total	144

X^2 UV-reflecting ornaments: $p = 0.001$.

There is a clear preference for ornaments exhibiting UV-reflections at bowers 1 – 4 collected by Satin Bowerbirds of the nominate subspecies *P. violaceus violaceus*.

Table 2.9 Ornaments found at bowers 5 – 6.

Bowers 5 – 6	# Ornaments
UV-reflecting	90
Non-UV-reflecting	42
Total	132

X^2 UV-reflecting ornaments: p = 0.00004.

There is a clear preference for ornaments exhibiting UV-reflections at bowers 5 – 6 collected by Satin Bowerbirds of the northern subspecies *P. violaceus minor*.

Table 2.10 Ornaments found at all 6 bowers.

Bowers 1 – 6	# Ornaments
UV-reflecting	181
Non-UV-reflecting	95
Total	276

X^2 UV-reflecting ornaments: p = 2.25976×10^{-7}.

There is a clear preference for ornaments exhibiting UV-reflections at bowers 1 – 6 collected by Satin Bowerbirds of both subspecies.

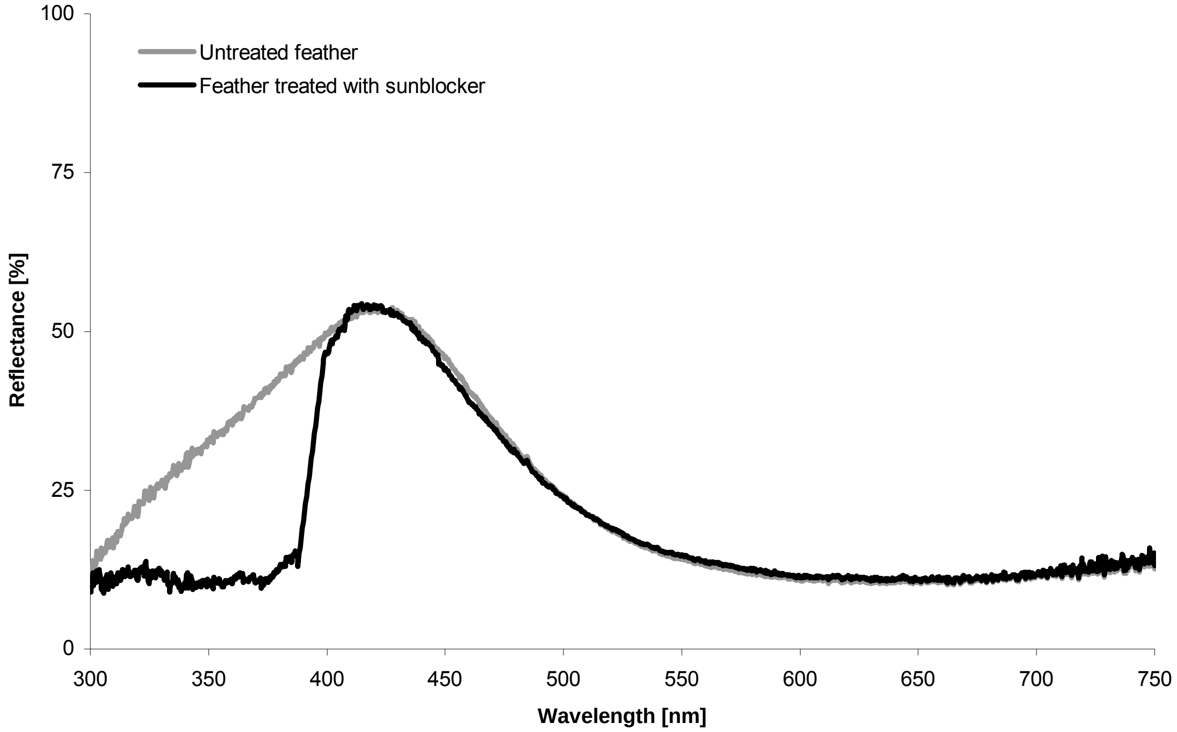

Fig. 2.1 Treated and untreated tail feathers of the Crimson Rosella *Platycercus elegans* with the sun block lotion NIVEA ® Sun-Spray LSF 30.

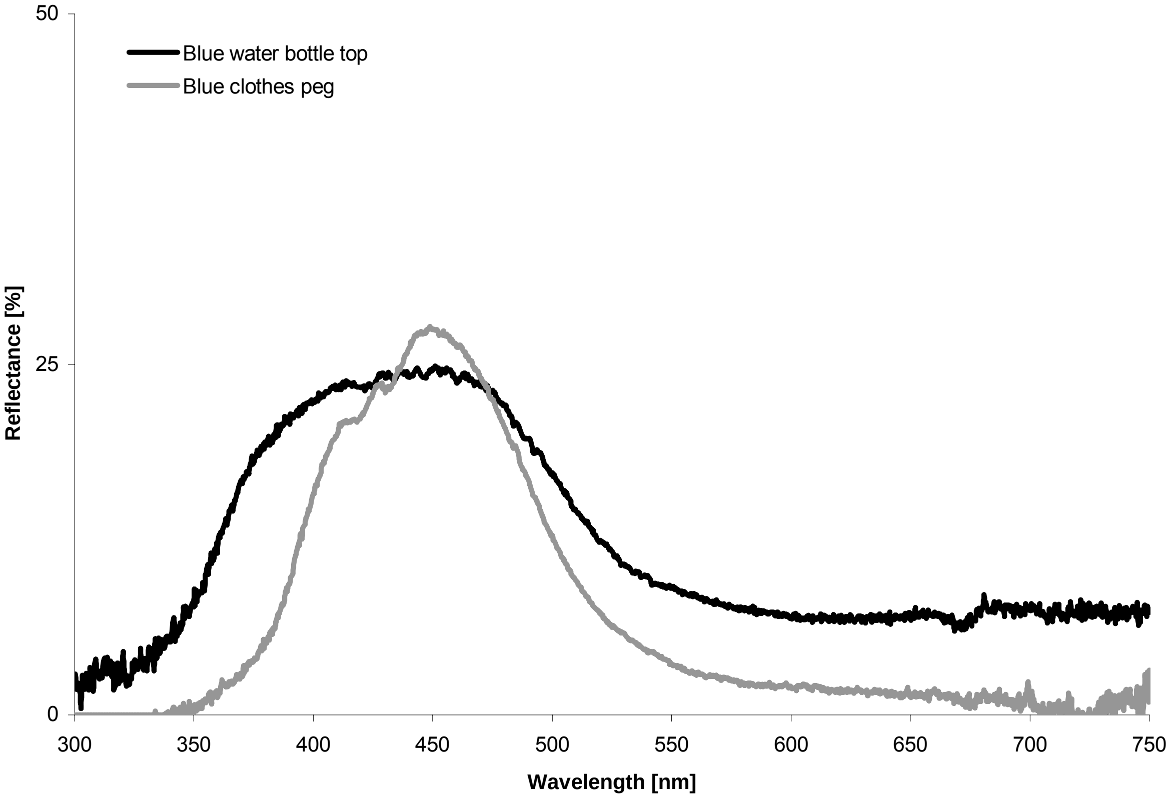

Fig. 2.2 Spectrum of a plastic water bottle top and a blue clothes peg as found at all bowers shows high amounts of UV – reflection.

Fig. 2.3 Satin's Bower decorated with *Solanum*-flowers.

Fig. 2.4 Satin Bowerbird's Habitat in the Royal National Park, New South Wales, Australia.

Fig. 2.5 Satin Bowerbird female (*Ptilonorhynchus violaceus*).

Fig. 2.6 Satin Bowerbird juvenile male (*Ptilonorhynchus violaceus*), with blue paper in bill.

Fig. 2.7 Satin Bowerbird male (*Ptilonorhynchus violaceus*).

Fig. 2.8 Satin's Bower with ornaments, tail feathers of a Crimson Rosella and plastic objects.

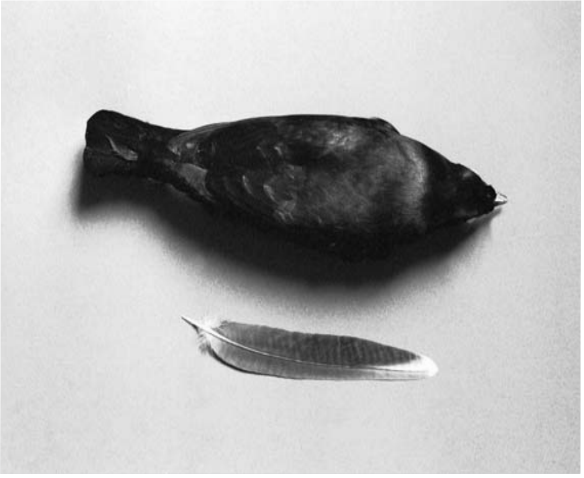

Fig. 2.9 Satin Bowerbird male with tail feather of a Crimson Rosella in normal light, B & W.

Fig. 2.10 Satin Bowerbird male with tail feather of a Crimson Rosella in UV light.

Fig. 2.11 Ornaments collected by a Satin Bowerbird in Daintree NP, Queensland, in sunlight.

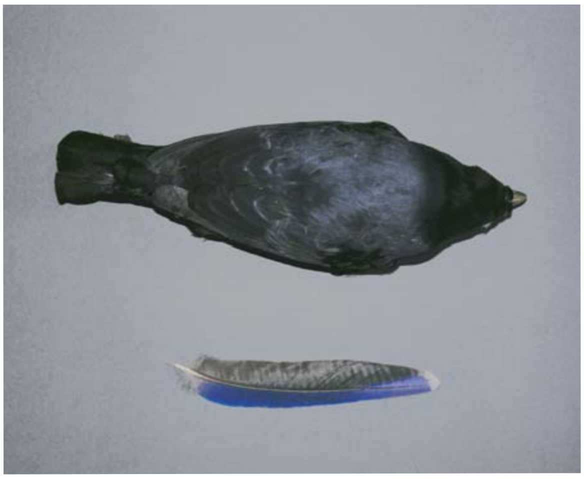

Fig. 2.12 Satin Bowerbird male with tail feather of a Crimson Rosella in sunlight,

Fig. 2.13 Ornaments collected by a Satin Bowerbird in Daintree NP, Queensland, in B & W.

Fig. 2.14 Ornaments collected by a Satin Bowerbird in Daintree NP, Queensland, in UV light.

Behavioral Experiment

Very rarely, 6 times in total, feathers were turned over to their non-coloured reverse side by the wind, and the bird came before they could be turned the other way round again. In all cases the bird ignored these feathers. Some few feathers, especially innermost tail feathers T_1 and some T_2 showed small parts of green next to blue. These feathers were also neglected by the birds and separated from the feathers used in the experiment in order not to influence the trail.

Table 2.11 Collection activities at bower 5.

Date and experiment No.	Number of untreated collected feathers	Number of treated collected feathers	Total number of collected feathers
Day 1			
No. 1	7	2	9
No. 2	3	3	6
No. 3	9	2	11
Total	19	7	26
X^2 untreated feathers for day 1 p = 0.019.			
Day 2			
No. 1	3	5	8
No. 2	2	6	8
No. 3	8	3	11
Total	13	14	27
X^2 untreated feathers for day 2 p = > 1.			
Day 3			
No. 1	6	1	7
No. 2	4	0	4
No. 3	2	3	5
Total	12	4	16
X^2 untreated feathers for day 3 p = 0.045.			
Day 4			
No. 1	9	3	12
No. 2	3	4	7
No. 3	7	4	11
Total	19	11	
X^2 untreated feathers for day 4 p = 0.144.			

Date and experiment No.	Number of untreated collected feathers	Number of treated collected feathers	Total number of collected feathers
Day 5			
No. 1	4	3	7
No. 2	6	2	8
No. 3	5	0	5
Total	15	5	20
X^2 untreated feathers for day 5 p = 0.0253.			
Day 6			
No. 1	5	3	8
No. 2	4	5	9
No. 3	1	7	8
Total	10	15	25
X^2 untreated feathers for day 6 p = > 1.			
Day 7			
No. 1	5	2	7
No. 2	3	3	6
No. 3	2	4	6
Total	10	9	19
X^2 untreated feathers for day 7 p = 0.818.			
Day 8			
No. 1	1	3	4
No. 2	7	0	7
No. 3	6	2	8
Total	14	5	19
X^2 untreated feathers for day 8 p = 0.025.			
Day 9			
No. 1	8	4	12
No. 2	1	2	3
No. 3	7	1	8
Total	16	7	23
X^2 untreated feathers for day 9 p = 0.062.			
Day 10			
No. 1	0	3	3
No. 2	5	4	9
No. 3	1	8	9
Total	6	15	21
X^2 untreated feathers for day 10 p = > 1.			

Table 2.12 Collection activities at bower 6.

Date and experiment No.	Number of untreated collected feathers	Number of treated collected feathers	Total number of collected feathers
Day 1			
No. 1	4	5	9
No. 2	5	6	11
No. 3	6	4	10
Total	15	15	30
X^2 untreated feathers for day 1 p = 1.			
Day 2			
No. 1	3	1	4
No. 2	4	0	4
No. 3	7	2	9
Total	14	3	17
X^2 untreated feathers for day 2 p = 0.008.			
Day 3			
No. 1	4	2	6
No. 2	7	1	8
No. 3	4	2	6
Total	15	5	20
X^2 untreated feathers for day 3 p = 0.025.			
Day 4			
No. 1	3	1	4
No. 2	1	2	3
No. 3	6	3	9
Total Day 4	10	6	16
X^2 untreated feathers for day 4 p = 0.287.			
Day 5			
No. 1	3	0	3
No. 2	5	4	9
No. 3	6	2	8
Total	14	6	20
X^2 untreated feathers for day 5 p = 0.078.			

Date and experiment No.	Number of untreated collected feathers	Number of treated collected feathers	Total number of collected feathers
Day 6			
No. 1	1	3	4
No. 2	2	7	9
No. 3	4	4	8
Total	7	14	21
X^2 untreated feathers for day 6 p = > 1.			
Day 7			
No. 1	1	4	5
No. 2	9	1	10
No. 3	8	4	12
Total	18	9	27
X^2 untreated feathers for day 7 p = 0.0651.			
Day 8			
No. 1	2	5	7
No. 2	7	2	9
No. 3	6	4	10
Total	15	11	26
X^2 untreated feathers for day 8 p = 0.432.			
Day 9			
No. 1	8	0	8
No. 2	5	2	7
No. 3	9	1	10
Total	22	3	25
X^2 untreated feathers for day 9 p = 0.0001.			
Day 10			
No. 1	4	4	8
No. 2	8	3	11
No. 3	8	3	11
Total	20	10	30
X^2 untreated feathers for day 10 p = 0.071.			

Table 2.13 Total collection activities at bowers 5 and 6.

Date and experiment No.	Number of untreated collected feathers	Number of treated collected feathers	Total number of collected feathers
Days 1 – 10 at bower 5	134	92	226
X^2 untreated feathers for days 1 - 10 $p = 0.005$			
Days 1 – 10 at bower 6	150	82	232
X^2 untreated feathers for days 1 - 10 $p = 8.0286 \times 10^{-6}$			
Days 1 – 10 at bowers 5 + 6	284	174	458
X^2 untreated feathers for days 1 - 10 $p = 2.7479 \times 10^{-7}$			

The untreated feathers exhibited a strong UV reflection and could be clearly distinguished from the feathers treated with UV blocking agent (Fig. 2.1). This seemingly affected the bowerbird's choice. At both bowers, no. 5 and 6 the bowerbirds preferred UV-blue feathers to blue feathers significantly ($p < 0.0001$). The bowerbirds collected between 3 and 12 feathers, with an average of seven to eight feathers (mean = 7.633   2.5) during one visit. A total of 458 feathers were taken away by the bowerbirds. All birds were mature male Satin Bowerbirds (Fig. 2.7) to collect the feathers except for experiment number 2 on the 6th as well as the 7th day, on which a juvenile male collected the feathers. A juvenile male could clearly be distinguished from a mature one by its plumage which closely resembles the female's (Fig. 2.5 and 2.6). The juvenile birds didn't show any difference in their behavior compared to adults. The gathered feathers were partly found at either of the two bowers and retaken at the end of each day. However, the destiny of 62 feathers remained unknown. Inner Crimson Rosella tail feathers which were the largest of all feathers were selected first and showed the most portions of blue or UV-blue respectively.

Discussion

Many natural ornaments collected by Satin Bowerbirds exhibit considerable amounts of ultraviolet light: Blue berries – as long as they have a waxy bloom, flowers, butterfly wings, and feathers. There are probably less natural blue colored objects without UV. This may explain the high abundance of UV blue colored artificial ornaments at the bowers. A random check of blue colored items of man made objects in an Australian supermarket revealed that most blue colors didn’t show a UV reflection at all. Although a male Satin Bowerbird would possibly collect any blue item it can find, studies on ornament stealing showed the preference for blue Crimson Rosella retrices and blue bottle tops (Wojcieszek 2006). In my observations these were the ornaments picked up and held in its beak by the male most frequently during courtship. Taken together, the results suggest the gathered objects consist of two colors, blue and UV-blue, the latter being the preferred color. For a human’s eye the decoration is uncolored blue. In my study no feathers of a Satin Bowerbird male were found at any bower, with the feathers only exhibiting light in the ultraviolet range. The birds are also known to reject flight feathers of male Satin Bowerbirds when offered to them (Borgia *et al.* 1987). This supports the innovation hypothesis, in which colors used in bowerbird courtship are innovate more than elaborate trains (Endler *et al.* 2005). The Satin Bowerbird is not unique in using moulted feathers in courtship. The Archbold’s Bowerbird (*Archboldia papuensis*) uses the head plumes from adult male King of Saxony Bird of Paradise (*Pteridophora alberti*) as bower decoration. The rarity and therefore novelty of these particular feathers is remarkable, each male takes between four to seven years to first attain them, suggesting that they were indicators of male fitness when used as bower decoration (Frith & Frith 1990). The male Spotless Starling (*Sturnus unicolor*) also uses moulted feathers to attract females. The feathers are put in the nest built by the male with the most colorful and/or UV reflecting surface facing upwards (Veiga 2005). Feather decorations are a key element in sexual display and serve as novelty fitness indicators for females. My study adds further details to the understanding of multicomponent sexual signaling in the sexual selective behavior of the Satin Bowerbird. The capability of Satin Bowerbirds seeing ultraviolet light allows the female to judge the quality of male UV colored plumage and bower construction which is believed to have evolved to provide females information of relative quality of males. Bower building bowerbirds are known to have evolved larger brains than the related non-bower building taxa (Madden 2001). This leads to the conclusion that relative brain size is related to bower complexity and suggests that sexual selection may drive gross brain enlargement. The Satin Bowerbird's courtship with its complex multicomponent signaling may be even more complex as we think it already is.

Summary

During courtship male Satin Bowerbirds are known to collect blue ornaments to decorate their bowers. In my study reflection spectrophotometry revealed significantly more UV-blue compared to unicolored blue collected ornaments, at all bowers surveyed. Via a behavioral choice experiment with feathers of the Crimson Rosella, partly treated with sun block lotion, a procedure previously conducted in UV-related behavioral studies, I was able to demonstrate the Satin Bowerbird's potential to see ultraviolet light. UV-vision allows the female to judge the quality of male UV colored plumage and bower construction which is believed to have evolved to provide females information about the relative quality of males.

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3. Is UV coloration in birds associated with light habitat variance?

Introduction

The adaptive significance of interspecific variation in avian coloration has been the subject of numerous studies (Darwin 1871, Hamilton & Zuk 1982, Endler 1993, Marchetti 1993, Finger & Burkhardt 1994, Endler & Thery 1996, McNaught & Owens 2002). Next to the “Species Isolation Hypothesis”, the “Light Environment Hypothesis” has been favored to explain interspecific plumage coloration (Marchetti 1993, Endler & Thery 1996, McNaught & Owens 2002). Birds live in different light environments, so-called “light habitats”, characterized by the surrounding ambient light. Light environments are caused by the geometry of the light paths, influenced by the weather conditions, and the time of day (Endler 1993). Perceived colors of animals depend upon the interaction between ambient light color and the reflectance color of the animal, e.g., feathers or bird plumage. As a result, a bird may have a different appearance in different light habitats; a color pattern may be relatively cryptic in some light habitats, while relatively conspicuous in others. Based on maximizing contrast against the background in the dominant ambient light environment, several authors have made predictions about which colors are most suitable in particular light habitats (Endler 1993, Marchetti 1993, Endler & Thery 1996, Thery 1996, Gomez & Thery 2004). Species that live in relatively closed habitats should have generally more reflective or brighter plumage than those species living in open habitats. This is due to the overall level of luminescence which is lower in relatively closed habitats such as forest habitats (Marchetti 1993). Not only the visible range of the light spectrum differs in various light habitats, but also the ultraviolet range differs significantly (Endler 1995).

Spectra measured in open habitats (Fig. 3.1) – as found in deserts, savannahs, or grasslands – resemble Standard Daylight (D65) spectra when taken in cloudy weather. The D65 standard describes the average spectral composition of noonday ambient light (with a light temperature of 6500 Kelvin) including the UV.

Sea habitats are light environments most exposed to the sun (Fig. 3.2). In addition to the radiation coming from above, ultraviolet light is also strongly reflected by seawater, ice or sand. Forests in particular exhibit much variation in their light environments (Fig. 3.3). Endler (1993) has structured forests into four major light habitats during day time independent of geographic regions: large gaps, small gaps, woodland shade, and forest shade. Compared to other light habitats the proportion of ultraviolet light, in contrast to the visible spectrum, is highest in forest shade (Endler 1993). At night-time, especially at nights with full moon (Fig. 3.4), the relative amount of UV light is higher at night than in the daytime, but the amount of light (a factor 100 times less) may not permit color detection, which may also apply to UV vision (Koivula *et al.* 1997).

However, although one or two supportive examples have been found in species favoring specific light habitats, there have been rather few statistically comparative tests dealing with a greater number of bird species (McNaught & Owens 2002). The overall aim of this study is to find out if the light environment has an effect on the development of UV reflective plumage coloration, if this is the case then species possessing UV phenomena would not be evenly distributed within each habitat.

Methods

Species selection

968 species from approximately 65 % of all bird families and from all 23 Orders following the taxonomic list of Sibley & Monroe (1990) were measured by means of reflection spectrophotometry. 5362 reflectance spectra were measured covering all colors in all plumage patches of a species. Most of the black, dark-grey and brown-colored feathers revealed a lack of substantial UV reflection which is supported by the results of previous work dealing with feather coloration (Burkhardt 1989, Finger *et al.* 1992, Hausmann *et al.* 2002, Eaton & Lanyon 2003). Therefore, the most colorful species in an Order were included as they were most likely to show distinctive UV reflection (Hausmann *et al.* 2002). Orders with few colored species, such as the Gruiformes, species were randomly

selected, but always from a colored species pool. Where possible, an average of 6 specimens per species of one subspecies of one geographical region were measured, all of them were adult birds. Only specimens in a good condition were taken which showed well-preserved colors. (Refer to the method section in Chapter 1 for the exact procedure and number of species measured in the different Orders).

For the purpose of this study, bird skins preserved at the Alexander Koenig Research Institute and Museum of Zoology in Bonn, Germany, The Natural History Museum in Tring, United Kingdom, and the American Museum of Natural History in New York were used for data collection. In the main, skins less than 20 years old were used to avoid failure due to possible color changes in older museum skins (Endler and Théry 1996, Hausmann *et al.* 2002, McNaught & Owens 2002). I define a bird as having distinctive UV coloration, (which I refer to as UV phenomena) when the spectrum shows a UV reflectance peak higher than 10 %. In order to include species lacking UV peaks, but with high amounts of UV reflecting plumage, I also speak of UV phenomena when any part of the UV reflectance spectrum exceeds the lowest reflection in the range of 400 to 700 nm. On account of this definition, white and light-colored feathers are excluded, despite their ability to reflect high amounts of UV light, contributing to overall brightness. (Refer to the method section in Chapter 1 for the exact procedure). With respect to the visual abilities of the birds, continuous reflection in the whole spectrum is a basic characteristic of white (Vorobyev *et al.* 1998) and significant amounts of UV have been found in nearly all white feathers (Eaton & Lanyon 2003).

Spectrophotometry and UV photography

Specimens and feathers were measured using reflection spectrophotometry via an Ocean Optics S2000 spectrometer and a pulsed xenon lamp (PX-2). A single fibre-optic probe was used to provide illumination from the light source and the reflected light was transferred to the spectrometer. Measurements using a standardized angle might not show UV reflections despite their existence. Therefore feathers were checked for UV reflection by measuring at different angles. The angle with the highest UV output was finally taken. Plumage patches were illuminated at angles of between 35° and 90° to the long axis of the feather patch from a top view at a distance of approximately 7 mm. The light was collected at the same angle. As a padding, a black velvet cloth was used to avoid stray light from the colored surfaces influencing the measurements. This was also used as a dark reference. As a white reference standard, a compressed tablet of barium sulphate (Ba SO_4) was used showing a white with a higher reflection intensity than the white standard included along with the Ocean Optics spectrometer. Measurements were made in the ambient light of a darkened room using the bifurcated cable UV/VIS 400UM from World Precision Instruments, illuminating a field of approximately 2-3 mm^2 with a 100 ms summation time.

The photos were taken with a Nikon D70 SLR digital body, a camera with a UV sensitive chip, the UV-Nikkor 105 mm lens with ED glass to avoid chromatic aberrations. Visible light was blocked using the U 360 Hoya filter and a BG 23 Heliopan filter blocked infrared light.

Habitat selection and statistics

I chose four habitats which could be easily distinguished from another primarily through their different light environments. All birds having their main activity during the night were assigned to the “night habitat,” independent of the natural environment in which they are usually found. Birds assigned to the “sea and ice” habitat had in common besides having their main activity assigned to the sea, the seashore, pack ice, icebergs and other coastal areas including watt, rock islands, and cliffs. “Open habitats” were characterized by areas undisturbingly exposed to the sun such as in the case of the savannahs, deserts, or grasslands. This light habitat included inshore water habitats such as rivers and streams as well as bodies of standing water such as lakes and lagoons as long as they were not covered by plants producing shady areas. Birds assigned to the “forest habitat” mainly live in the forest or in habitats with thick undergrowth. The “forest habitat” includes all habitats with no direct sun exposure. The 968 bird species measured were assigned to the four light habitat groups by the use of habitat characterization as described in Sibley & Monroe's (1990) list. The assignment was conducted following ecological aspects such as main territory, in which courtship, breeding, hatching, and foraging occurred. Sometimes, a species could be assigned to more than one light habitat. Assuming UV phenomena possibly play a role in intraspecific signaling; species were then assigned to the light habitat where courtship was conducted. For statistical analysis, I used the Chi^2 test, a non-parametric test with a significance level of 5%. Because of the 968 species surveyed, 348 species exhibited UV phenomena, therefore a probability level of 0.36 was assumed for the distribution of UV phenomena to be found in the declared habitats. H_0: there is no significant difference between the found and expected frequencies of UV phenomena within each light habitat. H_1: there is a significant difference.

Results

Only the measured species of the Order Strigiformes with the exception of the Burrowing Owl (*Speotyto cunicularia*), which is also active during the day, and the three Kiwi species from the Order Struthioniformes were assigned to the “night habitat” category. 45 species of the two Orders Anseriformes and Ciconiiformes were assigned to the “sea and ice” habitat (Table 1). Species belonging to the rest of the bird Orders were more or less equally assigned to the other two light habitat categories, with 386 species assigned to “open terrain” and 483 species assigned to the “forest” light habitat.

No UV phenomena were found in species assigned to the light habitats “night” and “ice and sea” whereas species assigned to the light habitat “open terrain” and “forest” exhibited 76 and 272 UV phenomena, respectively, with the latter being the only light habitat with more bird species exhibiting UV phenomena (56%) than without (Fig. 3.5).

My rejection of the null hypothesis allows me to conclude, that in all the four light habitats birds exhibiting UV phenomena were unevenly spread. In other words, the frequencies of the occurrence of UV phenomena are significantly different within each light habitat. With 272, significantly more species with UV phenomena ($p < 0.005$) were found in the forest light habitat than the 211 species without UV phenomena.

The bird species, which are known to live in regions with a lot of snow, such as the Snowy Owl, the Whooping Crane and the winter plumaged Ptarmigan, the feathers were not only white. The spectra of all three birds well exceeded into the UV region making the birds invisible in the UV reflecting snow, especially when compared with the spectrum of snow, which resembled the barium sulphate white standard (Fig. 3.6). The spectra of the white breast feathers of the Black-headed Gull also exceeded remarkably into the UV (Fig. 3.6).

Fig. 3.1 Light in „open habitats", as found in this African savannah, resemble Standard Daylight (D65) spectra, when taken in cloudy weather.

Fig. 3.2 The „sea and ice" habitat is the light habitat most exposed to the sun. In addition to the radiation coming from above, ultraviolet light is also strongly reflected by the sea, ice or sand.

Fig. 3.3 Most birds with UV phenomena were found in the „forest" light habitat. Compared to other light habitats, the proportion of ultraviolet light, in contrast to the visible spectrum, is highest in this habitat.

Fig. 3.4 Especially on nights with full moon the “night habitat” shows a high proportion of UV light compared to the rest of the spectrum. But probably because overall brightness is low, diurnal birds don't seem to develop highly UV reflective feather patches presumably used in courtship behavior.

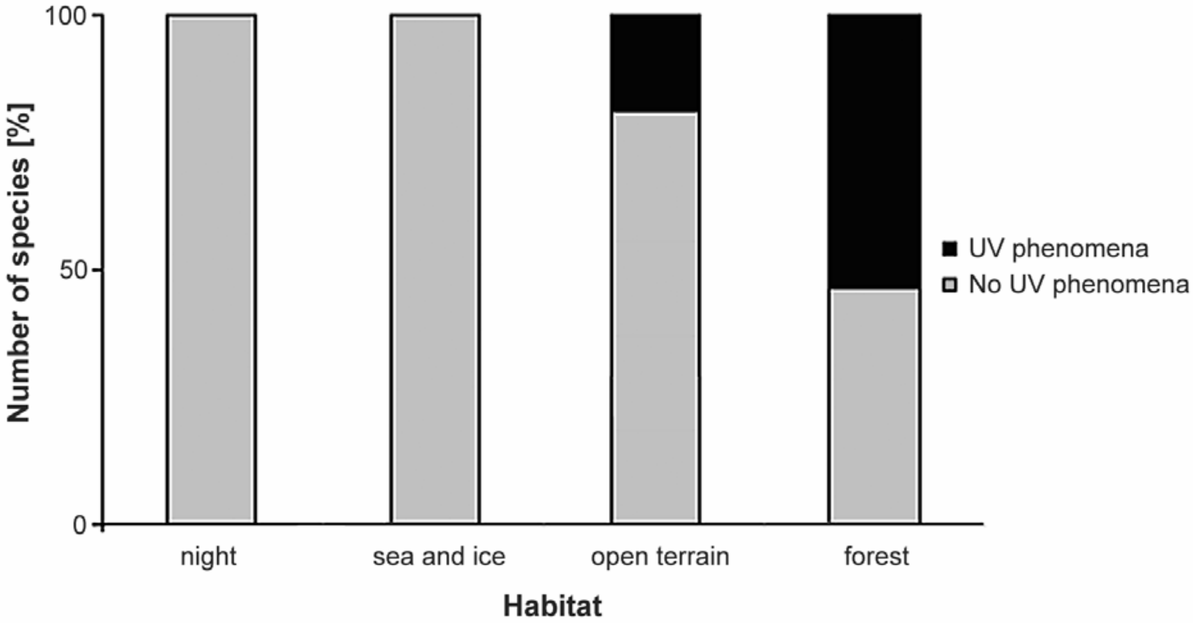

Fig. 3.5 Percentage of birds with UV phenomena found in the different habitats. Only in the forest habitat birds with UV phenomena dominated. Values were taken from the last row from Table 3.1.

Table 3.1 Proportion of UV phenomena defined to four light habitats. 968 bird species were divided into 4 distinct light habitat types according to their main occurrence. The Chi^2 test was used to test whether or not UV phenomena were evenly distributed in each light habitat. In all 4 light habitats UV phenomena were unevenly spread.

	Quantity of species with UV phenomena	Quantity of species without UV phenomena	p	species with UV phenomena in %
Night	0	54	3.56×10^{-8}	0
Sea and ice	0	45	4.87×10^{-7}	0
Open terrain	76	310	2.45×10^{-11}	20
Forest	272	211	1.39×10^{-20}	56
Total	348	620		

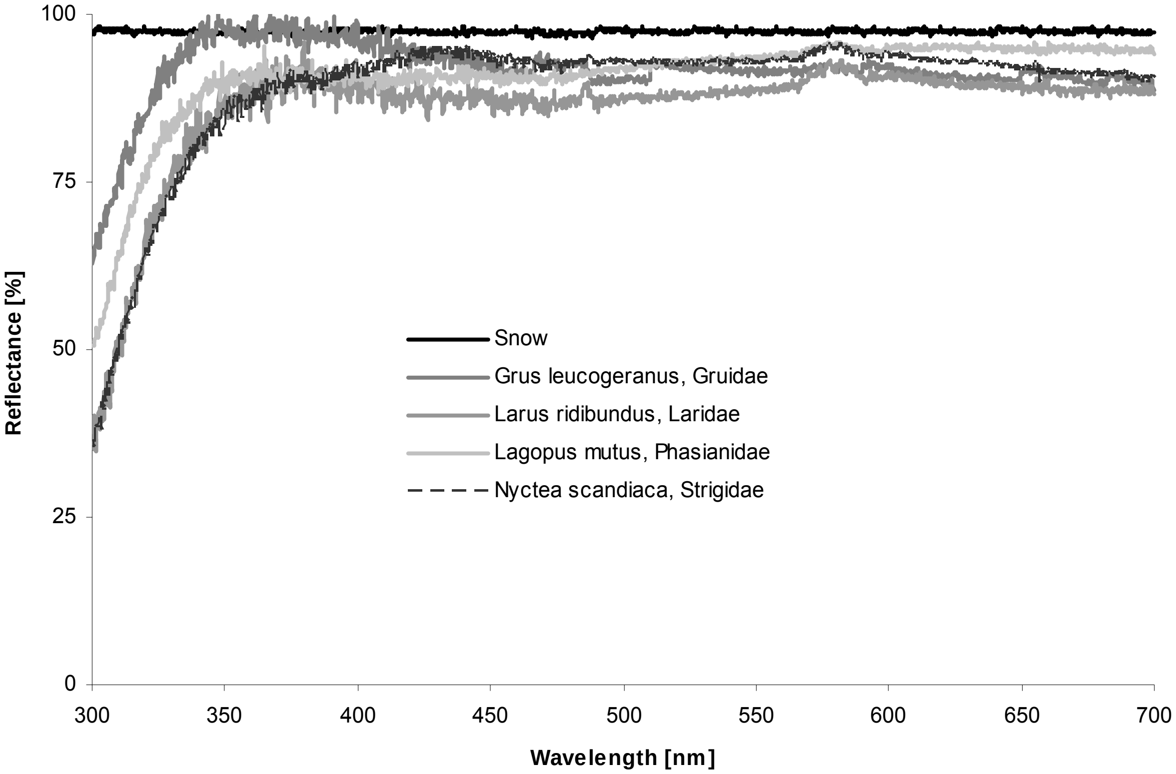

Fig. 3.6 Reflection spectra of snow as well as white breast feathers from birds living in areas with snow and water such as the Snowy Owl, the Ptarmigan, the Whooping Crane, and the Black-headed Gull. All spectra exceed well into the UV region making the birds invisible in the UV-reflecting snow (or sky) even for predators (or prey) with UV-vision.

Discussion

In agreement with the Light Environment Hypotheses, significant association was found between plumage coloration and habitat use. According to my definition of UV phenomena, a completely white bird or a white feather patch couldn't exhibit a UV phenomenon. Black, grey, and brown feathers very rarely reflect high amounts of UV (see Chapter 1). It therefore doesn't seem surprising that in the “sea and ice” habitat with many black and white colored birds, none were found to exhibit UV phenomena. But, there are seabirds with colored plumage parts, such as the yellow and orange feathers of some penguins, auks, and pelican species. However, none of those plumage patches measured, exhibited a UV phenomenon. To increase signal efficiency, it may be of advantage for a bird living in such a UV rich light habitat surrounded by UV reflecting sand, water, or ice, to evolve plumage patches with no UV reflection at all. We found many white feathers in seabirds such as the white breast feathers of the Black-headed Gull exceeding well into the UV region. It is a generally observable fact, seabirds being provided with bright white ventral feathers in contrast dark colored dorsal feathers. According to Tinbergen (1968), seabirds with bright white ventral plumage, could have an advantage when preying on fish, because the white feathers may reduce contrast to the bright white sky. If Tinbergen’s presumption is correct, then it would make sense for the white breast feathers of the Black-headed Gull and other seabirds to extend the reflection well into the UV region, as it is known that fish are also possess UV-vision (Jacobs 1992). The white feathers from birds living in areas with snow such as the breast feathers of the Snowy Owl, the Ptarmigan, as well as the Whooping Crane, resemble the reflection spectra of snow. All spectra exceed well into the UV region making the birds invisible in the UV-reflecting snow even for predators with UV-vision. In “open” habitats, a smaller quantity of birds with UV phenomena was found than statistically expected. The reason for this may lie in the fact that when UV is involved in intraspecific signaling in courtship behavior in many birds studied to date, UV is used as a communication signal in short distances (Andersson & Amundsen 1997, Andersson *et al.* 1998, Cuthill *et al.* 2000, Doucet 2003). This may be due to the fact that ultraviolet light scatters with increasing distance in contrast to light with longer wavelengths. Hence, many non-achromatic birds found in open habitats lacked UV phenomena, e.g., cranes, bustards, rails, or ducks where males perform their courtship activity at a notable distance from the observing female. The eyes of nocturnal birds are highly adapted to viewing in darkness because their retina is dominated by rods (Bowmaker & Martin 1978). Even though there is evidence for UV vision by a possible expression of a VS cone in at least one nocturnal species, with the Nightjar (*Caprimulgus europaeus*) in a behavioral experiment with Tengmalm's Owls (*Aegolius funereus*) it was revealed that they do not use UV vision in foraging (Koivula et al 1997, Ödeen & Håstad 2003). The fact that not a single UV phenomenon was found in the nocturnal birds surveyed suggests that UV does not play a role in intraspecific signaling related to plumage coloration.

By far the most species with UV phenomena were found in the "forest" light habitat. Many studies have been conducted on bird communities living in different ambient light conditions within forests, dividing forests into clusters of distinct light environments. On account of the shading of the trees and undergrowth, the overall luminescence is lowest in this light environment. Interestingly, the "forest shade" light habitat defined by Endler (1993), in relation to the visible spectrum, showed higher amounts of UV than any other light habitat (Endler, personal communication). This was the case with light habitats within forests and also compared to the others. Forests being the UV richest habitats may have an influence on the evolution of plumage colors favoring the expression of UV phenomena. This may explain the abundance of UV phenomena in forest birds found in my study. It is important to point out that the joint evolution of visual signals and vision can be strongly influenced by microhabitat choice. Each light habitat can easily be divided into numerous smaller habitats with different light conditions. This sometimes very effectively drives the evolution of intraspecific visual signals as found, e.g., in four sympatric manakin species. All four differently colored, forest- dwelling species place their leks at different vertical positions in the rainforest, with each species favoring a slightly different microhabitat with a specific spectral composition of ambient light (Heindl 2002, Heindl & Winkler 2003). Differences in plumage color between closely related species are a product of selection on signal efficiency which is an adaptive response to variation in light environments across habitats independent of their dimension (McNaught & Owens 2002). My results support the Light Environment Hypotheses and suggest that, in general, interspecific variation in plumage color among birds is strongly influenced by light environment.

Summary

The “Light Environment Hypotheses” is supported by my findings. My results suggest that, in general, interspecific variation in plumage color among birds is strongly influenced by the light environment. Four light habitats were chosen: open, sea and ice, forest, and night. Of 968 bird species plumages surveyed by means of reflection spectrophotometry, 348 revealed remarkable amounts of UV (UV phenomena). Birds of all 23 Orders according to Sibley & Monroe’s list (1990) were measured and assigned to one of the four light habitats. No UV phenomena were found in the “night” and the “sea and ice” habitat, few were found in open habitats, whereas 56% of the 425 surveyed species assigned to the forest habitat exhibited UV phenomena. Possible explanations for the inhomogeneous distribution of UV phenomena in the different light habitats with possible function as intraspecific signals are proposed and discussed.

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4. The distribution of UV phenomena in parrots

Introduction

In my survey in search of UV phenomena in 968 bird species of all Orders by far the most were found in the parrot Order, the Psittaciformes. 140 of the 143 species under study reflected considerable amounts of ultraviolet light (see Chapter 1). In some of the examined species, all the measured plumage parts exhibited a UV phenomenon. In others, similar colored feather patches did not exhibit UV. In contrast to most other birds, parrots do not use carotenoids for feather coloration. For over a century, biochemists have been aware that parrots use a unique system of pigmentation, but their biochemical identity has remained elusive until recently (Stradi *et al.* 2001, McGraw & Nogare 2005). The novel pigments were called Psittacofulvins, which are polyenal lipochromes. Although not many studies have been conducted on the distribution of these unique pigments in the parrot Order, a suit of five different Psittacofulvins was found in 44 species which was responsible for red color pigmentation (McGraw & Nogare 2005). In contrast to, e.g., the passerines, parrots do not acquire red plumage pigments from their diets but seem to manufacture them endogenously instead, although parrots were found to circulate high concentrations of both dietary and metabolically derived carotenoids through the blood at the time of feather growth at levels comparable to those found in many carotenoid-colored birds (McGraw & Nogare 2004, 2005). Furthermore, similar to other bird plumage colors, such as the carotenoids, the Psittacofulvins have been discovered to signal individual quality and parental investment (Masello & Quillfeldt 2003, Masello *et al.* 2004). Psittacofulvins are believed to be responsible for red, orange, and yellow pigmentation in the parrot Order (McGraw & Nogare 2004). However, some pigments must be responsible for the fluorescing properties found in at least 109 parrot species (Völker 1936, 1937; 1955, 1965; Arnold 2002). Several studies have revealed evidence that at least in Budgerigars (*Melopsittacus undulatus*) a minimum of two different pigments are responsible for the yellow pigmentation (Völker 1937, Driesen 1953, Schmidt 1961). Blue colors in parrots are derived from the physical structure of the feather. Green feathers, which are present in

85% of the psittacine species, are a combination of pigment and the physical structure of the feather (Nissen 1958; Dyck 1971a, 1971b, 1976; Nemésio 2001). Ultraviolet reflections, also caused by micro structural arrangements in the feather, are known to occur in parrot feathers (Nemesio 2001, Eaton & Lanyon 2003, Hausmann *et al.* 2003, Pearn *et al.* 2003). Although, not many parrots are known to be able to perceive UV light, behavioral choice experiments have proven that Budgerigars see ultraviolet light and moreover further studies have revealed that they possess UVS cones (Pearn *et al.* 2001, Arnold 2002, Pearn *et al.* 2003). In birds, the VS cones are the most widespread variety of short wave sensitive (SWS) receptors. Although designated “violet sensitivity cones” they are capable of perceiving ultraviolet light, but only with the UVS cones’ (ultraviolet sensitive cones) the maximum sensitivity lies in the UV region. Opsin coding studies indicated UV vision via UVS cones in another psittacine species, the Grey Parrot (*Psittacus erithacus*) (Ödeen & Håstad 2003). After having found so many intensely, UV reflecting feather patches while screening through all the bird Orders, the focus of this study lies on the parrot Order with its 359 species (Sibley & Monroe 1990, 1993, 1996) in order to establish how UV phenomena are distributed. As UV reflection in achromatic feathers only add to overall brightness and therefore white and grey feathers always reflect UV light, the focus of this study is on the chromatic plumage (Eaton & Lanyon 2003). Prescreening has revealed that UV phenomena are present in at least one feather patch in each species (see Chapter 1). In this study, 16 body regions have been selected to cover all the chromatic patches of a species. I wanted to find out if all the parrots have at least one chromatic feather patch exhibiting a UV phenomenon, and, if so, how many (if any) possess UV phenomena in all chromatic feather patches.

The parrot Order is very diverse; it is the third largest bird Order after the Passeriformes and the Ciconiiformes. Parrots mainly live in tropical regions and inhabit dry savannahs, open bushland as well as dense forest from sea level up to 4000 m (Sibley & Monroe 1990). Therefore, another aim of this study is to evaluate whether parrots with many UV phenomena are more likely than expected by chance to be associated with the habitat they live in. Furthermore, do birds, when living at higher altitudes, exhibit more UV phenomena than birds living in lower altitudes? It would be also interesting to know if fluorescence, which was discovered in 30% (109 species) of the parrot species is associated with the quantity of UV phenomena, as fluorescence is known to reduce ultraviolet light reflection in feathers (Pearn *et al.* 2001, Arnold 2002, Hausmann *et al.* 2003, Pearn *et al.* 2003).

Methods

Species considered

The aim of my study was to include all the species of the parrot Order Psittaciformes listed in Table 4.1. Scientific and vernacular names were retrieved from Sibley & Monroe's list (1990) including the corrections published 1993 and 1996. According to their taxonomy there are 347 living species and 12 species which have become extinct during the last three centuries, the list totals 359 species altogether. 335 species (93 %), including six extinct species, were measured by means of reflection spectrophotometry. CITES classifies the remaining 18 parrot species as vulnerable to critically endangered, which explains the absence in most collections. Measurements were conducted on bird skins found in the collections of the following institutions: Alexander Koenig Research Institute and Museum of Zoology in Bonn, Germany, The Natural History Museum in Tring, United Kingdom, the American Museum of Natural History in New York, USA, the Academy of Natural Sciences in Philadelphia, USA, the Australian Museum, Sydney, Australia, and the Queensland Museum, Brisbane, Australia. Where possible, skins less than 20 years old were used to avoid errors due to possible color changes in older museum skins (Endler and Théry 1996, Hausmann *et al.* 2002, McNaught & Owens 2002). I define a bird as having distinctive UV coloration, (which I refer to as UV phenomena) when the spectrum shows a UV reflectance peak greater than 10 %. In order to include species lacking UV peaks, but with high amounts of UV reflecting plumage, I also speak of UV phenomena when any part of the UV reflectance spectrum exceeds the lowest reflection in the range of 400 to 700 nm. On account of this definition, white and light-colored feathers are excluded, despite their ability to reflect high amounts of UV light, which contributes to their overall brightness (see the Method Section in Chapter 1 for the exact procedure). With respect to the visual abilities of the birds, continuous reflection in the whole spectrum is a basic characteristic of white (Vorobyev *et al.* 1998) and significant amounts of UV have been found in nearly all white feathers (Eaton & Lanyon 2003). 16 body regions were measured (Table 4.2) while trying to cover all colors in all plumage patches of a species. Usually, the outer webs of the primaries and secondaries were measured. Only, when the outer webs were achromatic, were the inner webs taken into account. In total 5376 reflectance spectra were measured. Due to sexual dimorphism being absent in the parrot Order, (with very few exceptions such as in the Eclectus Parrot (*Eclectus roratus)*) only one specimen per species was measured.

Fluorescence, habitat selection, altitude and statistics

The data used, concerning the occurrence of fluorescence in parrot species were collected by G. Pohland and P. Mullen in 2006. Parrots are mainland birds. In order to cluster the measured species into distinct habitat types the characterization described in Sibley & Monroe's (1990) work was used as a basis. In order to avoid overlapping, only two habitats were assigned, “forest” and “open” were characterized mainly by the different light environments. Birds assigned to the “Open Habitat” category mainly lived in areas undisturbingly exposed to the sun such as in the case of the savannahs, deserts, or grasslands. But also birds abundant in palm groves, woodland, deciduous forest, and forest edges were assigned to the open light habitat. Birds assigned to the “forest habitat” mainly live in the forest or in habitats with thick undergrowth. Many parrot species live in forests that can also be found in woodland or even in deserts or savannahs. I wanted to segregate the two light habitats as clearly as possible, therefore parrots present in forests as well as in habitats specifically exposed to the sun such as deserts or savannahs were always assigned to the “open” light habitat. Sibley & Monroe's (1990) list was also used for assignment. The analyzed species were again assigned to two different groups, species occurring 2000 m above sea level and species living up to 2000 m and below. Ultraviolet light is more intense at higher altitudes (Dvorkin 1999); the ultraviolet portion of the light spectrum is also known to be proportionately higher than in other light habitats such as, e.g., “open” light habitats. As a statistical approach, I therefore used the Chi^2 test, a non-parametric test defined for the following hypothesis: H_0: there is no significant difference between the found and expected frequencies of UV phenomena within each light habitat, altitude and occurrence of fluorescence. H_1: there is a significant difference. In every discrimination analysis including the habitat and altitude choice as well as in the fluorescence correlation a probability level of 0.5 was assumed. All measured species were taken into account.

Spectrophotometry and UV photography

Feathers and ornaments were measured using reflection spectrophotometry via an Ocean Optics S2000 spectrometer and a pulsed xenon lamp (PX-2). A single fibre-optic probe was used to provide illumination from the light source and the reflected light was transferred to the spectrometer. To exclude external light from the measurement area the probe was mounted in a hard rubber cover. The feathers were checked for UV reflection by measuring at different angles. The angle with the highest UV output was finally taken. Ornaments were considered UV-reflecting when spectrophotometric measurements showed a peak intensity of at least 15 % within the range of 320 – 400 nm. The photos were taken with a Nikon D70 SLR digital body, a camera with a UV sensitive chip, the UV-Nikkor 105 mm lens using the Hoya filter U 360 to block visible light and a Heliopan BG 23 to block infrared light.

Results

Altogether 165 of the 335 parrot species measured (49%), exhibited UV phenomena in all chromatic plumage patches. The White-tailed Black-Cockatoo (*Calyptorhynchus baudinii*) and the Slender-billed Black-Cockatoo (*Calyptorhynchus latirostris*) were the only two species lacking chromatic plumage patches (many white colored cockatoos, such as the White Cockatoo (*Cacatua alba*) have yellow colored patches on the inner webs of their primaries and secondaries). The feathers of 12 parrot species exhibited UV phenomena in black or dark brown plumage patches (Table 4.3). This is interesting because these feathers appear achromatic to humans but colorful to birds, only the UVS receptor being excited. Feathers solely reflecting in the UV are considered rare and are only known from a few bird species (Burkhardt & Finger 1991, Finger 1992, Andersson 1996, Hausmann *et al.* 2002). The distribution of UV phenomena varied, and if you just looked at the parrots' plumage color under normal light conditions, you could not predict the appearance or absence of UV phenomena nor judge the intensity of UV reflection. This can be best demonstrated by means of UV photography (Fig. 4.1 – 4.6). It seemed that most parrots reflected more UV at the front, crown and nape feathers with UV reflection being reduced at the back. Table 4.4 revealed associations between fluorescence, habitat, and altitude correlations between species with many patches reflecting ultraviolet light. There was no significant correlation between species living in the forest light habitat and birds exhibiting UV phenomena on every chromatic plumage patch. Also, the 56 parrot species found in altitudes of more than 2000 m were not significantly correlated with birds exhibiting UV phenomena at every chromatic plumage patch. Therefore, altitude and habitat choice seem to have no effect on the distribution of UV phenomena. However, species possessing fluorescing plumage parts had significantly less UV phenomena $p < 0.001$. Nearly all parrots with violet or deep blue colored feathers, such as found in the Rainbow Lorikeet (*Trichoglossus haematodus*) (Fig. 4.7) exhibited UV phenomena. The only exceptions were parrots from the genera *Loriculus,* the Hanging Parrots, and *Psittacula* and *Platycercus.* Here, many species were highly fluorescing and some fluorescing blue-green feather patches showed hardly any reflection in the UV. This is demonstrated in Fig. 4.8, where the spectrum of the non-UV turquoise, fluorescing throat of the Red-billed Hanging-Parrot (*Loriculus exilis*) shows almost no UV reflection and the UV-green breast feathers of the Festive Parrot (*Amazona festiva*) exhibit high amounts of UV, exhibiting a clear UV phenomenon. However, overall UV reflection in the genus *Pyrrhura* was remarkably low, although, none of the Parakeets had fluorescing body regions.

Table 4.1 Complete list of the world's parrot species. Latin and vernacular names derived from Sibley & Monroe, 1990 (including corrections of 1993 and Sibley 1996). Empty field in last row indicate species exhibiting UV phenomena in all measured chromatic regions. Data on fluorescence in parrot species were gathered by Pohland & Mullen 2006. * = species extinct, n.m. = not measured, a.p. = species with achromatic plumage only, O = open habitat, F = forest habitat

Species	Vernacular name	Habitat	Altitude (m)	Fluores-cence	Lack of UV-phenomena in at least 1 chromatic plumage patch
Agapornis canus	Grey-headed Lovebird	O	0-1000	x	x
Agapornis fischeri	Fischer's Lovebird	O	1100-1700	x	x
Agapornis lilianae	Lilian's Lovebird	O	600-1000	x	x
Agapornis nigrigenis	Black-cheeked Lovebird	O	600-1000	x	x
Agapornis personatus	Yellow-collared Lovebird	O	1100-1700	x	x
Agapornis pullarius	Red-headed Lovebird	O	0-1400	x	x
Agapornis roseicollis	Rosy-faced Lovebird	O	0-1600	x	x
Agapornis swindernianus	Black-collared Lovebird	F	0-1800	x	x
Agapornis taranta	Black-winged Lovebird	F	1300-3200	x	x
Alisterus amboinensis	Moluccan King-Parrot	F	0-1450		x
Alisterus chloropterus	Papuan King-Parrot	F	0-2800		x
Alisterus scapularis	Australian King-Parrot	F	0-1000	x	x
Amazona aestiva	Blue-fronted Parrot	F	0-1000		
Amazona agilis	Black-billed Parrot	F	0-2000	x	
Amazona albifrons	White-fronted Parrot	O	0-2000		
Amazona amazonica	Orange-winged Parrot	O	0-1100		
Amazona arausiaca	Red-necked Parrot	F	500-1500		
Amazona auropalliata	Yellow-naped Parrot	O	0-1000		
Amazona autumnalis	Red-lored Parrot	F	0-1100		
Amazona barbadensis	Yellow-shouldered Parrot	O	0-500		
Amazona brasiliensis	Red-tailed Parrot	F	0-500		
Amazona collaria	Yellow-billed Parrot	F	800-2000		
Amazona dufresniana	Blue-cheeked Parrot	F	1000-1700		
Amazona farinosa	Mealy Parrot	F	0-1100		
Amazona festiva	Festive Parrot	O	0-500		
Amazona finschi	Lilac-crowned Parrot	O	0-500		
Amazona guildingii	St. Vincent Parrot	F	800-2000	x	
Amazona imperialis	Imperial Parrot	F	800-2000		
Amazona kawalli	Kawall's Parrot	F	0-500		
Amazona leucocephala	Cuban Parrot	F	0-500		x
Amazona mercenaria	Scaly-naped Parrot	F	1600-3600		
Amazona ochrocephala	Yellow-crowned Parrot	F	0-1500		
Amazona oratrix	Yellow-headed Parrot	O	0-1500		
Amazona pretrei	Red-spectacled Parrot	F	0-500		
Amazona rhodocorytha	Red-browed Parrot	F	0-500		
Amazona tucumana	Tucuman Parrot	F	1800-2000	x	
Amazona ventralis	Hispaniolan Parrot	F	0-1000		
Amazona versicolor	St. Lucia Parrot	F	500-1500		
Amazona vinacea	Vinaceous Parrot	F	0-500		
Amazona viridigenalis	Red-crowned Parrot	F	0-1000		
Amazona vittata	Puerto Rican Parrot	F	0-500		
Amazona xantholora	Yellow-lored Parrot	O	0-500		
Amazona xanthops	Yellow-faced Parrot	O	0-1500		

Species	Vernacular name	Habitat	Altitude (m)	Fluores-cence	Lack of UV-phenomena in at least 1 chromatic plumage patch
**Anodorhynchus glaucus*	Glaucous Macaw	F	0-500		x
Anodorhynchus hyacinthinus	Hyacinth Macaw	F	0-500		
Anodorhynchus leari	Indigo Macaw	F	500-2000		
Aprosmictus erythropterus	Red-winged Parrot	O	0-1000	x	x
Aprosmictus jonquillaceus	Olive-shouldered Parrot	O	0-2600	x	x
Ara ambigua	Great Green Macaw	F	0-600		x
Ara ararauna	Blue-and-yellow Macaw	F	0-500		x
Ara auricollis	Yellow-collared Macaw	F	0-1500		
Ara chloropterus	Red-and-green Macaw	F	0-1400		x
Ara couloni	Blue-headed Macaw	O	500-2000		
**Ara cubensis*	Cuban Macaw				n.m.
Ara glaucogularis	Blue-throated Macaw	F	500-2000		
Ara macao	Scarlet Macaw	O	0-1000		x
Ara manilata	Red-bellied Macaw	O	0-500		
Ara maracana	Blue-winged Macaw	F	0-500		x
Ara militaris	Military Macaw	O	0-2500		
Ara nobilis	Red-shouldered Macaw	O	0-500		x
Ara rubrogenys	Red-fronted Macaw	F	1300-2400		
Ara severa	Chestnut-fronted Macaw	F	0-1000		
**Ara tricolor*	Hispaniolan Macaw	O	0-1000		
Aratinga acuticaudata	Blue-crowned Parakeet	O	0-400		
Aratinga aurea	Peach-fronted Parakeet	O	0-500		
Aratinga auricapilla	Golden-capped Parakeet	O	0-500		x
Aratinga cactorum	Cactus Parakeet	O	0-500		
Aratinga canicularis	Orange-fronted Parakeet	O	0-1500		
Aratinga chloroptera	Hispaniolan Parakeet	F	0-1000		
Aratinga erythrogenys	Red-masked Parakeet	O	0-2500		
Aratinga euops	Cuban Parakeet	F	0-500		
Aratinga finschi	Crimson-fronted Parakeet	O	0-500		
Aratinga guarouba	Golden Parakeet	F	0-500	x	x
Aratinga holochlora	Green Parakeet	O	0-2200		
Aratinga jandaya	Jandaya Parakeet	O	0-500		x
Aratinga leucophthalmus	White-eyed Parakeet	O	0-500		x
Aratinga mitrata	Mitred Parakeet	F	1000-2600		x
Aratinga nana	Olive-throated Parakeet	F	0-1100		x
Aratinga pertinax	Brown-throated Parakeet	O	0-1600		
Aratinga solstitialis	Sun Parakeet	O	0-1200		x
Aratinga strenua	Pacific Parakeet	O	0-1600		
Aratinga wagleri	Scarlet-fronted Parakeet	F	0-1600		x
Aratinga weddellii	Dusky-headed Parakeet	O	0-500		
Bolbopsittacus lunulatus	Guaiabero	O	0-500	x	x
Bolborhynchus aurifrons	Mountain Parakeet	O	0-4000		
Bolborhynchus aymara	Grey-hooded Parakeet	O	1700-4000		
Bolborhynchus ferrugineifrons	Rufous-fronted Parakeet	O	3000-3800		x
Bolborhynchus lineola	Barred Parakeet	O	750-3000	x	x
Bolborhynchus orbygnesius	Andean Parakeet	O	1200-6250		x

Species	Vernacular name	Habitat	Altitude (m)	Fluores-cence	Lack of UV-phenomena in at least 1 chromatic plumage patch
Brotogeris chiriri	Yellow-chevroned Parakeet	O	0-1560	x	
Brotogeris chrysopterus	Golden-winged Parakeet	O	0-1200	x	
Brotogeris cyanoptera	Cobalt-winged Parakeet	O	0-500	x	x
Brotogeris jugularis	Orange-chinned Parakeet	O	0-1400	x	x
Brotogeris pyrrhopterus	Grey-cheeked Parakeet	O	0-500		x
Brotogeris sanctithomae	Tui Parakeet	O	0-100		
Brotogeris tirica	Plain Parakeet	O	0-500		
Brotogeris versicolurus	Canary-winged Parakeet	O	0-300		
Cacatua alba	White Cockatoo	F	0-1500	x	x
Cacatua ducorpsii	Ducorps's Cockatoo	F	0-1500	x	x
Cacatua galerita	Sulphur-crested Cockatoo	O	0-1450	x	
Cacatua goffini	Tanimbar Cockatoo	O	0-500	x	x
Cacatua haematuropygia	Philippine Cockatoo	F	0-1500	x	x
Cacatua leadbeateri	Pink Cockatoo	O	0-500	x	x
Cacatua moluccensis	Salmon-crested Cockatoo	F	0-1500	x	
Cacatua ophthalmica	Blue-eyed Cockatoo	F	0-1000	x	x
Cacatua pastinator	Western Corella	O	0-1000	x	
Cacatua sanguinea	Little Corella	O	0-1000	x	x
Cacatua sulphurea	Yellow-crested Cockatoo	O	0-1200	x	x
Cacatua tenuirostris	Long-billed Corella	O	0-1000	x	x
Callocephalon fimbriatum	Gang-gang Cockatoo	F	0-2000	x	x
Calyptorhynchus banksii	Red-tailed Black-Cockatoo	O	0-1000	x	x
Calyptorhynchus baudinii	White-tailed Black-Cockatoo	F	0-500		a.p.
Calyptorhynchus funereus	Yellow-tailed Black-Cockatoo	F	0-1000	x	x
Calyptorhynchus lathami	Glossy Black-Cockatoo	F	0-500		
Calyptorhynchus latirostris	Slender-billed Black-Cockatoo	O	0-500		a.p.
Chalcopsitta atra	Black Lory	O	0-1000		
Chalcopsitta cardinalis	Cardinal Lory	F	0-1000		x
Chalcopsitta duivenbodei	Brown Lory	F	0-200		
Chalcopsitta sintillata	Yellow-streaked Lory	O	0-500		
Charmosyna amabilis	Red-throated Lorikeet	F	1000-2500		
Charmosyna diadema	New Caledonian Lorikeet				n.m.
Charmosyna josefinae	Josephine's Lorikeet	F	750-2200		
Charmosyna margarethae	Duchess Lorikeet	F	0-1350		
Charmosyna meeki	Meek's Lorikeet	F	500-2500		
Charmosyna multistriata	Striated Lorikeet	F	200-1800	x	x
Charmosyna palmarum	Palm Lorikeet	F	0-1000		
Charmosyna papou	Papuan Lorikeet	F	1450-3000		
Charmosyna placentis	Red-flanked Lorikeet	O	0-500		x
Charmosyna pulchella	Fairy Lorikeet	F	800-2100		
Charmosyna rubrigularis	Red-chinned Lorikeet	F	0-1500		
Charmosyna rubronotata	Red-fronted Lorikeet	F	0-850		
Charmosyna toxopei	Blue-fronted Lorikeet				n.m.
Charmosyna wilhelminae	Pygmy Lorikeet	F	500-2200		
**Conuropsis carolinensis*	Carolina Parakeet	O	0-1000		x

Species	Vernacular name	Habitat	Altitude (m)	Fluores-cence	Lack of UV-phenomena in at least 1 chromatic plumage patch
Coracopsis nigra	Black Parrot	O	0-500		
Coracopsis vasa	Vasa Parrot	O	0-1000		
Cyanoliseus patagonus	Burrowing Parakeet	O	0-1900		x
**Cyanopsitta spixii*	Little Blue Macaw	O	0-500		x
Cyanoramphus auriceps	Yellow-fronted Parakeet	F	0-2000	x	x
Cyanoramphus cookii	Norfolk Island Parakeet	F	0-500		
Cyanoramphus novaezelandiae	Red-fronted Parakeet	F	0-1000		x
**Cyanoramphus ulietanus*	Raiatea Parakeet				n.m.
Cyanoramphus unicolor	Antipodes Parakeet	O	0-500	x	
**Cyanoramphus zealandicus*	Black-fronted Parakeet				n.m.
Cyclopsitta diophthalma	Double-eyed Fig-Parrot	F	0-1600	x	x
Cyclopsitta gulielmitertii	Orange-breasted Fig-Parrot	O	0-800	x	x
Deroptyus accipitrinus	Red-fan Parrot	O	0-400		x
Eclectus roratus, female	Eclectus Parrot, female	O	0-1700		x
Eclectus roratus, male	Eclectus Parrot, male	O	0-1700		x
Enicognathus ferrugineus	Austral Parakeet	F	0-500		x
Enicognathus leptorhynchus	Slender-billed Parakeet	F	0-500		x
Eolophus roseicapillus	Galah	O	0-1000		
Eos bornea	Red Lory	F	0-1250		x
Eos cyanogenia	Black-winged Lory	O	0-500		
Eos histrio	Red-and-blue Lory	F	0-500		x
Eos reticulata	Blue-streaked Lory	F	0-500		
Eos semilarvata	Blue-eared Lory				n.m.
Eos squamata	Violet-necked Lory	O	0-500		
Eunymphicus cornutus	Horned Parakeet	F	0-500		
Forpus coelestis	Pacific Parrotlet	O	0-500		
Forpus conspicillatus	Spectacled Parrotlet	O	0-2000		
Forpus cyanopygius	Mexican Parrotlet	O	0-1320		
Forpus passerinus	Green-rumped Parrotlet	O	0-1800		
Forpus sclateri	Dusky-billed Parrotlet	O	0-500	x	x
Forpus xanthops	Yellow-faced Parrotlet	O	1700-1750		
Forpus xanthopterygius	Blue-winged Parrotlet	O	0-500		
Geoffroyus geoffroyi	Red-cheeked Parrot	O	0-1400	x	x
Geoffroyus heteroclitus	Singing Parrot	F	0-500		
Geoffroyus simplex	Blue-collared Parrot	F	800-2300	x	x
Geopsittacus occidentalis	Night Parrot	O	0-500	x	x
Glossopsitta concinna	Musk Lorikeet	O	0-500		
Glossopsitta porphyrocephala	Purple-crowned Lorikeet	F	0-500		x
Glossopsitta pusilla	Little Lorikeet	O	0-500		x
Graydidascalus brachyurus	Short-tailed Parrot	F	0-400		
Gypopsitta vulturina	Vulturine Parrot	F	0-500		
Hapalopsittaca amazonina	Rusty-faced Parrot	F	2000-3600		

Species	Vernacular name	Habitat	Altitude (m)	Fluorescence	Lack of UV-phenomena in at least 1 chromatic plumage patch
Hapalopsittaca fuertesi	Indigo-winged Parrot				n.m.
Hapalopsittaca melanotis	Black-winged Parrot	F	2500-3100		
Hapalopsittaca pyrrhops	Red-faced Parrot	F	1000-2500		
Lathamus discolor	Swift Parrot	O	0-500		x
Leptosittaca branickii	Golden-plumed Parakeet	F	1800-3500		
Loriculus amabilis	Moluccan Hanging-Parrot	O	0-500	x	x
Loriculus aurantiifrons	Orange-fronted Hanging-Parrot	F	0-1200	x	x
Loriculus beryllinus	Ceylon Hanging-Parrot	O	0-1600	x	x
Loriculus catamene	Sangihe Hanging-Parrot	O	0-500		x
Loriculus exilis	Red-billed Hanging-Parrot	F	0-800	x	x
Loriculus flosculus	Wallace's Hanging-Parrot				n.m.
Loriculus galgulus	Blue-crowned Hanging-Parrot	O	0-1250	x	x
Loriculus philippensis	Colasisi	F	0-2500	x	x
Loriculus pusillus	Yellow-throated Hanging-Parrot	F	0-1800	x	
Loriculus stigmatus	Sulawesi Hanging-Parrot	O	0-800	x	x
Loriculus tener	Green-fronted Hanging-Parrot				n.m.
Loriculus vernalis	Vernal Hanging-Parrot	O	0-2000	x	x
Lorius albidinuchus	White-naped Lory				n.m.
Lorius chlorocercus	Yellow-bibbed Lory	F	0-500		
Lorius domicella	Purple-naped Lory	F	500-700		
Lorius garrulus	Chattering Lory	F	0-500		x
Lorius hypoinochrous	Purple-bellied Lory	F	0-500		x
Lorius lory	Black-capped Lory	F	0-1750		x
*_Mascarinus mascarinus_	Mascarene Parrot				n.m.
Melopsittacus undulatus	Budgerigar	O	0-500	x	x
Micropsitta bruijnii	Red-breasted Pygmy-Parrot	F	1000-2300	x	x
Micropsitta finschii	Finsch's Pygmy-Parrot	F	0-750	x	
Micropsitta geelvinkiana	Geelvink Pygmy-Parrot	F	0-500	x	x
Micropsitta keiensis	Yellow-capped Pygmy-Parrot	F	0-500	x	x
Micropsitta meeki	Meek's Pygmy-Parrot				n.m.
Micropsitta pusio	Buff-faced Pygmy-Parrot	F	0-850	x	x
Myiopsitta monachus	Monk Parakeet	O	0-1560		
Nandayus nenday	Nanday Parakeet	O	0-500		
Nannopsittaca dachilleae	Amazonian Parrotlet				n.m.
Nannopsittaca panychlora	Tepui Parrotlet	F	750-1850		
Neophema chrysogaster	Orange-bellied Parrot	O	0-500	x	
Neophema chrysostoma	Blue-winged Parrot	O	0-500	x	x
Neophema elegans	Elegant Parrot	O	0-500	x	x
Neophema petrophila	Rock Parrot	O	0-500		x
Neophema pulchella	Turquoise Parrot	O	0-1000	x	x
Neophema splendida	Scarlet-chested Parrot	O	0-500	x	x
Neopsephotus bourkii	Bourke's Parrot	O	0-500		

Species	Vernacular name	Habitat	Altitude (m)	Fluores-cence	Lack of UV-phenomena in at least 1 chromatic plumage patch
Neopsittacus musschenbroekii	Yellow-billed Lorikeet	F	1100-3000		
Neopsittacus pullicauda	Orange-billed Lorikeet	F	2100-3800		
Nestor meridionalis	New Zealand Kaka	F	0-1000		
Nestor notabilis	Kea	O	1250-2500		
**Nestor productus*	Norfolk Island Kaka	O	0-500		
Northiella haematogaster	Bluebonnet	O	0-1000	x	x
Nymphicus hollandicus	Cockatiel	O	0-1500	x	
Ognorhynchus icterotis	Yellow-eared Parrot	F	2000-3400		
Oreopsittacus arfaki	Plum-faced Lorikeet	F	2000-3000		
Pezoporus wallicus	Ground Parrot	O	0-500		x
Phigys solitarius	Collared Lory	O	0-1000		
Pionites leucogaster	White-bellied Parrot	F	0-1500	x	x
Pionites melanocephala	Black-headed Parrot	O	0-1100	x	x
Pionopsitta barrabandi	Orange-cheeked Parrot	F	0-500		
Pionopsitta caica	Caica Parrot	F	0-1100		x
Pionopsitta haematotis	Brown-hooded Parrot	F	0-3100		x
Pionopsitta pileata	Pileated Parrot	F	0-500		
Pionopsitta pulchra	Rose-faced Parrot	F	0-2100		x
Pionopsitta pyrilia	Saffron-headed Parrot	F	0-1700		
Pionus chalcopterus	Bronze-winged Parrot	F	1400-2800		
Pionus fuscus	Dusky Parrot	F	0-1800		
Pionus maximiliani	Scaly-headed Parrot	F	0-500		
Pionus menstruus	Blue-headed Parrot	F	0-1500		
Pionus senilis	White-crowned Parrot	O	0-1600		x
Pionus sordidus	Red-billed Parrot	F	300-2200		x
Pionus tumultuosus	Speckle-faced Parrot	F	1200-3000		
Platycercus adscitus	Pale-headed Rosella	O	0-1500	x	x
Platycercus barnardi	Mallee Ringneck	O	0-1500	x	x
Platycercus caledonicus	Green Rosella	F	0-1000	x	x
Platycercus elegans	Crimson Rosella	F	0-1000	x	x
Platycercus eximius	Eastern Rosella	O	0-1000	x	x
Platycercus flaveolus	Yellow Rosella	O	0-1000	x	x
Platycercus icterotis	Western Rosella	O	0-1000	x	x
Platycercus venustus	Northern Rosella	O	0-1000	x	x
Platycercus zonarius	Port Lincoln Ringneck	F	0-1000	x	x
Poicephalus crassus	Niam-niam Parrot				n.m.
Poicephalus cryptoxanthus	Brown-headed Parrot	O	0-1000		
Poicephalus flavifrons	Yellow-fronted Parrot	F	1000-3000		
Poicephalus gulielmi	Red-fronted Parrot	F	0-3500		x
Poicephalus meyeri	Meyer's Parrot	O	0-1250		
Poicephalus robustus	Brown-necked Parrot	F	0-1000		x
Poicephalus rueppellii	Rueppell's Parrot	O	0-1250		
Poicephalus rufiventris	Red-bellied Parrot	O	0-2000		
Poicephalus senegalus	Senegal Parrot	O	0-2000		
Polytelis alexandrae	Alexandra's Parrot	O	0-1000	x	
Polytelis anthopeplus	Regent Parrot	O	0-1000	x	

Species	Vernacular name	Habitat	Altitude (m)	Fluores-cence	Lack of UV-phenomena in at least 1 chromatic plumage patch
Polytelis swainsonii	Superb Parrot	O	0-1000	x	x
Prioniturus discurus	Blue-crowned Racquet-tail	F	0-1750	x	x
Prioniturus flavicans	Yellowish-breasted Racquet-tail	F	0-1000	x	x
Prioniturus luconensis	Green Racquet-tail	F	0-1000		x
Prioniturus mada	Buru Racquet-tail				n.m.
Prioniturus montanus	Montane Racquet-tail	F	1000-2500	x	x
Prioniturus platenae	Blue-headed Racquet-tail	F	850-1700		x
Prioniturus platurus	Golden-mantled Racquet-tail	F	0-500	x	x
Prioniturus verticalis	Blue-winged Racquet-tail				n.m.
Prioniturus waterstradti	Mindanao Racquet-tail				n.m.
Probosciger aterrimus	Palm Cockatoo	F	0-1300		x
Prosopeia personata	Masked Shining-Parrot	F	0-2500		x
Prosopeia splendens	Crimson Shining-Parrot	F	0-2500		x
Prosopeia tabuensis	Red Shining-Parrot	F	0-2500		x
Psephotus chrysopterygius	Golden-shouldered Parrot	O	0-500	x	x
Psephotus dissimilis	Hooded Parrot	O	0-500	x	x
Psephotus haematonotus	Red-rumped Parrot	O	0-1000	x	x
*_Psephotus pulcherrimus_	Paradise Parrot	O	0-500	x	x
Psephotus varius	Mulga Parrot	O	0-500	x	x
Pseudeos fuscata	Dusky Lory	O	0-1800		
Psittacella brehmii	Brehm's Tiger-Parrot	O	1150-2800		x
Psittacella madaraszi	Madarasz's Tiger-Parrot	O	1200-2500		x
Psittacella modesta	Modest Tiger-Parrot	F	1700-2800		x
Psittacella picta	Painted Tiger-Parrot	F	2500-4000		x
Psittacula alexandri	Red-breasted Parakeet	F	0-1500	x	x
Psittacula calthropae	Layard's Parakeet	F	0-2000	x	x
Psittacula caniceps	Nicobar Parakeet	F	0-500	x	
Psittacula columboides	Malabar Parakeet	F	0-1500	x	x
Psittacula cyanocephala	Plum-headed Parakeet	O	0-1800	x	x
Psittacula derbiana	Derbyan Parakeet	O	2800-4000	x	x
Psittacula echo	Mauritius Parakeet				n.m.
Psittacula eupatria	Alexandrine Parakeet	F	0-1800	x	x
*_Psittacula exsul_	Newton's Parakeet				n.m.
Psittacula finschii	Grey-headed Parakeet	F	500-3600	x	
Psittacula himalayana	Slaty-headed Parakeet	F	500-2500	x	
Psittacula intermedia	Intermediate Parakeet				n.m.
Psittacula krameri	Rose-ringed Parakeet	O	0-1800	x	x
Psittacula longicauda	Long-tailed Parakeet	O	0-350	x	
Psittacula roseata	Blossom-headed Parakeet	O	0-900	x	
*_Psittacula wardi_	Seychelles Parakeet				n.m.
Psittaculirostris desmarestii	Large Fig-Parrot	O	0-1500	x	x
Psittaculirostris edwardsii	Edwards's Fig-Parrot	F	0-800	x	x
Psittaculirostris salvadorii	Salvadori's Fig-Parrot	F	0-400	x	x
Psittacus erithacus	Grey Parrot	O	0-2000		
Psitteuteles goldiei	Goldie's Lorikeet	F	1400-2800		

Species	Vernacular name	Habitat	Altitude (m)	Fluores-cence	Lack of UV-phenomena in at least 1 chromatic plumage patch
Psitteuteles iris	Iris Lorikeet	F	0-1500		
Psitteuteles versicolor	Varied Lorikeet	O	0-1000		x
Psittinus cyanurus	Blue-rumped Parrot	F	0-500		
Psittrichas fulgidus	Pesquet's Parrot	F	1000-2000		x
Purpureicephalus spurius	Red-capped Parrot	O	0-1000	x	
Pyrrhura albipectus	White-necked Parakeet	F	0-1000		
Pyrrhura calliptera	Brown-breasted Parakeet	F	1700-3400		x
Pyrrhura cruentata	Blue-throated Parakeet	F	0-500		x
Pyrrhura devillei	Blaze-winged Parakeet	F	0-1000		
Pyrrhura egregia	Fiery-shouldered Parakeet	F	700-1800		
Pyrrhura frontalis	Maroon-bellied Parakeet	F	0-1500		x
Pyrrhura hoematotis	Red-eared Parakeet	O	1200-2000		x
Pyrrhura hoffmanni	Sulphur-winged Parakeet	F	700-3000		x
Pyrrhura leucotis	White-eared Parakeet	F	0-500		x
Pyrrhura melanura	Maroon-tailed Parakeet	F	0-1950		x
Pyrrhura molinae	Green-cheeked Parakeet	F	0-2000		x
Pyrrhura orcesi	El Oro Parakeet	F	600-1000		x
Pyrrhura perlata	Crimson-bellied Parakeet	F	0-500		
Pyrrhura picta	Painted Parakeet	F	0-2000		x
Pyrrhura rhodocephala	Rose-headed Parakeet	F	800-3050		x
Pyrrhura rupicola	Black-capped Parakeet	F	0-300		
Pyrrhura viridicata	Santa Marta Parakeet				n.m.
Rhynchopsitta pachyrhyncha	Thick-billed Parrot	O	1500-3400		x
Rhynchopsitta terrisi	Maroon-fronted Parrot	O	1800-3100		x
Strigops habroptilus	Kakapo	O	0-1250		x
Tanygnathus gramineus	Black-lored Parrot				n.m.
Tanygnathus lucionensis	Blue-naped Parrot	F	0-1000	x	
Tanygnathus megalorynchos	Great-billed Parrot	O	0-500	x	
Tanygnathus sumatranus	Blue-backed Parrot	F	0-500		
Touit batavica	Lilac-tailed Parrotlet	F	0-1700		x
Touit costaricensis	Red-fronted Parrotlet				n.m.
Touit dilectissima	Blue-fronted Parrotlet	F	0-1720		x
Touit huetii	Scarlet-shouldered Parrotlet	F	0-400		x
Touit melanonotus	Brown-backed Parrotlet	F	0-500		x
Touit purpurata	Sapphire-rumped Parrotlet	O	0-400		
Touit stictoptera	Spot-winged Parrotlet	F	600-2300		x
Touit surda	Golden-tailed Parrotlet	F	0-2000		
Trichoglossus chlorolepidotus	Scaly-breasted Lorikeet	O	0-500		
Trichoglossus euteles	Olive-headed Lorikeet	F	0-2300		
Trichoglossus flavoviridis	Yellow-and-green Lorikeet	F	500-2000		
Trichoglossus haematodus	Rainbow Lorikeet	F	0-1400		
Trichoglossus johnstoniae	Mindanao Lorikeet	F	1000-2500		
Trichoglossus ornatus	Ornate Lorikeet	O	0-1000		
Trichoglossus rubiginosus	Pohnpei Lorikeet	O	0-300		

Species	Vernacular name	Habitat	Altitude (m)	Fluores-cence	Lack of UV-phenomena in at least 1 chromatic plumage patch
Trichoglossus rubritorquis	Red-collared Lorikeet	F	0-500		
Triclaria malachitacea	Blue-bellied Parrot	F	0-500		
Vini australis	Blue-crowned Lorikeet	O	0-500		
Vini kuhlii	Kuhl's Lorikeet	O	0-500		
Vini peruviana	Blue Lorikeet	O	0-500		
Vini stepheni	Stephen's Lorikeet	O	0-500		
Vini ultramarina	Ultramarine Lorikeet	O	0-500		x

Table 4.2 Measurement chart used in reflection spectrophotometry in the parrot Order.

Body region	Sequence (= file extension)
forehead	001
crown	002
nape	003
back	004
rump	005
uppertail coverts	006
tail, middle part	007
tail, tip	008
throat	009
breast	010
belly	011
undertail coverts	012
wrist + Alula	013
greater upper wing coverts	014
secondaries (outer web)	015
primaries (outer web)	016

Table 4.3 Parrot species with UV phenomena in achromatic feathers.

Species	Color	Body region
Alisterus scapularis	black	006, 007, 008
Amazona brasiliensis	black	007
Chalcopsitta atra	black	every region
Chalcopsitta duivenbodei	brown	every region
Charmosyna josefinae	black	002, 003, 006, 012
Charmosyna margarethae	black	002, 003
Charmosyna pulchella	black	002, 003
Neophema elegans	black	016
Pionus tumultuosus	black	008
Polytelis anthopeplus	black	016
Pseudeos fuscata	black, brown	every region
Trichoglossus haematodus	deep-blue black	003


Fig. 4.1 Scarlet Macaw (*Ara macao*) in sunlight.


Fig. 4.2 Scarlet Macaw (*Ara macao*) in B&W.


Fig. 4.3 Scarlet Macaw (*Ara macao*) in UV light.


Fig. 4.4 Red-winged Parrot (*Aprosmictus erythropterus*) in B&W.


Fig. 4.5 Red-winged Parrot (*Aprosmictus erythropterus*) in sunlight.


Fig. 4.6 Red-winged Parrot (*Aprosmictus erythropterus*) in UV light.


Fig. 4.7 Rainbow Lorikeet (*Trichoglossus haematodus*) Blue feathers are nearly always blue-UV.

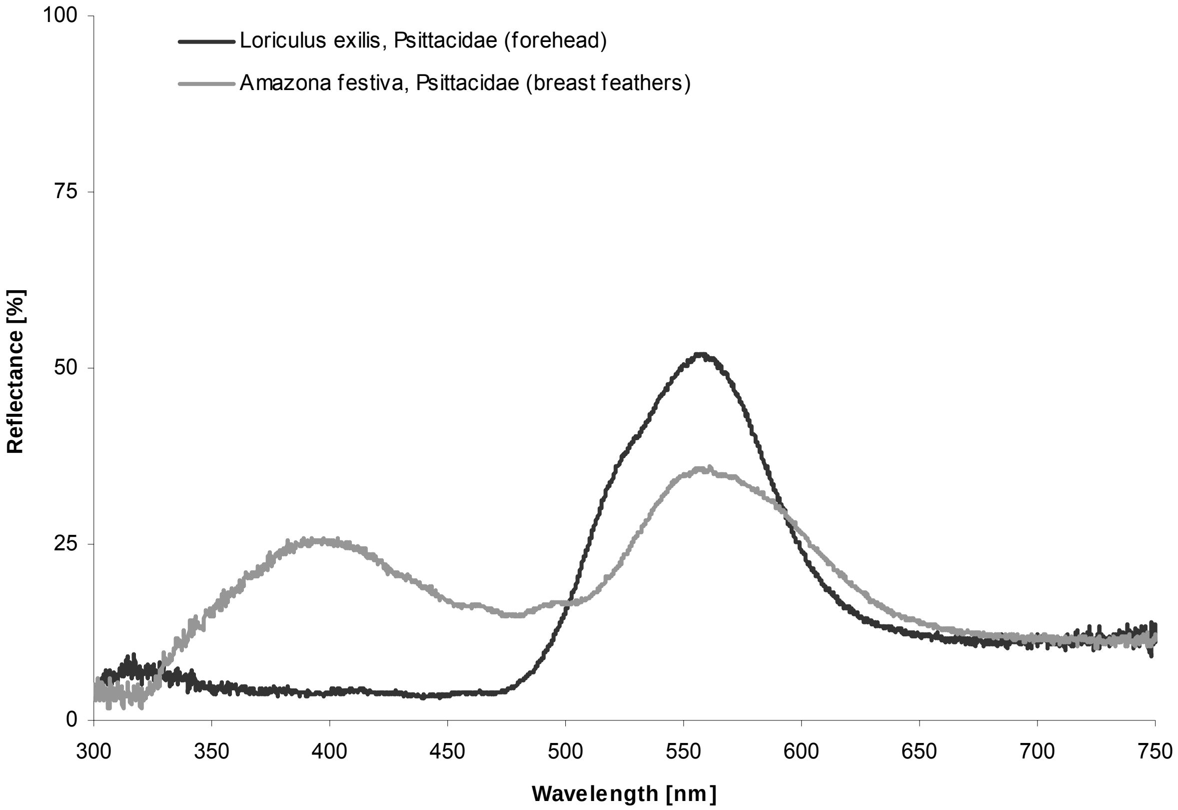

Fig. 4.8 Spectrum of the non-UV turquoise, fluorescing throat of *Loriculus exilis.* The UV-green breast feathers of *Amazona festiva* exhibit high amounts of UV reflectionand show a clear UV phenomenon.

Table 4.4 The Chi^2 test was performed on parrot species in which all chromatic plumage patches exhibit UV phenomena and parrots lacking UV phenomena in at least one chromatic plumage patch – correlated with habitat, altitude and fluorescence.

	Forest habitat	Open habitat	Parrots found at an altitude > 2000 m	Fluorescence
No. of species with at least 1 chromatic plumage patch lacking UV phenomena (taken from Table 4.3)	89	79	27	75
No. of species in which all chromatic plumage patches exhibit UV phenomena (taken from Table 4.3)	91	74	29	22
p-value	0.881	0.686	0.789	< 0.001

Discussion

Although I did not manage to measure all the parrot species, the quantity of UV phenomena found in the Psittaciformes is remarkable. 14 of the 18 living parrot species not measured have at least one distinct blue feather patch, and because blue feathers nearly always reflect UV it is most probable that these parrots have at least one plumage patch exhibiting a UV phenomenon. Species whose plumage exhibited high quantities of UV phenomena were thought to be found more frequently in forests. This is due to the assumption that UV may be a good medium for signaling over short distances as UV is more rapidly degraded over long distances than longer wavelengths due to particle scatter (Andersson 1996, Hausmann *et al.* 2003). It has also been assumed that UV reflective plumage would be more effective to act as a signal in a UV richer environment, such as at high altitudes. But because there is no correlation between UV phenomena quantity and habitat selection or altitudinal occurrence, it seems that UV phenomena are a plesiomorphic trait in the parrot Order, an original character, probably found in the most ancestral forms. My results support Nemésio's assumption (2001) who suggested that the feather structure that enables birds to reflect blue light are plesiomorph. He claims that this structure might be a synapomorphy of the Psittaciformes and the Passeriformes which have previously been suggested to be sister groups. This could also be the case with UV phenomena which are also structural based and are nearly always associated with blue coloring. Fluorescence is significantly, positively associated with species possessing non-UV chromatic plumage patches. Blue and blue-green (turquoise) feathers often reflected considerable amounts of ultraviolet light. Sometimes, not always, non-UV blue and non-UV blue-green feather patches fluoresce. Some parrot species, such as the Philippine Hanging Parrot (*Loriculus philippinensis*), were the only exceptions where blue feathers exhibited no UV light at all. All of these particular feather patches showed strong fluorescence when illuminated with a UV-lamp. Many of them lie adjacent to strongly UV-reflective plumage parts, such as the violet-UV colored cheek feathers and the yellow fluorescent crown feathers of the Budgerigar. Probably the main evolutionary drive for this lies not in developing fluorescence itself but in the strong contrast between UV-reflecting and non-UV-reflecting plumage, such as is found in the Budgerigar, as has been proposed in earlier studies (Pearn *et al.* 2001, Eaton & Lanyon 2003, Hausmann *et al.* 2003). To date there is evidence for only two of the 347 living parrot species being able to see ultraviolet light (via UVS cones) – the Budgerigar and the Grey Parrot. The high quantity of UV reflecting chromatic feather patches found in this Order supports evidence that UV vision is frequent and it would be promising to conduct further UV vision related behavioral experiments on more parrot species. It also would be interesting to know if UV phenomena in parrots are used as signals in courtship behavior and if they are, are if they also serve as indicators for male fitness or quality as found in birds with UV reflecting plumage of other bird Orders (Borgia 1986, Keyser & Hill 1999, Doucet & Montgomerie 2003).

Summary

All of the 347 living parrot species but 18 were measured at 16 different body regions by means of reflection spectrophotometry. Every parrot species possessing chromatic plumage patches exhibited considerable amounts of ultraviolet light in at least one plumage patch. 50 % of the measured species exhibited considerable amounts of UV light in all chromatic plumage patches. No significant correlation was found between parrots which were UV reflective in all chromatic plumage patches and their occurrence in UV rich habitats such as in high altitudes and forests. Parrots possessing fluorescing plumage regions did not exhibit UV reflections in all chromatic plumage patches significantly. It is suggested that UV phenomena are a plesiomorph trait in the parrot Order. This special morphology in the feather structure can probably be found in the most ancestral forms.

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5. Are UV reflections in hummingbirds altitude-dependent?

Introduction

The White-vented Violet-ear (*Colibri serrirostris*) was the first avian taxon for which ultraviolet light perception was experimentally demonstrated (Huth & Burkhardt 1972). Though it is still not known whether hummingbirds perceive ultraviolet light through a VS or a UVS cone, several studies on trochilid visual abilities were conducted. Evidence was found for the detection of ultraviolet light in three additional species (Goldsmith & Goldsmith 1979, Goldsmith 1980, Goldsmith *et al.* 1981). These, the Black-chinned Hummingbird (*Archilochus alexandri*), the Blue-throated Hummingbird (*Lampornis clemenciae*), and the Magnificent Hummingbird (*Eugenes fulgens*) were trained to make visual discriminations between lights of different spectral composition (Goldsmith 1980). The iridescent colors in hummingbird feathers are of structural origin and caused by interference of different sized layers. It was found that the surface of the colored barbules consisted of a mosaic of colored elliptical. Thin elliptical melanin bodies filled with air bubbles form a non-homogenous layer. Two different structures are necessary to create interference. In hummingbirds these are the mosaic-like structures in the upper surface of the barbules and the air-containing cells of the platelets (Rensch 1927, Greenewalt 1960). The density of hummingbird species is highest in tropical regions. They live in regions as diverse as savannahs, open bushland but also thickets and cloud forests (Schuchmann 1999). Hummingbirds are known to inhabit extremly high altitudes, with several Andean species occuring in the páramo with exceeding altitudes of 5000 m (Pearson 1953, Schuchmann & Abersfelder 1986, Schuchmann *et al.* 2000).

With the exception of very few studies which included only a minority of trochilid species (Bleiweiss 1994, Eaton & Lanyon 2003), hummingbirds have never been subject to superior reflection spectrophotometric examinations. Bleiweiss (1994) conducted UV-related research on three species of sunangels (*Heliangelus* spp.). His findings show the presence of UV reflecting patches at the gorgets of male and male-like females indicating that the resemblance extends into the UV, which supports the hypothesis that they have evolved a convergent resemblance.

Hausmann *et al.* (2002) have found many UV reflections particularly in iridescent colored plumage patches although not having measured a single hummingbird species. Therefore, in this study I focus on the trochilid Order with c. 328 species with the majority possessing iridescent feathers in order to establish how UV phenomena are distributed. Furthermore, another aim of this study is to evaluate whether hummingbirds with many UV phenomena are more likely than expected by chance to be associated with the habitat they live in. Furthermore, do trochilids, inhabiting higher altitudes, exhibit UV phenomena compared to birds living in lower altitudes?

Methods

Species considered

The aim of my study was to include all the species of the hummingbird Order Trochiliformes. Scientific and vernacular names were retrieved from the Handbook of the Birds of the World, Volume 5 (Schuchmann 1999). 311 of the 328 species (95 %) were measured by means of reflection spectrophotometry. Measurements were conducted on bird skins found in the collections of the following institutions: Alexander Koenig Research Institute and Museum of Zoology in Bonn, Germany; The Natural History Museum in Tring, United Kingdom; the American Museum of Natural History in New York, USA, and the Academy of Natural Sciences in Philadelphia, USA. Where possible, skins less than 20 years old were used to avoid errors due to possible color changes in older museum skins (Endler & Théry 1996, Hausmann *et al.* 2002, McNaught & Owens 2002). I define a bird as having distinctive UV coloration, when the spectrum shows a UV reflectance peak greater than 10 %. In order to include species lacking UV peaks, but with high amounts of UV reflecting plumage, I also speak of UV phenomena when any part of the UV reflectance spectrum exceeds the lowest reflection in the range of 400 to 700 nm (see the Method Section in Chapter 1 for the exact procedure). With respect to the visual abilities of the birds, continuous reflection in the whole spectrum is a basic characteristic of white (Vorobyev *et al.* 1998) and significant amounts of UV have been found in nearly all white feathers (Eaton & Lanyon 2003). All colors in all plumage patches of a species were measured. Sexual dimorphism is a common trait in the hummingbird Order, when available female specimens were included in the study.

Habitat selection, altitude, and statistics

In order to cluster the measured species into distinct habitat types the characterization described in the “Handbook of the Birds of the World,” Volume 5 (Schuchmann 1999) was used as a basis. To avoid overlapping, only two habitats were assigned, “forest” and “open” which were characterized mainly by the different light environments. Birds assigned to the “open habitat” category mainly lived in areas undisturbingly exposed to the sun such as in the case of savannahs, deserts, or páramo/puna grasslands. But also birds abundant in woodland, deciduous forest, and forest edges were assigned to the open light habitat. Birds assigned to the “forest habitat” mainly live in the forest or in habitats with thick undergrowth. Analogous to the habitat classification accomplished with the parrots (see Chapter 4) I wanted to segregate the two light habitats as clearly as possible, therefore hummingbirds present in forests as well as in habitats specifically exposed to the sun such as rocky slopes or savannahs were always assigned to the “open” light habitat. The “Handbook of the Birds of the World,” Volume 5 (Schuchmann 1999) was also used for assignment. The analyzed species were again designated to two different groups, species living up to 2000 m and below and species also occurring 2000 m above sea level. Ultraviolet light is more intense at higher altitudes (Hailmann 1977, Andersson 1996, Dvorkin 1999). The ultraviolet portion of the light spectrum is also known to be proportionately higher than in other light habitats, such as, e.g., “open” light habitats. As a statistical approach, I used the Chi^2 test, a non-parametric test.

The following hypotheses were defined: H_0: there is no significant difference between the found and expected occurrence of birds possessing UV phenomena in the light habitats and different altitudes. H_1: there is a significant difference. Of the 328 hummingbird species 165 only occur below 2000 m and 163 can also be found above 2000 m. Therefore, in the discrimination analysis I first checked altidunilal distribution (probability level of 0.5) and second habitat occurence of taxa (probability level 0.5).

Spectrophotometry and UV photography

Feathers and ornaments were measured using reflection spectrophotometry via an Ocean Optics S2000 spectrometer and a pulsed xenon lamp (PX-2). A single fibre-optic probe was used to provide illumination from the light source and the reflected light was transferred to the spectrometer. To exclude external light from the measurement area the probe was mounted in a hard rubber cover. The feathers were checked for UV reflection by measuring at different angles. The angle with the highest UV output was finally taken. Ornaments were considered UV-reflecting when spectrophotometric measurements showed a peak intensity of at least 10 % within the range of 320 – 400 nm. The photos were taken with a Nikon D70 SLR digital body, a camera with a UV sensitive chip, the UV-Nikkor 105 mm lens using the Hoya filter U 360 to block visible light and a Heliopan BG 23 to block infrared light.

Results

29 of the 311 hummingbird species measured (9%), exhibited UV phenomena in at least one plumage patch (Table 5.1). The distribution of UV phenomena varied, and just by looking at the hummingbirds’ different colored feather patches under normal light conditions, the appearance or absence of UV phenomena could not be predicted. Neither could the intensity of UV reflections be judged. This is best demonstrated by means of UV photography (Fig. 5.1 – 5.3): Whereas the iridescent green breast feathers of the Sparkling Violet-ear (*Colibri coruscans*) do not reflect ultraviolet light, the blue throat feathers, which appear much darker to the human observer, exhibit a bright UV phenomenon (Fig. 5.3). The Green-breasted Mango (*Anthracothorax prevostii*) was included for comparative reasons to demonstrate the absence of UV phenomena in the dark blue breast and throat. The UV reflecting patches were predominantly found at the head, with forehead and throat feathers dominating. The Saw-billed Hermit (*Ramphodon naevius*) was the only hummingbird found to possess UV phenomena at its retrices. Flight

feathers never reflected ultraviolet light. Table 5.2 reveals associations between species exhibiting UV phenomena and habitat and altitude occurrence. There was no significant correlation between species living in the proportionately UV-richer forest light habitat and birds exhibiting UV phenomena. But, species with UV phenomena and altitudinal occurrence above 2000 m correlated significantly $p < 0.05$. Therefore, living in high altitudes seems to have an effect on the evolution of UV phenomena in trochilids. Most feather colors in hummingbirds are iridescent and of structural origin. But, compared to non-iridescent, structural feathers of, e.g., blue crown feathers of Blue Tits (*Parus caruleus*), iridescent plumage patches of hummingbirds exhibit spectra much narrower in appearance. Although, quite a few hummingbird species occur in the high Andean páramo region, the Ecuadorian Hillstar (*Oreotrochilus chimborazo*) was the only species found to reveal a UV phenomenon living at altitudes higher than 3600 m. The deep violet feathers on the forehead of the Ecuadorian Hillstar reflected remarkable amounts of UV light, being the only plumage patch found exhibiting higher amounts of ultraviolet light than in the visible spectrum. UV phenomena were predominantly found in males. Only in three species the females exhibited UV phenomena, but in all three cases the males reflected ultraviolet light as well (Table 5.1). In contrast to the findings in the parrots and passerines the UV peaks most commonly were found in the range between 370 – 400 nm (see Chapter 1).

Fig. 5.1 Violet Sabrewing (*Campylopterus hemileucurus*), Sparkling Violet-ear (*Colibri coruscans*), Amethyst-throated Sunangel (*Heliangelus amethysticollis*), Green-breasted Mango (*Anthracothorax prevostii*).

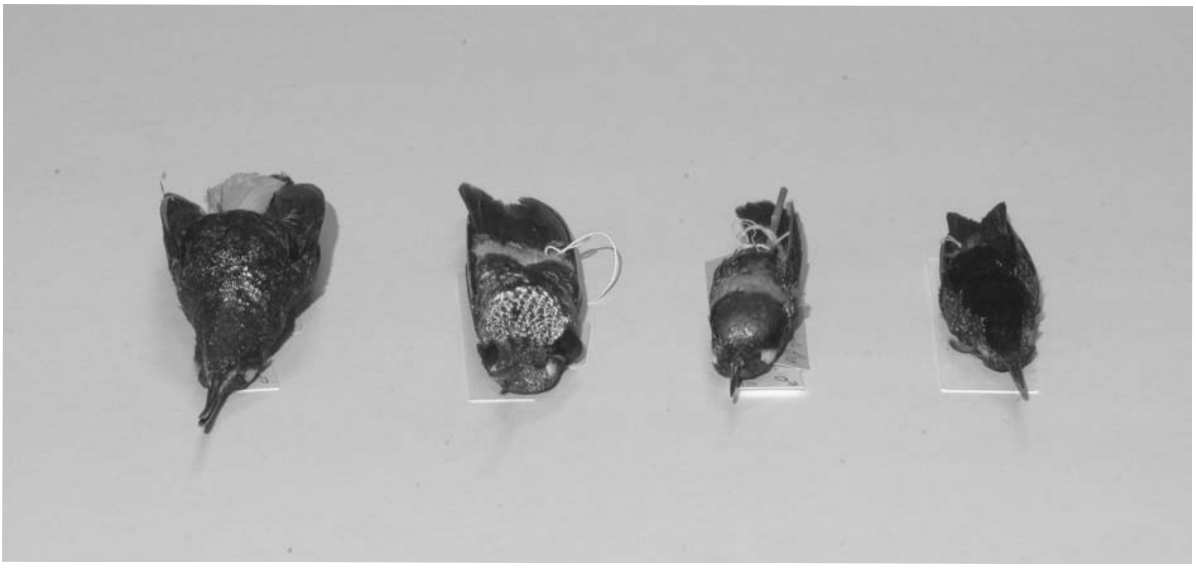

Fig. 5.2 Violet Sabrewing (*Campylopterus hemileucurus*), Sparkling Violet-ear (*Colibri coruscans*), Amethyst-throated Sunangel (*Heliangelus amethysticollis*), Green-breasted Mango (*Anthracothorax prevostii*) in B&W.

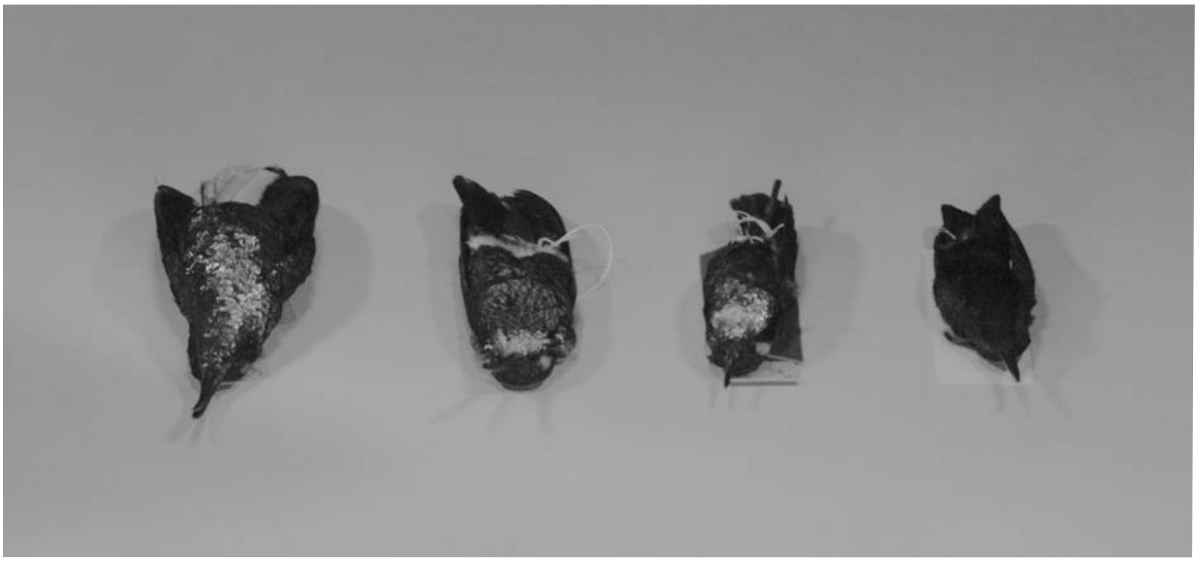

Fig. 5.3 Violet Sabrewing (*Campylopterus hemileucurus*), Sparkling Violet-ear (*Colibri coruscans*), Amethyst-throated Sunangel (*Heliangelus amethysticollis*), Green-breasted Mango (*Anthracothorax prevostii*) in UV.

5.1 Hummingbird taxa with UV phenomena. Latin and vernacular names derived from the Handbook of the Birds of the World, Volume 5 (Schuchmann 1999). O = open habitat, F = forest habitat, m = male, f = female.

No.	Species, Scientific Name	Gender	UV-exhibiting patch	Habitat	Habitat Abr.	Altitude (m)
1	Augastes geoffroyi	m	ear coverts	humid forest	F	800-2500
2	Augastes lumachellus	m	nape	Open scrub	O	950-1600
3	Campylopterus falcatus	m	crown	humid forest	F	900-3000
4	Campylopterus hemileucurus	m	throat	humid forest	F	400-2400
5	Campylopterus villaviscensio	m	forehead	woodland	O	750-1700
6	Chalcostigma herrani	m	throat	shrubbery	O	2700-3600
7	Colibri coruscans	m	rump, throat	humid forest	F	900-3600
8	Colibri delphinae	m, f	throat	woodland	O	500-2800
9	Colibri serrirostris	m	throat, breast, side of neck	savannah	O	500-2500
10	Colibri thalassinus	m	throat, rump	forest edge	O	600-3000
11	Doryfera johannae	m	forehead, rump	humid forest	F	400-1600
	Doryfera johannae	f	rump, forehead			
12	Doryfera ludovicae	m	rump, forehead	humid forest	F	900-2200
	Doryfera ludovicae	f	forehead			
13	Eulampis jugularis	m	breast	forest	F	800-2000
14	Heliangelus amethysticollis	m	throat	forest	F	1800-3300
15	Heliangelus mavors	m	throat	humid forest	F	1000-3000
16	Heliangelus clarisse	m	throat	forest edge	O	2000-3600
17	Heliangelus regalis	m	throat	forest	F	1350-2200
18	Heliangelus viola	m	throat	forest	F	2150-3000
19	Heliangelus micraster	m	throat	forest	F	2300-3400
20	Heliangelus strophianus	m	throat	humid forest	F	1200-2800
21	Heliangelus exortis	m	throat	forest	F	1500-3400
22	Lampornis amethystinus	m	throat	humid forest	F	500-3000
23	Metallura eupogon	m	throat	elfin forest edge	O	2100-3600
24	Microchera albocoronata	m	back	open woodland	O	0-1000

No.	Species, Scientific Name	Gender	UV-exhibiting patch	Habitat	Habitat Abr.	Altitude (m)
25	Oreotrochilus chimborazo	m	forehead	rocky slopes	O	3500-5200
26	Ramphodon naevius	m	tail T1	forest	F	0-900
27	Sephanoides fernandensis	m	crown	woodland	O	0-500
28	Topaza pella	m	throat, breast	humid forest	F	0-500
29	Topaza pyra	m	throat, breast	humid forest	F	0-500

Table 5.2 The Chi^2 test was performed on hummingbird species in which at least 1 plumage patch exhibited UV phenomena and correlated with habitat and altitudinal occurrence. UV phenomena in hummingbirds seem to be altitude depended.

	Forest habitat	Open habitat	Hummingbirds found at altitudes < 2000 m	Hummingbirds found at altitudes > 2000 m
No. of species exhibiting UV phenomena in at least 1 plumage patch (taken from Table 5.1)	18	11	9	20
p-value	0.194		0.041	

Discussion

My results demonstrate that most UV reflections in trochilids were found at the gorgets and forehead of males, plumage most commonly used in courtship behavior (Stiles 1982, Bleiweiss 1994), suggesting that hummingbirds communicate with the aid of UV. No UV phenomena were found in the hummingbird’s flight feathers. This may be due to the rapid movement of the wings which are too fast to be appraised by females and therefore may be inconvenient to act as display areas for sexual signaling. It would also be disadvantageous for primaries and secondaries to produce structural colors (which are the origin of UV reflection) because this could result in instability of the feather (Rensch 1927). UV peaks most commonly were found in the range between 370 - 400 nm which point towards the presence of VS cones rather than UVS cones.

Living at high altitudes seems to have an effect on the evolution of UV phenomena in hummingbirds. However, the Ecuadorian Hillstar (*Oreotrochilus chimborazo*) was the only high Andean bird living in the páramo region found to exhibit UV phenomena. At elevations of 4000 m UV light is four times as intensive as it is on sea level (Dvorkin 1999). Patches of ice, water, and the leaves of plants, growing in these heights, such as from *Espeletia* spp. (Asteraceae) are found to be covered with white hairs, add to an UV-rich environment. Most birds found to exhibiting UV phenomena inhabit sub-páramo regions between 2000 and 3600 m. This habitat is characterized by dense vegetation, thickets, and moving on downwards, humid cloud forest. Hummingbirds probably choose UV rich habitats with less UV reflecting surrounding objects to enhance contrast. The iridescent feathers especially at the throat or forehead (where most UV reflecting patches were found) are carefully steered towards a potential mate. Especially in these habitats, where light conditions are poor, it may be of an advantage for birds reflecting light only at relatively small angles. The onlooker's position is important and a proper angle is needed in order to see iridescent feather patches. Therefore, iridescent colors may provide a more directional signal for display than other plumage colors (Bailey 1978). This may be also true for ultraviolet reflections. The UV phenomena found in the trochilids also were particularly angle dependent, reflecting light at the same angle as in the visible spectrum. Furthermore, the peaks found in the ultraviolet range were as narrow as found in the visible spectrum in contrast to spectra of UV reflecting patches found in non-iridescent feathers, e.g., in parrots. Thus, it can be concluded that UV reflections in hummingbirds may are of iridescent nature, too. A predator has to be just in the right light angle to see an iridescent feather patch, which may be a relatively rare incident. Thus, the detection of iridescent prey by stationary predators would be difficult (Bailey 1978).

Male hummingbirds use their iridescent plumage in a variety of contexts. This presentation includes nuptial flights, sexual displays, and aggressive encounters, associated with nectar-centered feeding territoriality (Stiles 1982, Bleiweiss 1985). Because promiscuous breeding systems, which is commonly found in trochilids, thought to be associated with high levels of sexual selection, the bright male plumage and sexual dichromatism, a characteristic of most hummingbirds are consistent with the sexual selection theory (Selander 1972). It has been proposed that UV reflections when used as signals may act as amplifiers of behavioral traits (Zahavi & Zahavi 1997, Hausmann *et al.* 2002). If UV phenomena play a role in signaling, this may very well be the case with hummingbirds. Especially in trochilids, iridescent colors are not only used as color patterns themselves but are incorporated in complex courtship behavior related traits, such as vocal advertising, aggressive territorial defending behavior, and during agonistic flights. The found UV reflections in male display related visual traits may act as an additional visual component, signalling no more or less than the rest of the visual iridescent color pattern presented in courtship.

Summary

All of the 328 hummingbird species but 17 were measured by means of reflection spectrophotometry. 29 species were found to exhibited considerable amounts of ultraviolet light in at least one plumage patch. UV phenomena were predominantly found in males and in plumage patches used in courtship, such as in gorgets and the forehead. Assuming that UV reflective plumage would be more effective to act as a signal in a UV richer environment, the hummingbirds were assigned to their altitudinal occurrence and habitat. While no significant correlation was found between trochilids which exhibited UV phenomena and their occurrence in the proportionately UV-richer forest habitats a significant positive correlation was found with species inhabiting altitudes higher than 2000 m. The found UV reflections in male display related visual traits may act as an additional visual component.

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Synopsis

In my survey, altogether 1439 (15 %) of the 9702 bird species listed in Sibley & Monroe's taxonomic list (1990, 1993) were measured by means of reflection spectrophotometry at different museum collections in Europe, the United States, and Australia. Species of every bird Order were studied in search of birds possessing UV reflecting plumage patches. In contrast to surveys conducted previously, I used varying angles for measurement due to strongly angle-dependent reflection, especially in structural and iridescent colors. Of the following Orders all the species were completely surveyed: Struthioniformes, Tinamiformes, Craciformes, Turniciformes, Galbuliformes, Upupiformes, Coliiformes, Apodiformes, Trochiliformes and Musophagiformes. 335 (93 %) of all the parrot species (Psittaciformes) were measured. In particular, the colored plumage regions exhibited high proportions of UV reflections. A significant positive correlation was found between bird Orders with species which are believed to possess VS cone types, and Orders in which most species had their UV maxima between 380 – 399 nm. Orders with species which are assumed to have UVS cone types correlated significantly with Orders in which most species had their UV maxima between 300 – 379 nm respectively. My results suggest that, in general, interspecific variation in plumage color among birds is strongly influenced by the surrounding light and thus my findings support the "Light Environment Hypotheses". Four light habitats were chosen: "open", "sea and ice", "forest", and "night". The plumages of 968 bird species were surveyed, 348 revealed remarkable amounts of UV. The measured birds were assigned to one of the four light habitats. No UV phenomena were found in the "night" and the "sea and ice" habitat, few were found in open habitats, whereas 56% of the 425 surveyed species assigned to the forest habitat exhibited UV phenomena. Possible explanations for the inhomogeneous distribution of UV phenomena in the different light habitats with possible function as intraspecific signals are proposed and discussed. Special emphasis lay on the parrot and hummingbird Orders. All the hummingbird species were surveyed and all of the 347 living parrot species (but 18) were measured at 16 different body regions. Every parrot species possessing chromatic plumage patches exhibited considerable amounts of ultraviolet light in at least one plumage patch. 50 % of the measured species exhibited considerable amounts of UV light in all chromatic plumage patches. Only 29 species of hummingbirds were found to exhibit UV phenomena. No significant correlation was found between parrots which were UV reflective in all chromatic plumage patches and their occurrence in UV-rich habitats such as in high altitudes and forests. Parrots possessing fluorescing plumage regions did not exhibit UV reflections in all chromatic patches to a significant extent. It is proposed that UV phenomena are a plesiomorph trait in the parrot Order and it is thus suggested that this special morphology in the feather structure can probably be found in the most ancestral forms. In contrast to the findings of the parrots, my results show a significant positive correlation between hummingbirds exhibiting UV phenomena and altitudinal occurrence. Evidence for altitude dependent evolution of UV reflecting plumage traits could be shown for the first time. To test whether UV phenomena are used in signaling in species with pure UV phenomena, (birds appearing literally black to humans) the Satin Bowerbird (*Ptilonorhynchos violaceus*) was chosen as an example and a behavioral choice experiment was conducted. With the help of feathers of the Crimson Rosella, partly treated with sun block lotion, a procedure previously conducted in UV-related behavioral studies, I was able to demonstrate the Satin Bowerbird’s potential to see ultraviolet light. During their courtship male Satin Bowerbirds are known to collect blue ornaments to decorate their bowers. In my study reflection spectrophotometry revealed significantly more UV-blue compared to unicolored blue collected ornaments, at all bowers surveyed. UV-vision allows the female to judge the quality of male UV colored plumage and bower construction which is believed to have evolved to provide females information about the relative quality of males. My study supports the concept that birds of many more groups may see UV light than have been apparent to date. The large number of species exhibiting UV phenomena indicates their use as potential signals such as is the case with the Satin Bowerbird whose UV reflecting plumage has been the subject of numerous studies. The brightness of UV reflecting feather patches is lower in museum bird specimens compared to live birds measured (McNett & Marchetti 2005). This leads to the conclusion that the intensity of UV reflections found in my study tend to be underestimated rather than overestimated.

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UV light, plumage coloration, feathers, parrots, hummingbirds, Satin Bowerbird, light habitat.

Bibliography of photographs

With the exception of Fig. 3.2, all photographs were taken by Peter Mullen and Georg Pohland / SUNBIRD IMAGES. Fig. 3.2 was made by Werner Forster / SUNBIRD IMAGES.

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Erklärung

Hiermit erkläre ich, die vorliegende Arbeit selbständig verfasst, keine anderen als die angegeben Quellen und Hilfsmittel benutzt und die Zitate kenntlich gemacht zu haben. Die vorliegende Arbeit wurde weder von mir noch sonstigen Personen anderweitig als Dissertation eingereicht. Es gab keine früheren Promotionsversuche. Einzelne Kapitel wurden bereits bei Fachzeitschriften eingereicht und akzeptiert. Ich lehne eine Zulassung von Zuhörern bei der Disputation ab.