# Spectral Data of Avian Plumage

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Dedicated to the memory of

***Knöpfchen***

“The light that burns twice as bright burns for half as long and you have burned so very, very brightly”

(Blade Runner, 1982)

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## General Introduction

Avian coloration has evolved to serve the different requirements of the bearer. Colors can result from pigments, incorporated into the feather structure as well as structural properties. The majority of birds are diurnal and rely heavily on visual orientation and communication. Hence, a vivid palette of colors is extant in the entire Class Aves. Coloration can be involved in recognition of age, sex, and health condition and plays an important role in signaling and camouflage. A certain color can either facilitate the perceiver to derive information from it or to avoid recognition. Plumage and plumage coloration are reliable sources of information for conspecifics. It can provide indications about condition or parasite load (Hamilton & Zuk 1982, Zuk *et al.* 1990) and even structural color can potentially signal feather quality and abrasion resistance (Fitzpatrick 1998). Thus, plumage brightness can also be associated with male mating success (Stein & Uy 2006). Since feathers are dead structures, color changes depend on abrasion, fading as well as on, replacement of the entire plumage. This information is certainly valid during the lifetime of its bearer but is not intended to last after death. Above all, in a living bird this information is frequently renewed by molt.

Color vision enables animals to discriminate hue and chroma of any object they naturally encounter. It frequently comprises further visual properties, such as luminance information or polarization recognition. Coloration itself is the vision ecological counterpart fine tuned to ambient light conditions and visual capacities of the addressed organisms.

Avian color vision exceeds the limits of human color vision. Using discrimination experiments, it had been possible to demonstrate, for the first time, that a bird's perception encompasses ultraviolet wavelengths (Huth & Burkhardt 1972, Wright 1972). Further studies revealed a great number of birds capable of perceiving UV (Bennett & Cuthill 1994, Cuthill *et al*. 2000, Hart 2001a). Different approaches contributed evidence that UV-vision is a widespread phenomenon in the class Aves. Electroretinography (Chen *et al.* 1984, Chen & Goldsmith 1986) as well as microspectrophotometry (Maier & Bowmaker 1993) provided data to support this hypothesis and moreover even genetic evidence in a great number of species was

provided by Ödeen & Håstad (2003). Furthermore, avian color vision is unique in other respects. Besides a potential capability of polarization recognition the bird's retina contains more different cone types than the human eye. So called double cones seem to play a role in motion detection (Campenhausen & Kirshfeld 1998, Jones & Osorio 2004). Avian vision receptors are protected by colored oil droplets that can act as edge filter to facilitate precise wavelength discrimination (Govardowskii 1983, Goldsmith *et al*. 1984, Bowmaker *et al.* 1997, Vorobyev & Osorio 1998, Hart *et al*. 2000, Hart 2001b, Vorobyev 2003).

Individuals of different bird species, even though equally sized and shaped, can sometimes easily be distinguished by their color (Fig. 1 & 2). However, in some cases, a single specimen might be misjudged to be affiliated to several populations, depending on the angle of observation (Fig. 3 – 5). Therefore, carefully color analyses have been subject to different approaches during the last century.

Plumage coloration is a well established standard means for categorization and identification of birds. It enables taxonomists as well as field workers to distinguish species, sexes, and, to a certain degree, ages of an observed population. Although phylogenetic information can be derived by new DNA analysis methods using feathers from museum bird skins (Ellegren 1991), they suffer from covering entire populations of certain taxa, unlike morphometrical data (Leeton *et al*. 1993).

Two major fields of interest are frequently addressed by the analysis of plumage coloration. In taxonomic research, in which a great number of museum skins are analyzed, plumage coloration acts as morphometrical data. Ecological or behavioral investigations put implications of plumage coloration to the test. Therefore, the nature of the required data is different. The major interest of research based on museum skins is to establish if accurate and reliable information can be derived from plumage, especially in plumage colors as it might be void due to different mechanisms of decay.

Fig. 1 Northern Cardinal (*Cardinalis cardinalis*).

Fig. 2 Blue Grosbeak **(***Passerina caerulea*).

Fig. 3 Purple-throated Mountain-gem, male (*Lampornis calolaema*) throat appearing green.

Fig. 4 Purple-throated Mountain-gem, male (*Lampornis calolaema*) throat appearing violet.

Fig. 5 Purple-throated Mountain-gem, male (*Lampornis calolaema*) throat appearing purple.

Owing to increasing knowledge about color vision and color formation, researchers nowadays place high demands on the acquisition of spectral data. It has to withstand increasing requirements in respect of accuracy, reproducibility and meeting the visual deficiencies of human examiners. Therefore, attention has been focused on the value of spectrophotometric methodologies. Reflection spectrophotometry is the most conservative way to treat a specimen in order to obtain morphometrical data, contrary to methods based on extraction of pigments (e.g., Mahler *et al*. 2003). Moreover, specimens are prevented from damage, as there is no need to extract feathers or tissue for DNA-analysis (Leeton *et al*. 1993) or twist the specimen when measuring size.

An applicable standard for color characterization to facilitate unrestricted use of museum bird skins concerning plumage colors for taxonomic and related research purposes has still to be established.

References

Bennett, A. T. D. & Cuthill, I. C. 1994. Ultraviolet vision in birds: what is its function? *Vision Res.* 34: 1471-8.

Bowmaker, J. K., Heath, L. A., Wilkie, S. E. & Hunt, D. M. 1997. Visual pigments and oil droplets from six classes of photoreceptor in the retinas of birds. *Vision Res.* 37: 2183-94.

Campenhausen, M. V. & Kirschfeld, K. 1998. Spectral sensivity of the accessory optic system of the pigeon. *J. Comp. Physiol. A* 183: 1-6.

Chen, D. M., Collins, J. S. & Goldsmith, T. H. 1984. The ultraviolet receptor of bird retinas. *Science* 225: 337-40.

Chen, D. M. & Goldsmith, T. H. 1986. Four spectral classes of cone in the retinas of birds. *J. Comp. Physiol. A* 159: 473-479.

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

Ellegren, H. 1991. DNA typing of museum birds. *Nature* 354: 113.

Fitzpatrick, S. 1998. Colour schemes for birds: structural coloration and signals of quality in feathers. *Annales Zoologici Fennici* 35: 67-77.

Goldsmith, T. H., Collins, J. S. & Licht, S. 1984. The cone oil droplets of avian retinas. *Vision Res.* 24: 1661-71.

Govardovskii, V. I. 1983. On the role of oil drops in colour vision. *Vision Res.* 23: 1739-1740.

Hamilton, W. D. & Zuk, M. 1982. Heritable true fitness and bright birds: A role for parasites? *Science* 218: 384-387.

Hart, N. S., Partridge, J. C., Cuthill, I. C. & Bennett, A. T. D. 2000. Visual pigments, oil droplets, ocular media and cone photoreceptor distribution in two species of passerine bird: the Blue Tit (*Parus caeruleus* L.) and the Blackbird (*Turdus merula* L.). *J. Comp. Physiol. A* 186: 375-87.

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

Hart, N. S. 2001b. Variations in cone photoreceptor abundance and the visual ecology of birds. *J. Comp. Physiol. A* 187: 685-97.

Huth, H. H. & Burkhardt, D. 1972. Der spektrale Sehbereich eines Violettohr-Kolibris. *Naturwissenschaften* 59: 650.

Jones, C. D. & Osorio, D. 2004. Discrimination of orientated visual textures by poultry chicks. *Vision Res.* 44: 83-89.

Leeton, P., Christidis, L. & Westerman, M. 1993. Feathers from museum bird skins: a good source of DNA for phylogenetic studies. *Condor* 95: 465-466.

Mahler, B., Araujo, L. S. & Tubaro, P. L. 2003. Dietary and sexual correlates of carotenoid pigment expression in dove plumage. *Condor* 105: 258-267.

Maier, E. J. & Bowmaker, J. K. 1993. Colour vision in the passerine bird, *Leiothrix lutea*: Correlation of visual pigment absorbency and oil droplet transmission with spectral sensivity. *J. Comp. Physiol. A* 172: 295-301.

Ödeen, A. & Håstad, O. 2003. Complex distribution of avian color vision systems revealed by sequencing the SWS1 opsin from total DNA.
*Mol. Biol. Evol.* 20: 855-61.

Stein, A. C. & Uy, J. A. C. 2006. Plumage brightness predicts male mating success in the lekking Golden-Gollared Manakin, *Manacus vitellinus*. *Behav. Ecol.* 17: 41-47.

Vorobyev, M. & Osorio, D. 1998. Receptor noise as a determinant of colour thresholds. *Proc. R. Soc. Lond. B* 265: 351-358.

Vorobyev, M. 2003. Coloured oil droplets enhance colour discrimination. *Proc. R. Soc. Lond. B* 270: 1255-1261.

Wright, A. A. 1972. The influence of ultraviolet radiation on the pigeon's color discrimination. *J. Exp. Anal. Behav.* 17: 325-337.

Zuk, M., Johnson, K., Thornhill, R. & Ligon, J. D. 1990. Parasites and male ornaments in free-ranging and captive Red Jungle Fowl. *Behaviour* 114: 232-248.

# 1 Spectral data acquisition of avian plumage - A practical approach

## 1.1 Introduction

Feathers exhibit a wide spectrum of colors. They are effective tools in avian optical signaling and enable human investigators to obtain a variety of information about a particular specimen. The need for objective characterization has been recognized for a long time. With respect to different research goals, different approaches have been made to gather quantitative and qualitative data about plumage coloration. Nevertheless, different promising attempts have been made in several research groups, to develop methods for spectral data acquisition of avian plumage. Most of these attempts failed to meet practical requirements in terms of manageability, accuracy, or reproducibility. Only few of them had been carefully tested using critical experiments.

### Acquisition of spectral data

As a simple method to readily obtain basic information about many different birds, comparisons of descriptions or illustrations as well as photos from ornithological field guides or handbooks were carried out (Baily 1978, Fitzpatrick 1998). Amundsen *et al*. (1997) used information obtained by a human observer. Consistence was ensured by retaining the same observer. Another possibility is to take photographs of the specimen in question and analyze these according to color (Villafuerte & Negro 1998, Massaro *et al*. 2003, Badyaev & Young 2004). Using human perception as a means of color analysis encounters serious difficulties. Examinations are unsatisfactory due to the subjectivity and partial color blindness of the human observer who, at least, is incapable of perceiving ultraviolet light (Grill & Rush 2000, Thorpe 2002, Eaton 2005). Certain color standards, such as the Munsell Color Standards, the “LAB system” or CIE tristimulus values, were used in order to objectify analysis (Dyck 1966, Smithe 1975, Burtt 1986, Grill & Rush 2000). Since UV-coloration in avian plumage is known to play an important role in avian signaling (Huth & Burkhardt 1972, Maier 1993, Bleiweiss 1994, Bennett *et al*. 1997, Andersson *et al*. 1998, Church *et al*. 1998, Cuthill *et al*. 2000, Pearn *et al*. 2001, Arnold *et al*. 2002,

Hausmann *et al*. 2003), and was proved to be a widespread phenomenon (Eaton & Lanyon 2003), it is essential to take this wavelength into account. Ultraviolet components in avian plumage spectra are crucial for analyzing coloration. While UV occurs frequently in feathers, it is invisible to the human investigator, though it is a common property of avian color vision. It might easily elude the observer but it is an essential part of avian vision ecology. Hence, it is of major interest to learn about the distribution of this chromophoric element, in order to be able to take any signaling-related implications and evolutionary traits of this wavelength band into consideration. As the human visual system is not sensitive to ultraviolet hues (Goldsmith 1980; Burckhardt 1989; Burckhardt & Finger 1991; Jacobs 1992, 1993; Bennett *et al*. 1994; Finger & Burckhardt 1994; Burkhardt 1996; Shi & Yokohama 2003), technical aids are necessary to uncover their nature.

Lubnow & Niethammer (1964) already tested spectrophotometric techniques on avian plumage and emphasized their potentials for taxonomy. In the following, further studies had been conducted using different spectrophotometric equipment (Selander *et al*. 1964, Kniprath 1967, Hill 1998). The increased sensitivity of spectrophotometric techniques compared with the Munsell Color Standards became a topic of discussion (Zuk & Decruyenaere 1994).

Regrettably, with regard to gathering spectral data, a feather is not a Lambert reflector, i.e., light is reflected directionally and hence reflection is not diffuse. Moreover, a feather's surface is characterized by uneven barbs and barbules. The feather itself is curved, thus making it difficult to find an even area with homogenous reflectance properties, not to mention a perfectly diffuse reflectance. Nevertheless, spectral information of the feather can be crucially influenced by diffuse or specular gloss in terms of desaturation or even concealment of actual chromatic reflections. However, even reflections of the latter type might be an integral part of potential signals. Therefore, some researchers use integrating spheres which encompass reflection angles of an entire hemisphere (e.g., Bleiweiss 2004). However, the information, which can be obtained with this setup, is limited, as any directionally occurring hues are heterodyned by others.

Among others, Jan Dyck (1966) pioneered reflection spectrophotometry dealing in relation to avian plumage coloration. He made the first studies to determine feather pigments and structures by means of reflection spectrophotometry. As he recognized the value of reflection curves for investigating biological colors, he had tested the implications of the illumination angle in fruit-doves *Ptilinopus* sp. and *Ducula* sp. (Dyck 1987, 1992). As the feather does not represent a plane homologous colored surface, reflecting angle sectors changed dramatically, depending on the illumination geometry. Specimens illuminated with their head towards a lamp exhibited a small angle sector in *Ducula* but a broader range for *Ptilinopus*. Rotating the specimen by 180° caused the peak reflections to increase in both birds. When illuminating the birds 90° to their body axis, the reflections were predominately directed towards the incident light and the difference between the two specimens was remarkably low. This basic experiment stresses to the investigator not to underestimate the impact of the measuring angle.

As far as reflection spectrophotometry is concerned, only a few measuring angles had been used frequently. Those using coincident illumination and reading angles, chose perpendicular angles (Andersson & Amundsen 1997, Keyser & Hill 1999, Eaton & Lanyon 2003, Shawkey *et al*. 2003, Doucet *et al*. 2004, Reneerkens & Korsten 2004, Eaton 2005, Hofmann *et al*. 2006) or angles of 45° (Andersson *et al*. 1998, Gomez & Voisin 2002, Stein & Uy 2006). Some authors preferred to use measuring geometry without coincident measurement and reading angles (Hausmann *et al*. 2003, McNaught & Owens 2002). Even although the application of spectral data has been successfully tested by Schmitz-Ornés (2006), the reliability of spectral data itself is still questioned.

In order to evaluate measuring geometry, Cuthill *et al*. (1999) analyzed different measuring angles with respect to the iridescent coloration. They reported different hues in one feather patch, depending on the viewing and illumination geometry. The most in-depth analysis so far was carried out by Osorio & Ham (2002). In their study, reflectance properties of variably orientated and illuminated feathers had been observed. 15 feathers of structurally colored bird species were tested. They reported crucial differences in directional attributes due to the formation of chromophoric elements.

Formation of colors

Völker (1961a) already noted that, even under optimal illumination conditions, it is impossible to estimate from a color, the nature of the corresponding pigments.

The surface of a feather does not exhibit periodically repeating structures. Moreover, the differently arranged quill, barb (ramus), and barbule (radius) diffract the light in various directions (Frank 1939). This light is reflected repeatedly by juxtaposed feather parts, or even within the keratin structure itself, and hence, only very small amounts of light are lost. Thus, a diffuse reflection from a feather appears as white, as long as no light absorbing pigments are involved.

Chromophoric elements in feathers can be located in both the feather barbs and the barbules (Bancroft *et al*. 1923, Frank 1939). Besides granular melanins, diffuse or flake-like pigments add to overall feather color. They can produce red, yellow, orange, green, blue, and violet as well as achromatic hues. The resulting coloration depends on the density of the respective pigments. The effects of coloration are supported by morphology, position, and orientation of rami and radia (Frank 1939).

Another infrequent carrier of chromophoric elements is the so-called powder coloration, e.g., in the neck feathers of the Red-crested Bustard (*Eupodotis ruficristata*). These feathers are covered with a small scale-like powder which contains the respective color (Völker 1964; Berthold 1968).

Chromophoric elements in avian feathers are subject to different mechanisms of color production. The latter can be grouped into the main categories of color addition and color subtraction. Color addition occurs in structural coloration and color subtraction derives from pigment-based coloration. Structural colors are produced by physical interactions of light waves with nanometer-scale structures. All chromatic structural colors of birds originate from coherent light scattering. They differ only in the array of chromophoric structures. These are multilayer reflectors with a distinct relation to the wavelength of light (Raman 1935; Durrer 1965; Prum *et al*. 1998, 1999a, 1999b, 2002; Parker 2000, Prum 2006). The resulting coloration can include iridescent hues. Incoherent scattering produces white reflections (Prum 2006).

Feathers are composed of keratins which contribute to overall light refraction (Brush 1978). Structural colors emerge as a consequence of size, spatial distribution and the refractive indices of different molecules (i.e., melanin (2.0) and keratin (1.55) (Durrer & Villiger 1962)). These molecules can also serve as pigments. Some structural colors are not strictly “non pigmentary” colors if they are produced by nanometer-scale physical structures that consist of pigments (Prum 2006). Therefore, structural coloration can be an effect of interference of light by small melanin granules (Dyck 1987, 1992). The variety of structural arrangements from which colors are generated is innumerable.

A particular type of structural coloration is represented by iridescence. Iridescence is the optical phenomenon of changing color according to the angle of observation (Land 1972, Fox 1976). The common structural configurations in feathers, producing bright colors of the iridescent and non-iridescent type, evidently exclude one another (Auber 1956). Durrer & Villiger (1975) classified iridescent colors according to their intensity (i.e., brightness). They proposed different structural elements of feathers which result in iridescent colors. These are differently shaped and arranged melanin granula (Durrer & Villiger 1962, 1966). With regards to reflection spectrophotometry, iridescent coloration is expected to produce a great variability of spectra in relation to the measuring angle.

Avian pigments fall into general chemical categories, i.e., melanins, carotenoids, porphyrins, psittacofulvins (Völker 1947, 1955, 1963; Brush 1978; McGraw & Nogare 2004, 2005; Hudon 2005). Unlike structural colors, in general pigment-based coloration is not based on reflection but on absorption. Nevertheless, even in pigment-based coloration, a structural chromophoric element can serve as a background which contributes at least to brightness (Shawkey & Hill 2005). In this case the structure would act as a white canvas, underling the actual color.

In order to create plumage coloration, pigments are transferred to developing feather keratinocytes from pigments cells that migrate into the tubular feather germ from the dermis (Prum & Williamson 2002). Pigments are not entirely synthesized de novo and the influence of diet on pigmentation has been widely established (Giersberg & Stadie 1932; Brush & Power 1976; Brush 1978, 1990; Mahler *et al*. 2003).

Furthermore, Weber (1961) found evidence that color aberrations may be due to spatial conditions, independently of nutritional components. Hence, specimens held in captivity have to be treated carefully when being considered for spectral analysis.

Pigments are usually incorporated into the feather keratin during feather formation and only certain exceptional species, e.g., the Bearded Vulture (*Gypaetus barbatus)*, exhibit adventitious colors. These result from the deposition of ferrous oxides, picked up from the environment (Berthold 1965, 1967, 1968). Regular pigments can be located in both the feather barbs (rami) and the barbules (radia). Lipochromes are generally to be found in the rami but are occasionally in the radia as well.

Melanins are the most common and widely distributed class of pigments in bird feathers (Hudon 2005), contributing to most feather colors (Frank 1939). Melanins exhibit a granular structure and are distributed in organisms in differently shaped pigment bodies. The latter can be round, oval or rod-like, including intermediate forms. The darker melanins are classified as eumelanins, the brighter as phaeomelanins (Frank 1939, Lubnow 1963). Melanins play a crucial role as underlying pigments and light refracting elements in structural blue colors.

Further widespread pigments, contributing to avian plumage coloration, are the carotenoids. Pigments of this class are derived from diet and metabolically modified since they are incorporated in tissues or integumentary structures. The nutritional control of carotenoids can imply high physiological costs for its bearer (McGraw *et al*. 2004). This distinguishes them from both melanins and structurally induced coloration. Carotenoids are stored in oil droplets which are used as a storage vesicle until they are incorporated in keratin during feather formation. They are metabolically transformed from the precursors to those molecules used for inducing colors.

The resulting hues depend on the respective carotenoids, their relative concentration and the overall concentration of all pigments (Inoye *et al*. 2001). However, carotenoids are generally resistant to the negative effects light exposure (Völker 1962).

Porphyrins are predominately found in light protected plumage areas and natal plumage. In the Red-crested Bustard (*Eupodotis ruficristata*), they are located in the ornamental feathers. While the most widespread substance Kopoporphyrin is degraded by light, the copper binding Turacin is stable to light (Völker 1947, 1961a, 1961b, 1964, 1965; With 1967).

Psittacofulvins are synthesized endogenously by parrots which use them instead of carotenoids (Hudon 2005). Psittacofulvins are lipid-soluble and red, orange, or yellow in color (McGraw & Nogare 2004).

Purpose of present study

Some authors (e.g., Endler 1990) argue that the geometry of reflectance spectroradiometer must be designed to match, as closely as possible, the geometry of the viewing conditions in nature. Andersson and Prager (2006) discussed different alignments for the reflection spectrophotometric sampling of feathers. These included different angles of illumination as well as reading. They propose using the alignment of coincident normal, i.e., reading and illumination angles are the same and the reflection probe is adjusted perpendicular to the surface. The brightest reflections are characterized by a comparably low background noise. In order to operate with an optimal signal-to-noise ratio, it is indispensable to test for the brightest reflecting observation angle.

However, when dealing with spectral data, the potential a priory variation in plumage coloration has to be taken into account. Variation can be subject to seasonal changes, sexual dichromatism, maturity or intraspecific polymorphism. Furthermore, dietary dependency of coloration as well as possible diseases or molt should be considered when dealing with spectral information (see Chapter 2).

In my study, the overall variability of feather reflections is to be analyzed. A consistent methodology for obtaining spectral data of avian plumage will be proposed. In order to cope with practical inherent necessities, the most commonly used spectrophotometric measuring geometry is employed, i.e., a portable reflection spectrophotometer and a reflection probe consisting of a bifurcated cable with coincident illumination and reading fibers.

Study goals:

A survey is to be carried out, testing reliability of reflection spectrophotometric data acquired from avian plumage.

The significance of solid angles, with respect of an optimal signal-to-noise ratio, is to be analyzed.

A suitable technique is to be established for general spectral data acquisition of avian plumage.

## 1.2 Material and methods

A specially made spectrophotometric measuring device has been developed for the ongoing work (Fig. 6). This device exhibits a measuring geometry facility allowing a variable solid angle to be locked at any desired position ensuring equidistant piloting above the surface. With this essential tool, it is possible to gather spectral data using a stopless adjustable reflection probe head. The position of the reflection probe can be altered in both elevation and rotation as well as in distance to the specimen's surface. This arrangement allows for selecting any steradian of a hemisphere, with the respective sample positioned exactly in the centre of the fundamental plane. The sample is fixed into position during the entire measurement.

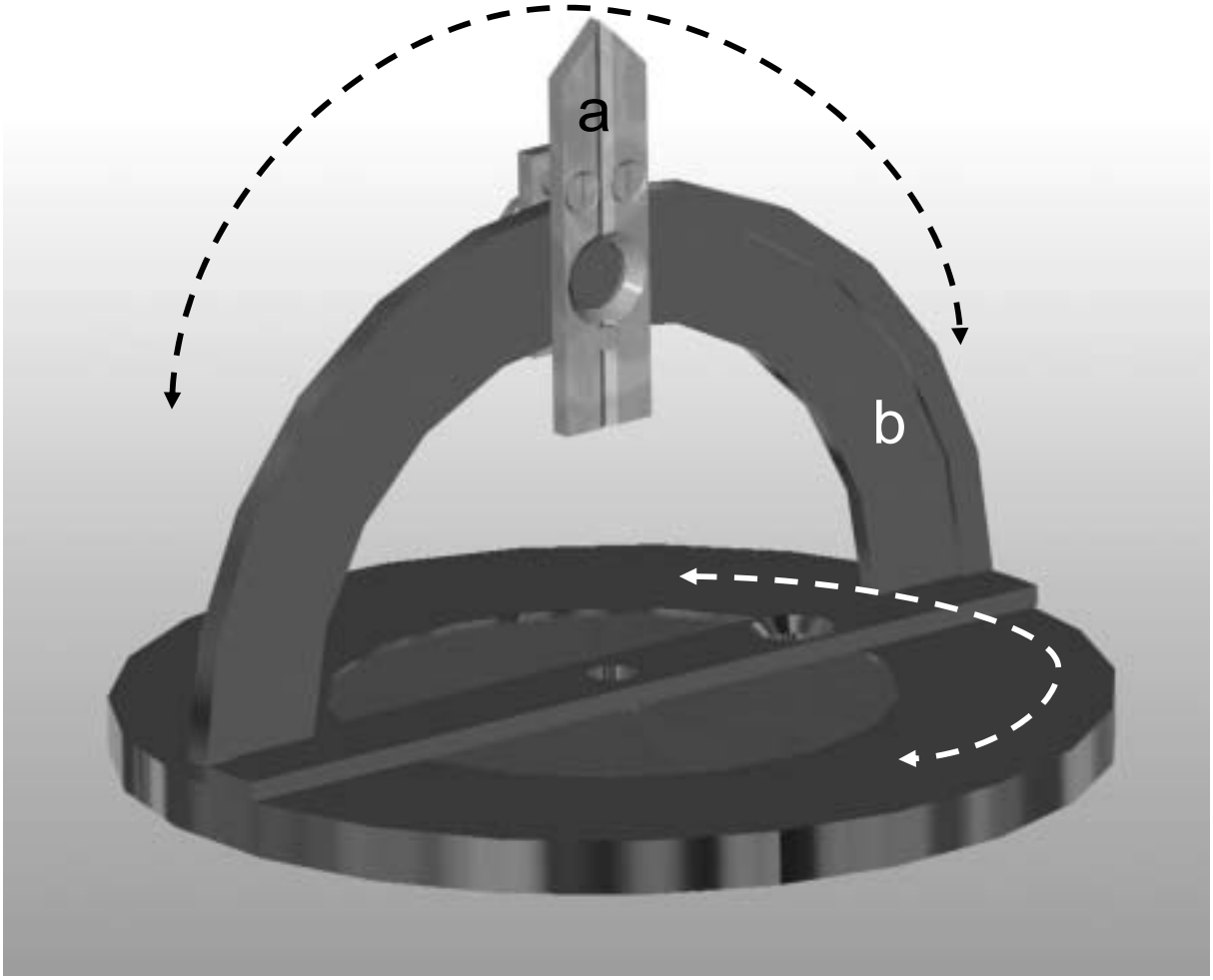



Fig. 6 Spectrophotometric measuring device. The reflection probe mounting (a) can be shifted along the semicircular bar; allowing for any desired vertical angle, representing the respective elevation level. The entire construction (b) is designed to rotate around the centered sample, thus facilitating the adoption of any required rotation sector.

Reflectance spectra were taken using an Ocean Optics USB 2000 spectrometer, with a Xenon pulse light source, providing both, wavelengths of the visible spectrum and ultraviolet light. Measurements were calibrated against a compressed pill of barium sulphate ($BaSO_4$), a black velvet cloth being used as a dark reference. Measurements were taken in the absence of ambient light in a darkened room using as reflection probe 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 measuring head was fixed to the measuring device, equidistantly 20 mm above the examined sample. All reflectance data were evaluated between the wavelengths 300 and 750 nm.

108 different feathers or plumage parts were spectrally analyzed. A single measurement represents the mean of 6 subsequently conducted measurements at the same spot. From each feather or plumage part, 169 different solid angles were taken into consideration. Data was subsequently obtained, starting with an elevation of 30° and a rotation of 0° according to the feather quill. Osorio & Ham (2002) defined elevation as the difference between illumination and reading angles. They referred to the elevation level as the azimuth. In my study, the angle between illumination and reading fibers is 0° owing to the default geometry of the standard bifurcated reflection probe. The term azimuth was rejected and replaced by elevation level, as it can easily be confused with the rotation sector due to its similar use in astronomy. Furthermore, the orientation of the sample itself was not changed. The measuring device was turned anti-clockwise in steps of 30° until a complete circle had been measured. Additionally, two angles were taken into account, i.e., 90° according to the rami and 270° respectively. Thereafter the elevation level was raised to 35° and another circle was completed. This procedure was repeated in elevation steps of 5°. At the elevation of 90°, a single measurement was conducted. This procedure resulted in a total amount of 18 252 single measurements (representing overall 109 512 measurements). Data gathering below the elevation level of 30° cannot be done as, when using the reflection spectrophotometer, the measured spot will expand exaggeratedly and generate adulterated spectra.

Single feathers or entire plumage parts were both tested. When plumage parts were analyzed, the arrangement of the measurement device was in accordance with the main direction of the feathers. When single feathers were tested, the arrangement was based on to the quill. Single feathers, including tail feathers, were exclusive from the left side of the bird's body. Spectral data were gathered from the upside of the outer web. Only exceptionally clean, unaltered feathers or plumage parts with an immaculate surface integrity and condition were considered in this study. The specimens were exclusively males of each species, unless designated otherwise.

Analyzed specimens are listed in Table 1.

Table 1 Analyzed specimen.

| Color | Color Type | Species | Family | Plumage Part |
|---|---|---|---|---|
| Red | Iridescent | *Topaza pyra* | Trochilidae | Belly |
| Red | Iridescent | *Selasphorus rufus* | Trochilidae | Throat |
| Red | Iridescent | *Meleagris ocellata* | Phasianidae | Upper wing coverts |
| Red | Iridescent | *Cinnyricinclus leucogaster* | Sturnidae | Tertials |
| Red | Iridescent | *Aix sponsa* | Anatidae | Secondaries |
| Red | Iridescent | *Topaza pella* | Trochilidae | Breast |
| Red | Structural | *Eos histrio* | Psittacidae | Primaries |
| Red | Structural | *Calyptorhynchus banksii* | Psittacidae | Tail |
| Red | Structural | *Trogon personatus* | Trogonidae | Belly |
| Red | Structural | *Pericrocotus miniatus* | Campephagidae | Primaries |
| Red | Structural | *Cardinalis cardinalis* | Cardinalidae | Tail |
| Red | Structural | *Colaptes auratus* | Picidae | Tail |
| Red | Pigment | *Campephilus melanoleucos* | Picidae | Crest |
| Red | Pigment | *Dendrocopos major* | Picidae | Under tail coverts |
| Red | Pigment | *Nectarinia senegalensis* | Nectariniidae | Breast |
| Red | Pigment | *Chrysolophus pictus* | Phasianidae | Tail |
| Red | Pigment | *Eupodotis senegalensis* | Otididae | Back |
| Red | Pigment | *Tauraco erythrolophus* | Musophagidae | Primaries |
| Red | Pigment | *Tragopan satyra* | Phasianidae | Belly |
| Yellow | Iridescent | *Nectarinia reichenowi* | Nectariniidae | Lesser upper wing coverts |
| Yellow | Iridescent | *Anthracothorax recurvirostris* | Trochilidae | Tail |
| Yellow | Iridescent | *Chlorostilbon aureoventris* | Trochilidae | Belly |
| Yellow | Iridescent | *Heliangelus micraster* | Trochilidae | Throat |
| Yellow | Iridescent | *Meleagris ocellata* | Phasianidae | Upper wing coverts |
| Yellow | Iridescent | *Caloenas nicobarica* | Columbidae | Upper wing coverts |
| Yellow | Iridescent | *Parotia lawesii* | Paradisaeidae | Breast |
| Yellow | Structural | *Aratinga guarouba* | Psittacidae | Tail |
| Yellow | Structural | *Touit dilectissima* | Psittacidae | Tail |
| Yellow | Structural | *Chrysolophus pictus* | Phasianidae | Crown |
| Yellow | Structural | *Gubernatrix cristata* | Cardinalidae | Tail |
| Yellow | Structural | *Gymnostinops montezuma* | Icteridae | Tail |
| Yellow | Structural | *Colaptes auratus* | Picidae | Primaries |

| Color | Color Type | Species | Family | Plumage Part |
|---|---|---|---|---|
| Yellow | Pigment | *Melanerpes candidus* | Picidae | Belly |
| Yellow | Pigment | *Trogon rufus* | Trogonidae | Belly |
| Yellow | Pigment | *Balearica pavonina* | Gruidae | Scapulars |
| Yellow | Pigment | *Aptenodytes patagonicus* | Spheniscidae | Ear-coverts |
| Yellow | Pigment | *Dinopium benghalense* | Picidae | Back |
| Yellow | Pigment | *Paradisaea minor* | Paradisaeidae | Flank-coverts |
| Green | Iridescent | *Campylopterus falcatus* | Trochilidae | Back |
| Green | Iridescent | *Nectarinia famosa* | Nectariniidae | Back |
| Green | Iridescent | *Anthreptes aurantium* | Nectariniidae | Back |
| Green | Iridescent | *Pharomachrus mocinno* | Trogonidae | Upper tail coverts |
| Green | Iridescent | *Chrysococcyx cupreus* | Cuculidae | Tail |
| Green | Iridescent | *Polyplectron malacense* | Phasianidae | Tail |
| Green | Structural | *Psittacula krameri* | Psittacidae | Tail |
| Green | Structural | *Aprosmictus erythropterus* | Psittacidae | Tail |
| Green | Structural | *Prioniturus platurus* | Psittacidae | Tail |
| Green | Structural | *Merops bullockoides* | Meropidae | Tertials |
| Green | Structural | *Ailuroedus buccoides* | Ptilonorhynchidae | Tail |
| Green | Structural | *Ptilinopus occipitalis* | Columbidae | Tail |
| Green | Pigment | *Tauraco porphyreolophus* | Musophagidae | Breast |
| Green | Pigment | *Somateria mollissima* | Anatidae | Crown |
| Green | Pigment | *Ithaginis cruentus* | Phasianidae | Belly |
| Green | Pigment | *Jacana spinosa* | Jacanidae | Primaries |
| Blue | Iridescent | *Campylopterus falcatus* | Trochilidae | Throat |
| Blue | Iridescent | *Anthreptes aurantium* | Nectariniidae | Nape |
| Blue | Iridescent | *Nectarinia coccinigastra* | Nectariniidae | Belly |
| Blue | Iridescent | *Anthreptes longuemarei* | Nectariniidae | Back |
| Blue | Iridescent | *Damophila julie* | Trochilidae | Belly |
| Blue | Iridescent | *Cosmopsarus regius* | Sturnidae | Tertials |
| Blue | Iridescent | *Pavo cristatus* | Phasianidae | Throat |
| Blue | Iridescent | *Aix sponsa* | Anatidae | Secondaries |
| Blue | Structural | *Coracias caudata* | Coraciidae | Primaries |
| Blue | Structural | *Barnardius zonarius* | Psittacidae | Tail |
| Blue | Structural | *Coracias abyssinica* | Coraciidae | Secondaries |
| Blue | Structural | *Dacelo leachii* | Alcedinidae | Tail |

| Color | Color Type | Species | Family | Plumage Part |
|---|---|---|---|---|
| Blue | Structural | *Acryllium vulturinum* | Numididae | Breast |
| Blue | Structural | *Cyanocorax caeruleus* | Corvidae | Tail |
| Ultraviolet | Structural | *Chalcopsitta atra* | Psittacidae | Tail |
| Ultraviolet | Structural | *Anthreptes longuemarei* | Nectariniidae | Tail |
| Ultraviolet | Structural | *Pionus seniloides* | Psittacidae | Tail |
| Ultraviolet | Structural | *Urocissa erythrorhyncha* | Corvidae | Tail |
| Ultraviolet | Structural | *Ptilonorhynchus violaceus* | Ptilonorhynchidae | Back |
| Ultraviolet | Structural | *Myophonus caeruleus* | Turdidae | Upper wing coverts |
| Brown | Pigment | *Steatornis caripensis* | Steatornithidae | Secondaries |
| Brown | Pigment | *Pavo cristatus* (Female) | Phasianidae | Primaries |
| Brown | Pigment | *Turdus iliacus* | Redwing | Tail |
| Brown | Pigment | *Buteo buteo* | Accipitridae | Primaries |
| Brown | Pigment | *Sylvia atricapilla* (Female) | Sylviidae | Crown |
| Brown | Pigment | *Streptopelia decaocto* | Columbidae | Secondaries |
| Brown | Structural | *Chalcopsitta duivenbodei* | Psittacidae | Secondaries |
| Grey | Lacking UV | *Grus virgo* | Gruidae | Upper wing coverts |
| Grey | Lacking UV | *Aptenodytes patagonicus* | Spheniscidae | Back |
| Grey | Lacking UV | *Otus leucotis* | Strigidae | Tail |
| Grey | Lacking UV | *Eolophus roseicapillus* | Psittacidae | Primaries |
| Grey | Lacking UV | *Urocolius macrourus* | Coliidae | Back |
| Grey | Lacking UV | *Aptenodytes forsteri* | Spheniscidae | Back |
| Grey | Containing UV | *Polyplectron emphanum* | Phasianidae | Tail |
| Grey | Containing UV | *Lanius excubitor* | Laniidae | Primaries |
| Grey | Containing UV | *Motacilla alba* | Motacillidae | Tail |
| Grey | Containing UV | *Sitta europaea* | Sittidae | Tail |
| Grey | Containing UV | *Streptopelia turtur* | Columbidae | Secondaries |
| Grey | Containing UV | *Anser anser* | Anatidae | Upper wing coverts |
| White | Lacking UV | *Cacatua galerita* | Psittacidae | Secondaries |
| White | Lacking UV | *Garrulus glandarius* (Albino) | Corvidae | Nape |
| White | Lacking UV | *Pavo cristatus* (Albino) | Phasianidae | Primaries |
| White | Lacking UV | *Campylopterus hemileucurus* | Trochilidae | Tail |
| White | Lacking UV | *Galbula dea* | Galbulidae | Throat |
| White | Lacking UV | *Somateria spectabilis* | Anatidae | Breast |
| White | Containing UV | *Argusianus argus* | Phasianidae | Eyespot |
| White | Containing UV | *Plectophenax nivalis* | Emberizidae | Secondaries |

| Color | Color Type | Species | Family | Plumage Part |
|---|---|---|---|---|
| White | Containing UV | *Nyctea scandiaca* | Strigidae | Secondaries |
| White | Containing UV | *Dacelo novaeguineae* | Alcedinidae | Breast |
| White | Containing UV | *Ceryle rudis* | Alcedinidae | Throat |
| White | Containing UV | *Lagopus lagopus* | Phasianidae | Breast |
| Special | Multiphase | *Plegadis falcinellus* | Threskiornithidae | Upper wing coverts |
| Special | Adventitious | *Gypaetus barbatus* | Accipitridae | Belly |
| Special | Multiphase | *Columba palumbus* | Columbidae | Nape |

Reflectance integrals represent the overall brightness of the resulting spectra. In order to obtain information about reflectance quantity, integrals of all spectra were calculated. To assess the significance of each individual, solid angle data were processed. The 10 angles of brightest reflection were listed for the individual samples. Furthermore, the mean reflectance integrals were calculated for any elevation level as well as for each rotation sector. The 3 angles with the highest integrals were determined and listed for further analysis. The latter were again incorporated into the evaluation of rotation sectors and elevation levels. Additionally, the entire hemisphere, represented by the analyzed steradians, was divided into clusters of similar solid angles. These clusters encompass four rotation sectors combined with four elevation levels, thus resulting in 16 steric clusters. The rotation angles are uniformly partitioned into 330°-30°, 60°-120°, 150°-210° and 240°-300°, constituting a range of 90°. Elevation levels are partitioned into 30°-40°, 45°-55°, 60°-70° and 75°-85°, representing a range of 15°. The additionally recorded data of 90° and 270° in base relative to the rami was not introduced to spatial clusters due to the variability of their actual rotation angle. The elevation level of 90° has been treated separately as it lacks rotational information. In order to test the reliability of spectral data, the standard deviation was calculated for all integrals of each analyzed feather or plumage part as well as the mean standard deviation for every elevation level and rotation sector. The variability, represented by the mean standard deviation, was calculated for all samples.

Red, yellow, green, blue, and ultraviolet feathers were categorized as chromatic, brown, grey, and white feathers being categorized as achromatic. Chromatic feathers and plumage parts were analyzed independently. Achromatic feathers and plumage parts were pooled, owing to the fact that variation within each of these is solely due to the reflectance properties of the feather's surface. In order to avoid overestimating these achromatic characteristics, the analyzed samples were assessed as one.

Black feathers have not been taken into consideration because light reflection is, by definition, not an integral part of their chromatic properties. The occasional appearance of brightness is entirely evoked by reflections caused by a potentially glossy feather surface. A black feather does not contain any spectral information.

Chromatic feathers and plumage parts were divided into iridescent, structural, and pigment based. Iridescent of course is a structural color. Feathers have been classified as iridescent if the hue changes according to the angle of observation. None of the UV-colored feathers were classified as iridescent as preliminary measurements did not reveal such characteristic. Structural colors might also be pigment-based if the structure exhibits a certain array of, e.g., melanin granular. Furthermore, feather colors have also been classified as structural if the coloration is based upon a combination of pigmentation and structural colors. In most cases, this has been proved by the presence of UV-reflections which are based on nanometer-scale physical structures. Information about UV-reflections has been obtained from preliminary experiments. Coloration has been classified as pigment-based, if it highly depends upon the chromophoric effects of pigmentation and is, furthermore, to a large extent independent of the structural properties of the feather.

White and grey feathers were categorized into those exhibiting or not exhibiting ultraviolet reflections. Even though UV-reflectance does not drop to zero, there is a significant difference between white or grey spectra which continue into the ultraviolet. These were classified as exhibiting ultraviolet reflectance when brightness does not decrease in wavelength longer than 350 nm. Those cases were classified as not exhibiting ultraviolet reflectance when the spectral curve dramatically decreases at wavelengths lower than 400 nm.

Data obtained from the Glossy Ibis (*Plegadis falcinellus*), Bearded Vulture (*Gypaetus barbatus*), and Common Wood-Pigeon (*Columba palumbus*) were treated separately. The underlying chromophoric elements differ significantly from regular feathers. *Plegadis falcinellus* and *Columba palumbus* represent a special type of structural coloration, resulting in a polyphase reflectance curve. The sample of *Gypaetus barbatus* represents adventitious coloration, in contrast to the usually studied chromophoric elements which are physiologically incorporated into the plumage during feather genesis.

## 1.3 Results

The results are presented for each sample individually (see Appendix). The data includes the integral range, i.e., the part of the spectrum which has been considered for analysis. The total average values as well as the percentage value of all integrals of the respective spectra were calculated. A list of the 10 highest integrals, representing the 10 brightest spectra was added. Furthermore, the mean integral values were calculated relating to each elevation level and as well as to each rotation sector. The respective standard deviations are listed, containing both the total values and the percentage. Mean values and respective standard deviations do not exist for the elevation of 90° because the latter is not composed of different rotation sectors. From both elevation levels and rotation sectors, 3 angles of brightest reflections were sorted out and listed for further data processing. The frequency of occurrence of the latter was calculated for each color type as well as for the entire analyzed feathers. This facilitates the demonstration of the significance of the respective angles for the spectral properties.

Angles corresponding to feather barbs do not represent a definite orientation as the arrangement of the rami is variable. They are marked as R90 and R270, according to their orientation relative to the rami of 90° and 270° respectively.

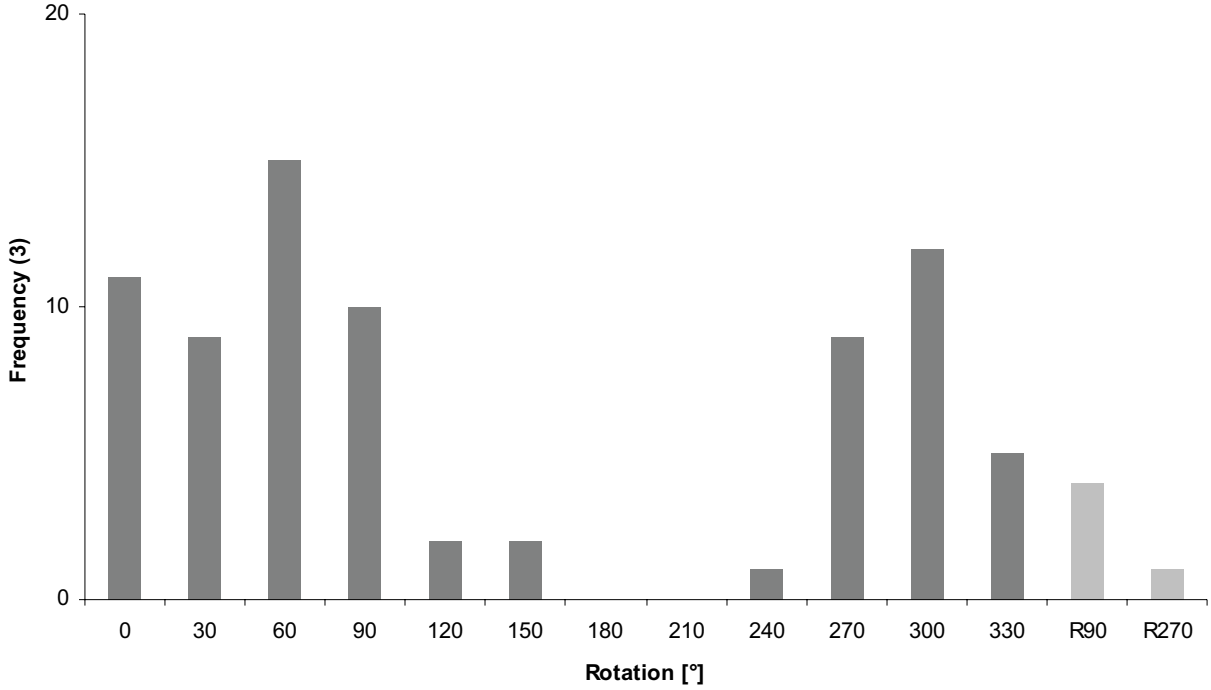
The frequently used elevation level of 90° did not produce the brightest reflections in any analyzed feather or plumage part. The widely used elevation level of 45° resulted in the top-ten scores of brightest reflections, 69 times in all chromatic feathers.

Figs. 7 – 14 show the frequency of respective angles resulting in the highest integrals of the corresponding spectra. The frequency has been calculated from the mean brightness of each level. In order to group data, the 3 top score average integrals of each sample were selected. These are incorporated in the calculation of frequency without being ranked.

The additional sectors referring to orientation in relation to the rami (R90 and R270) are highlighted as they can’t be assigned to a definite arrangement.

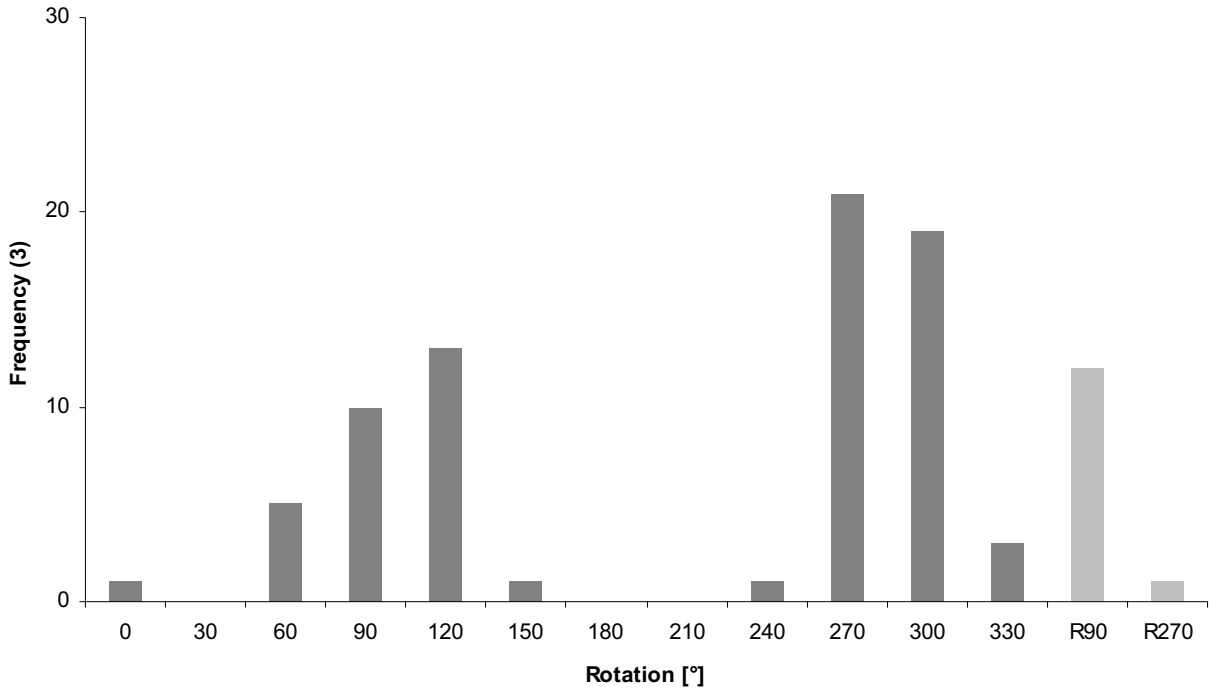
## Rotation sectors

Fig. 7 Rotation sectors of iridescent colors.




Generally two clusters can be distinguished in this figure with a gap between 120° and 240°.

Fig. 8 Rotation sectors of structural colors.




The distribution of bright reflecting sectors is accurate with a maximum at 270°.

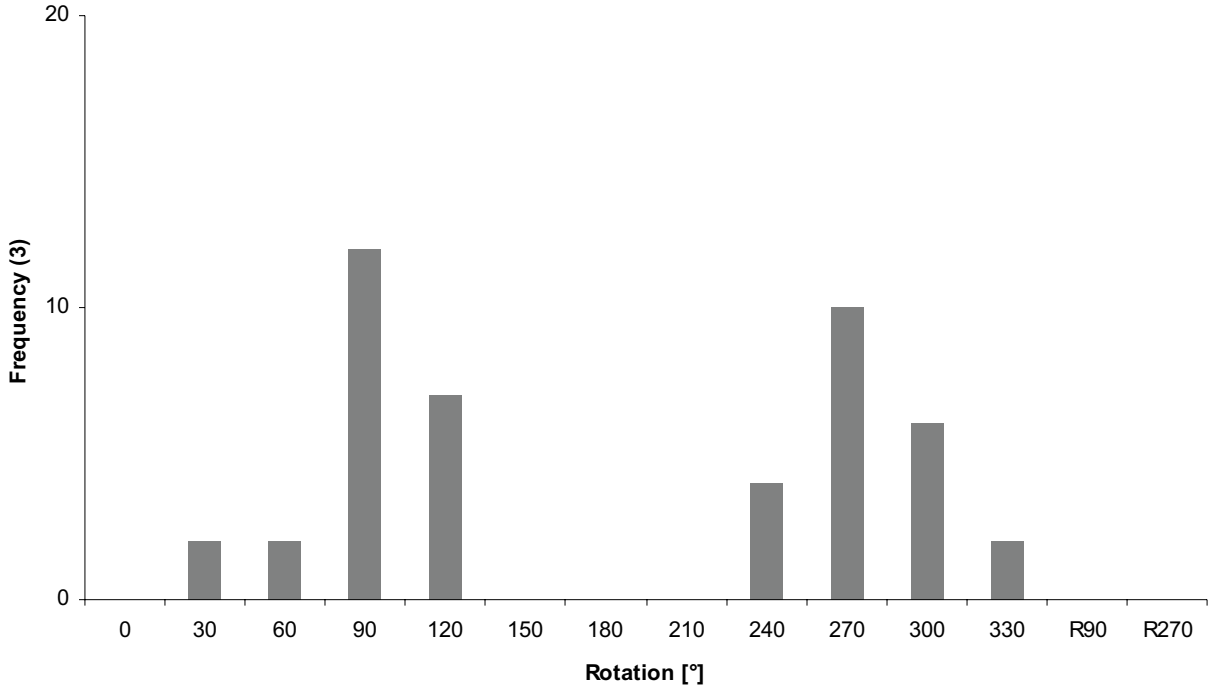



Fig. 9 Rotation sectors of pigment based colors.
Clearly, 2 clusters can be seen with a high at 90° and another peak at 270°.

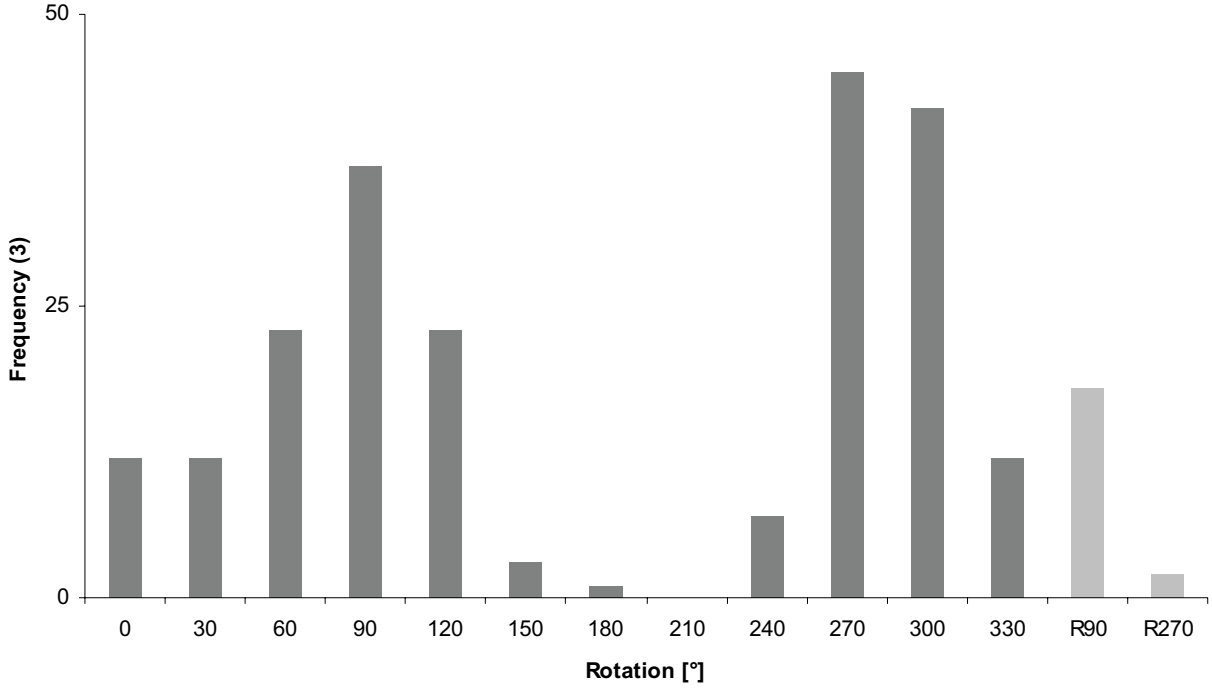
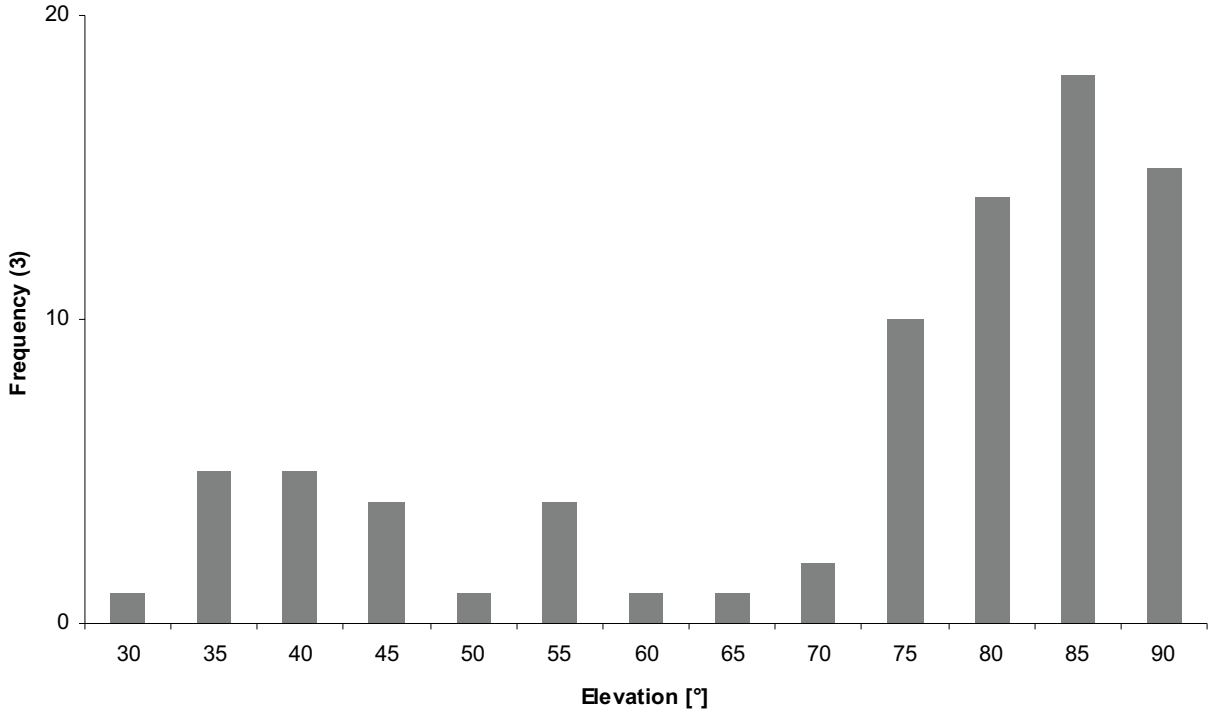



Fig. 10 Rotation sectors of all analyzed samples.

The analysis of all samples makes it possible to distinguish between two groups of highly reflecting sector with peaks at 90° and 270°.

## Elevation levels

Fig. 11 Elevation levels of iridescent colors.




A high frequency is found at 75°-90° with a maximum at 85°. In this range, the best results regarding brightest reflections were obtained. Another small cluster lies at low elevation levels but its magnitude is far below, that of the top levels.

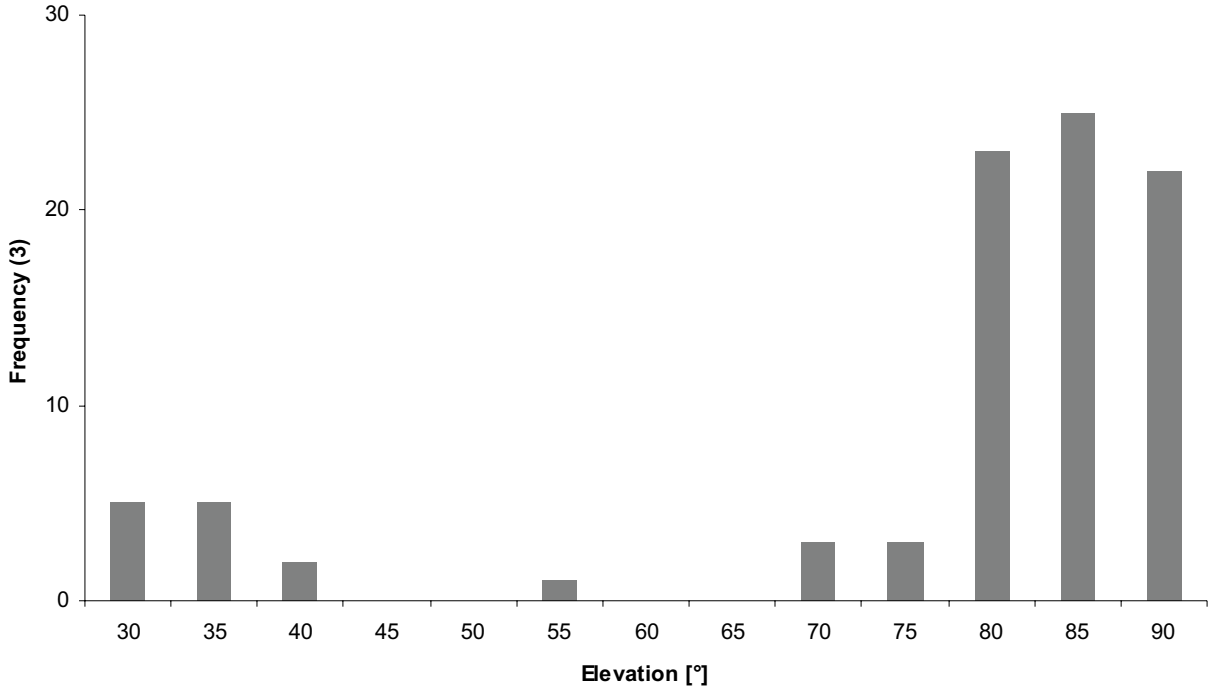



Fig. 12 Elevation levels of structural colors.
Again the highest results are obtained at 80°-90° with a maximum at 85°.

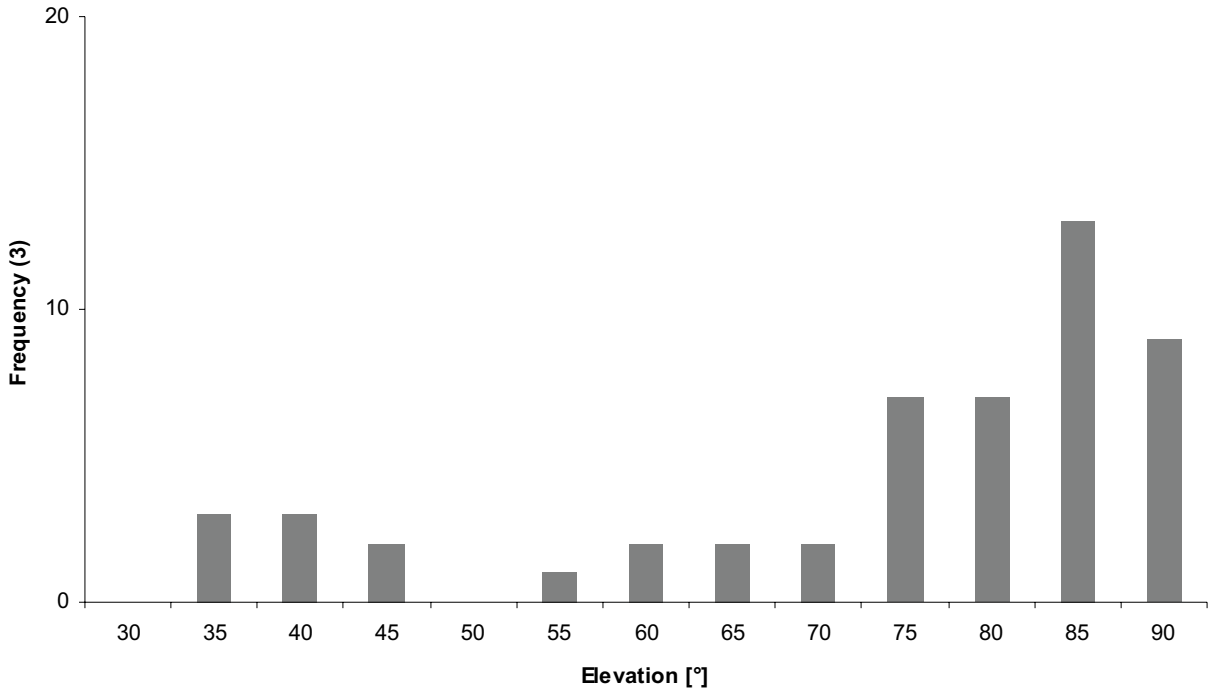



Fig. 13 Elevation levels of pigment based colors.
Even though the allocation appears more consistent, the clear maximum is at 85°.

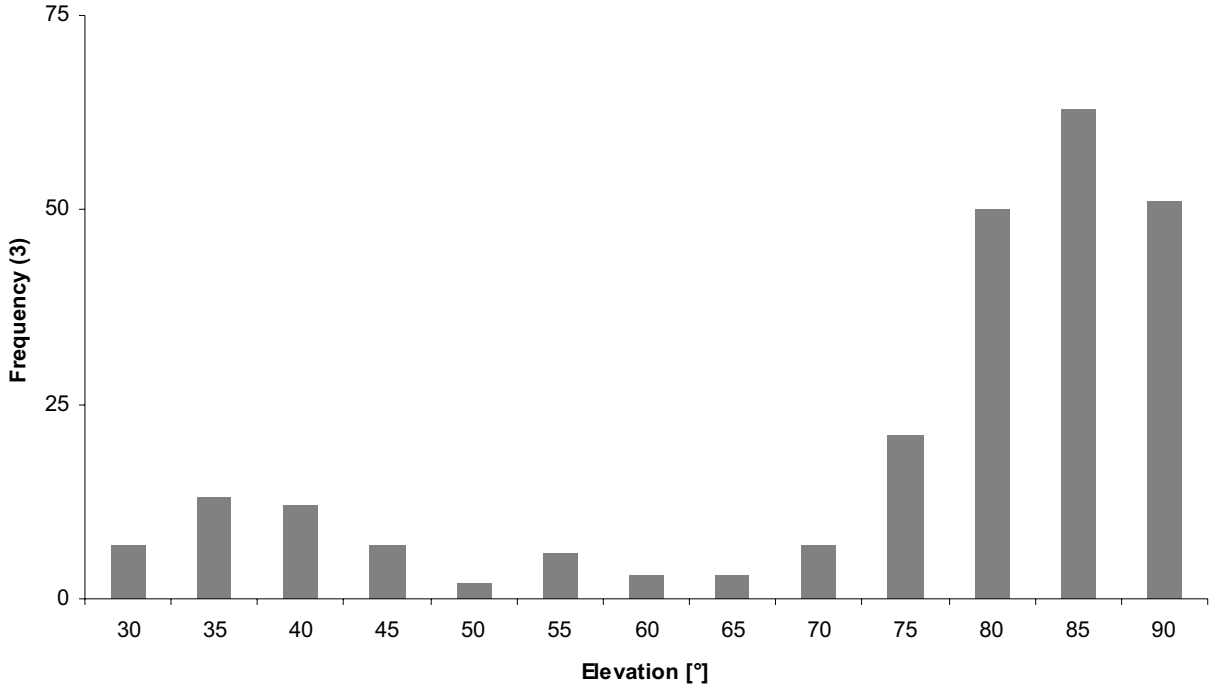



Fig. 14 Elevation sectors of all analyzed samples.
The analysis of all samples confirms the strong tendency for high integrals at elevation levels of 80°-90°. Remarkably, the 90° level does not result in the highest frequency.

Spectral data within groups of clustered steradians

The first digit of a group represents the rotation sector as follows:

1 → 330°, 0° and 30°

2 → 60°, 90° and 120°

3 → 150°, 180° and 210°

4 → 240°, 270° and 300°

The second digit represents the elevation level as follows:

1 → 30°, 35° and 40°

2 → 45°, 50° and 55°

3 → 60°, 65° and 70°

4 → 75°, 80° and 85°

E.g., the combination 3:2 signifies the group of angles in the sector of 150°-210° at an elevation of 45°-55°.

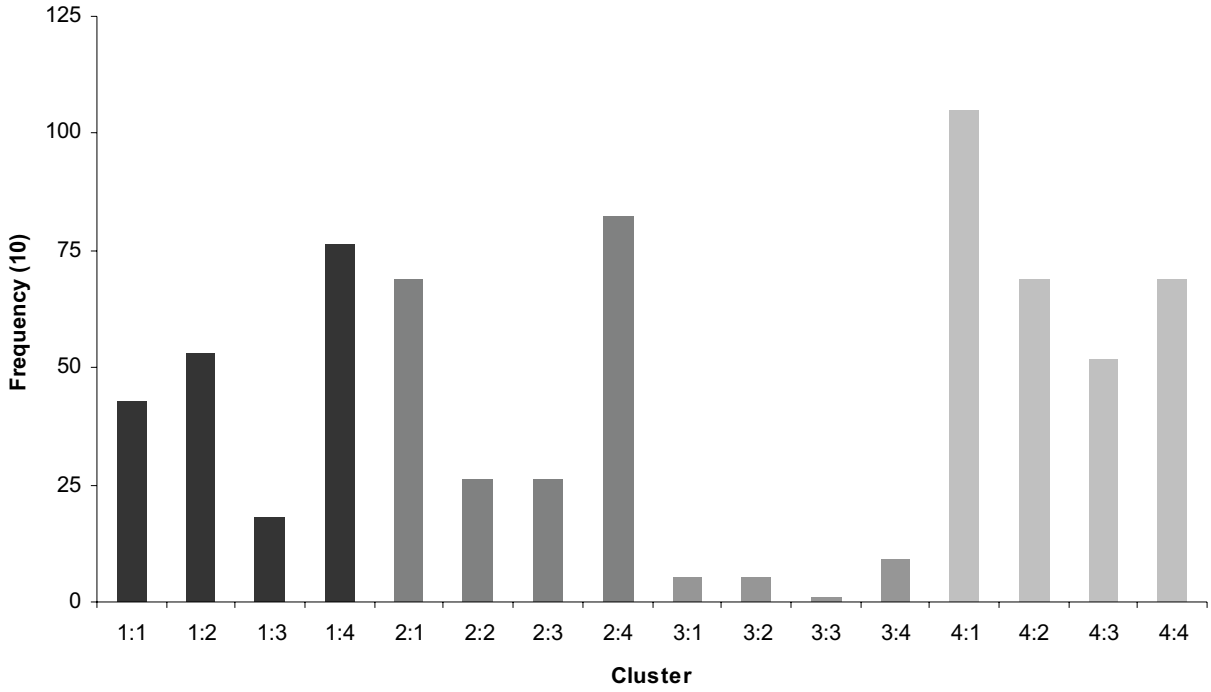



Fig. 15 Spectral data within groups of clustered steradians.
The combined treatment of grouped solid angles demonstrates the dramatically inhomogeneous reflectance properties at different measuring angles.

Variability of data obtained from various solid angles

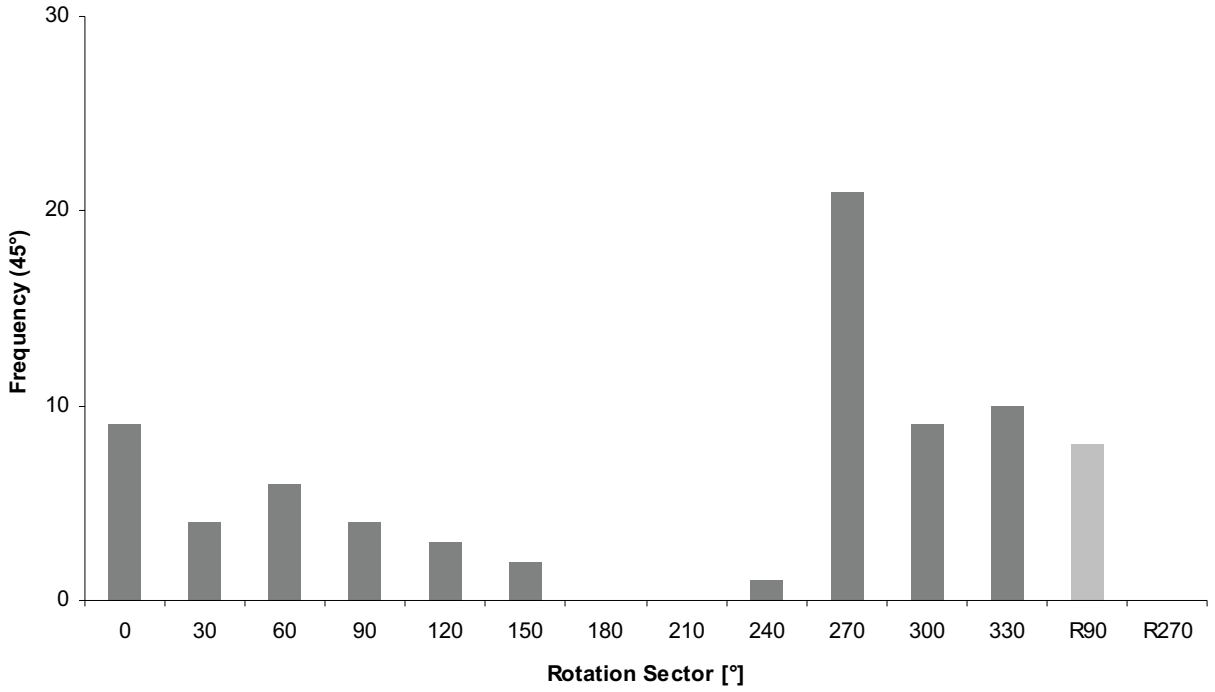



Fig. 16 Variability in the occurrence of bright reflections at elevation of 45°.
Even in a single elevation level, great variability of suitable rotation sectors occurs. The sector most likely to produce the expedient result is at 270°.

As great variability occurs, it is mandatory to take it into account in order to evaluate the reliability of certain solid angles. In publications dealing with reflection spectrophotometry, usually the elevation level is specified but only a few indicate the rotation sector as well. Fig. 16 shows the possible variability that has to be considered in spectral analysis even in a single elevation level. Hence, it demonstrates the necessity to check for the most reliable angle beforehand. Variability has been tested using mean standard deviation of the respective data.

The total variability in iridescent feather coloration is 85.2%

The total variability in structural feather coloration is 36.94%

The total variability in pigment based feather coloration is 32.68%

The total variability in all analyzed feathers and plumage parts is 51.95%

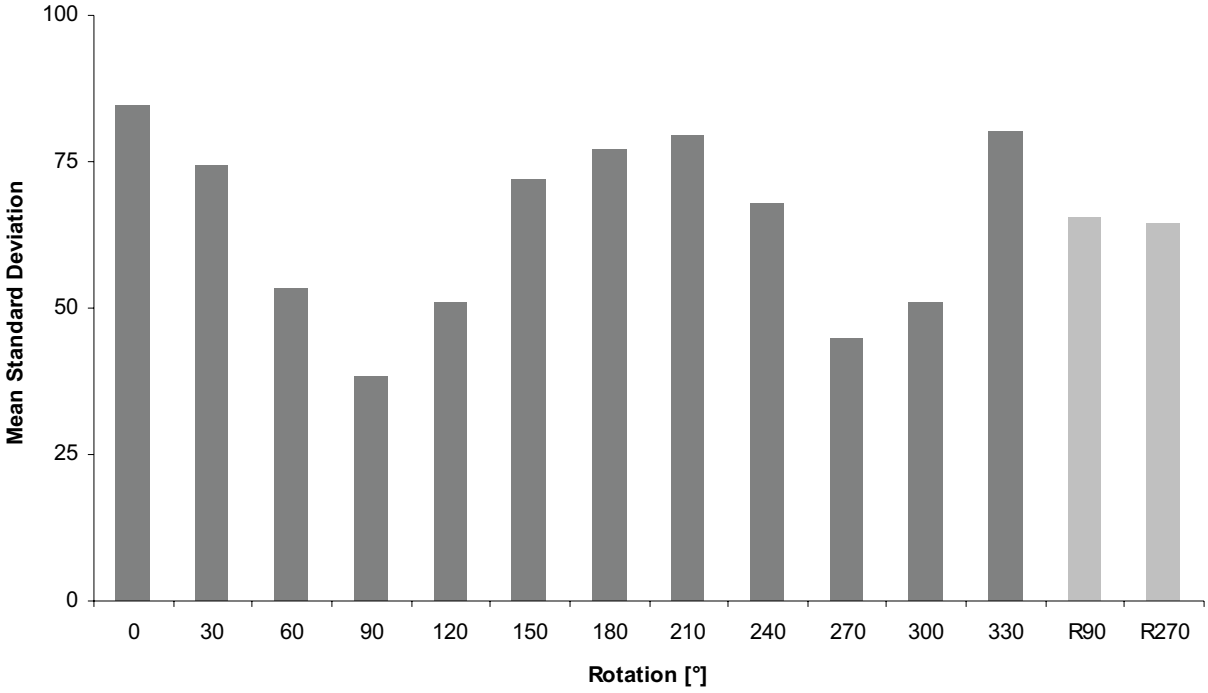



Fig. 17 Mean standard deviation of rotation sectors in iridescent feathers.
The standard deviation is lowest at 90° and 270° while the highest is shifted by almost 90° respectively.

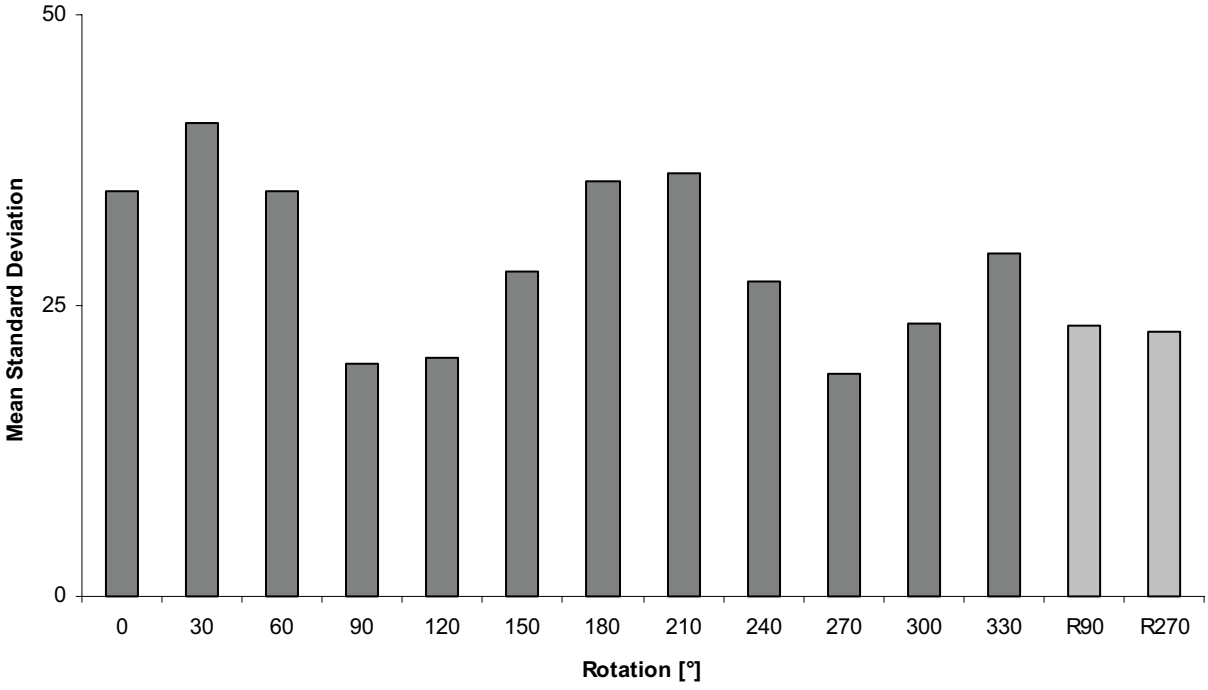



Fig. 18 Mean standard deviation of rotation sectors in feathers with structural coloration.
The results are similar to those of iridescent feathers. Again, standard deviation is lowest at 90° and 270° even though altogether it is about half as much.

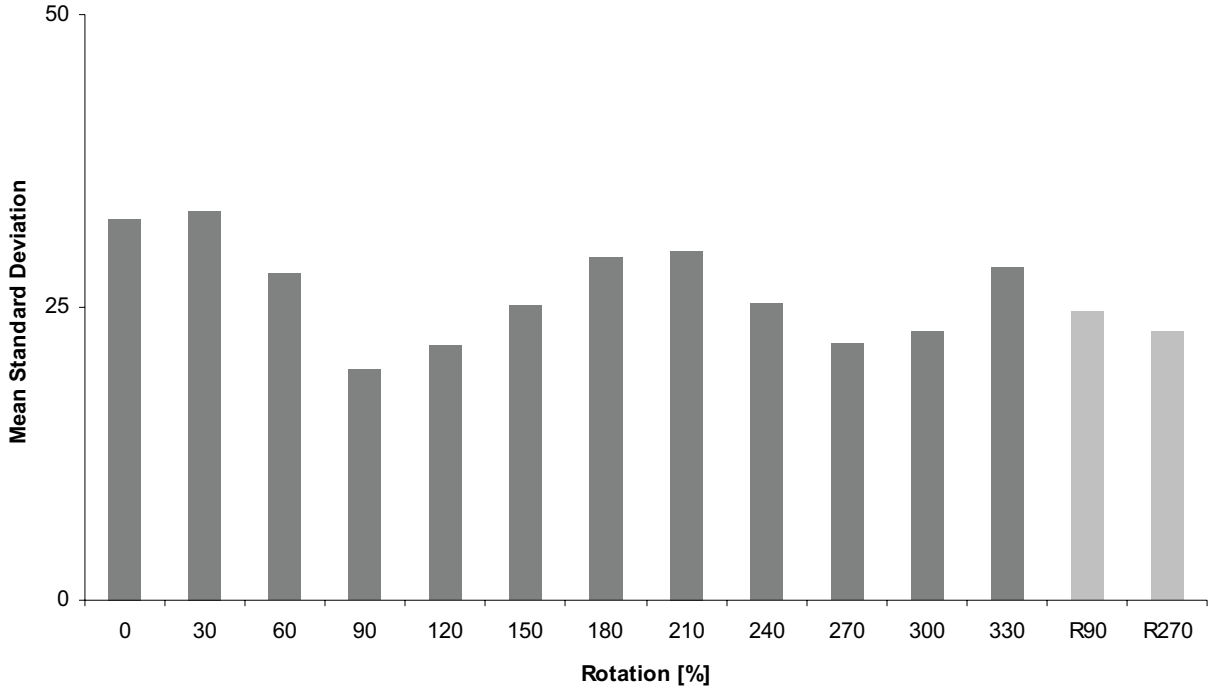



Fig. 19 Mean standard deviation of rotation sectors in feathers with pigment based coloration. Again, standard deviation is lowest at 90° and 270°. Overall variability is comparatively low.

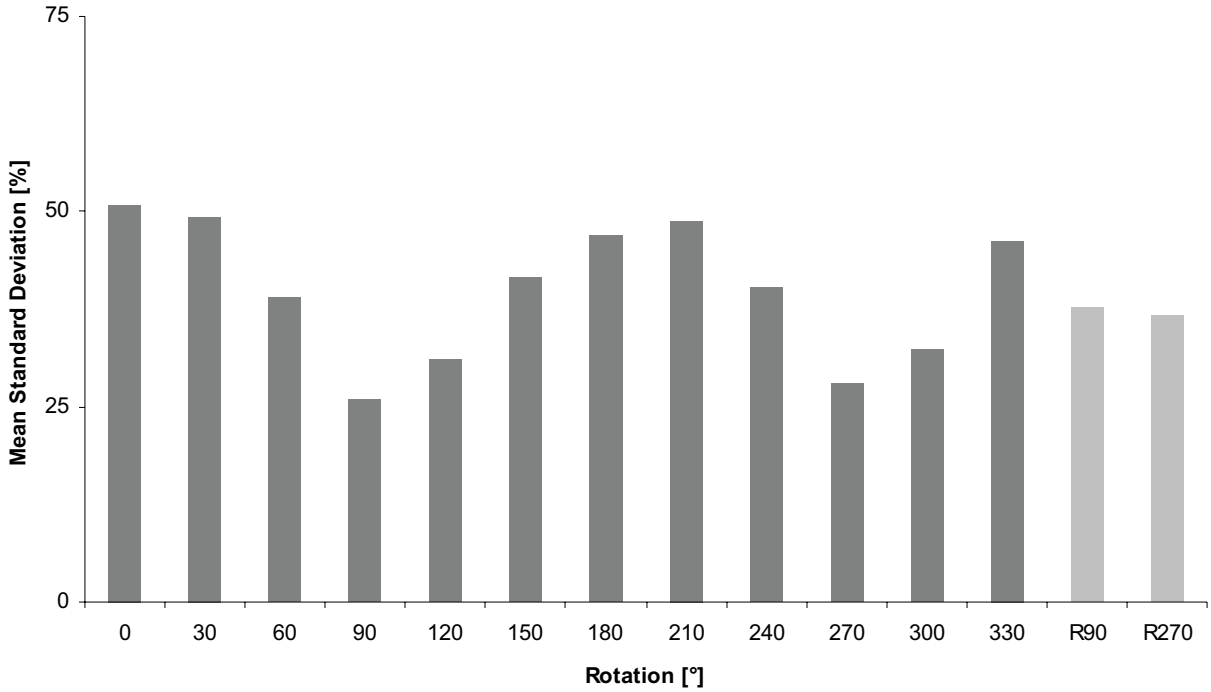



Fig. 20 Mean standard deviation of rotation sectors in all analyzed samples.
The tendency of minimal standard deviation at 90° and 270° is confirmed.

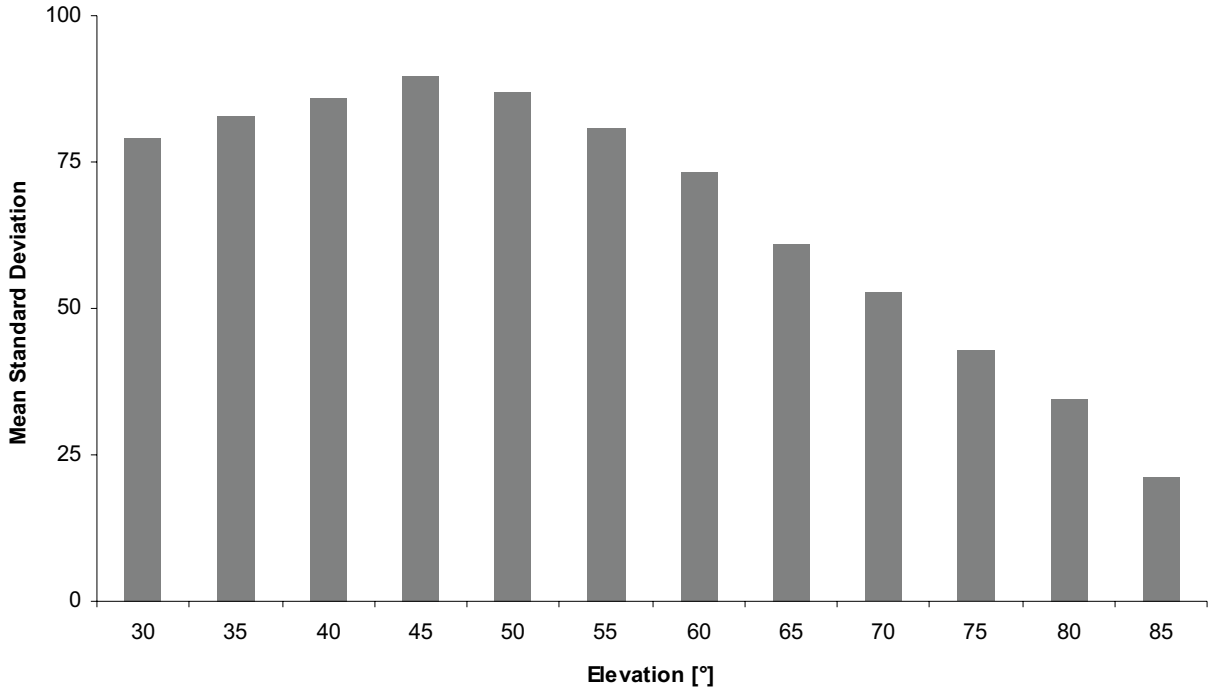



Fig. 21 Mean standard deviation of elevation levels in feathers with iridescent coloration. Mean standard deviation is high at low elevation levels, with a peak at 45°. It continuously decreases at higher elevations.

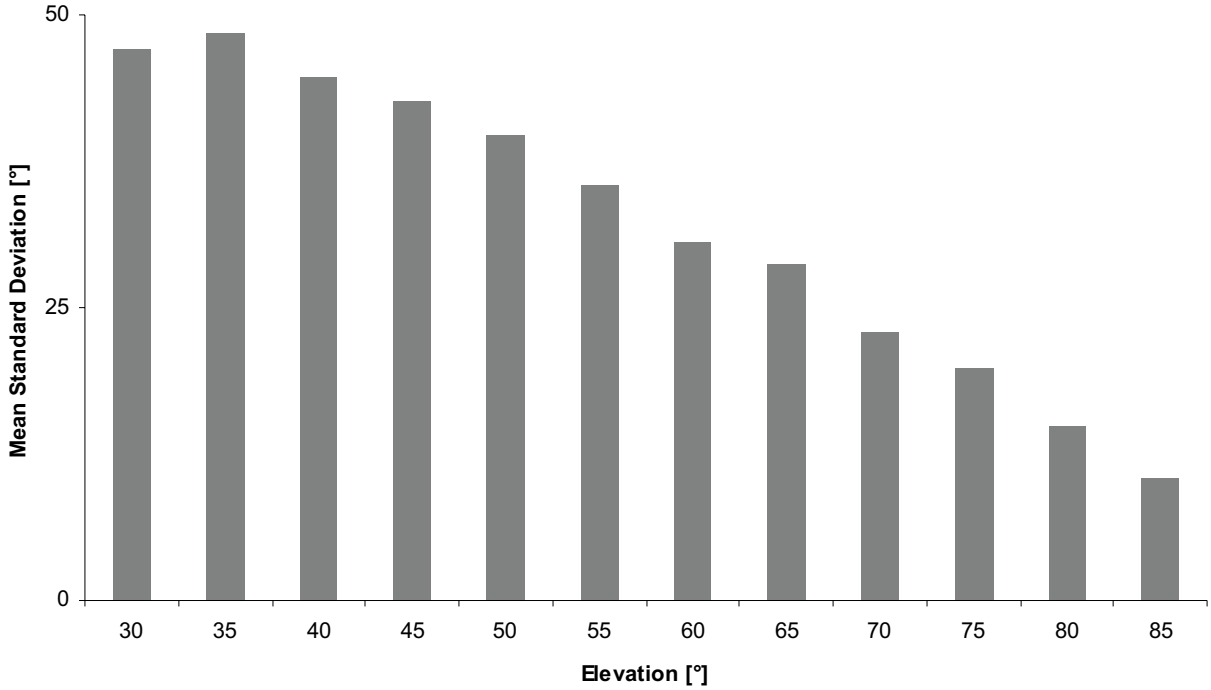



Fig. 22 Mean standard deviation of elevation levels in feathers with structural coloration. Mean standard deviation is continuously decreasing to a minimum at 85°.

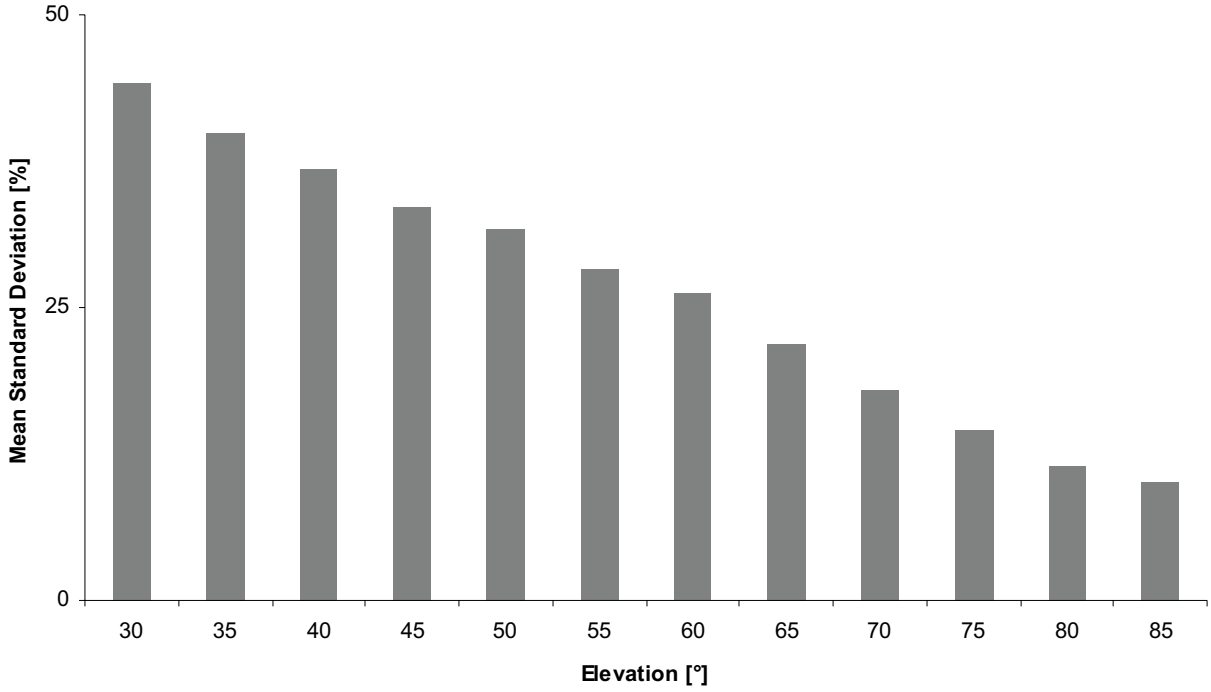



Fig. 23 Mean standard deviation of elevation levels in feathers with pigment-based coloration. Standard deviation is decreasing over the entire range.

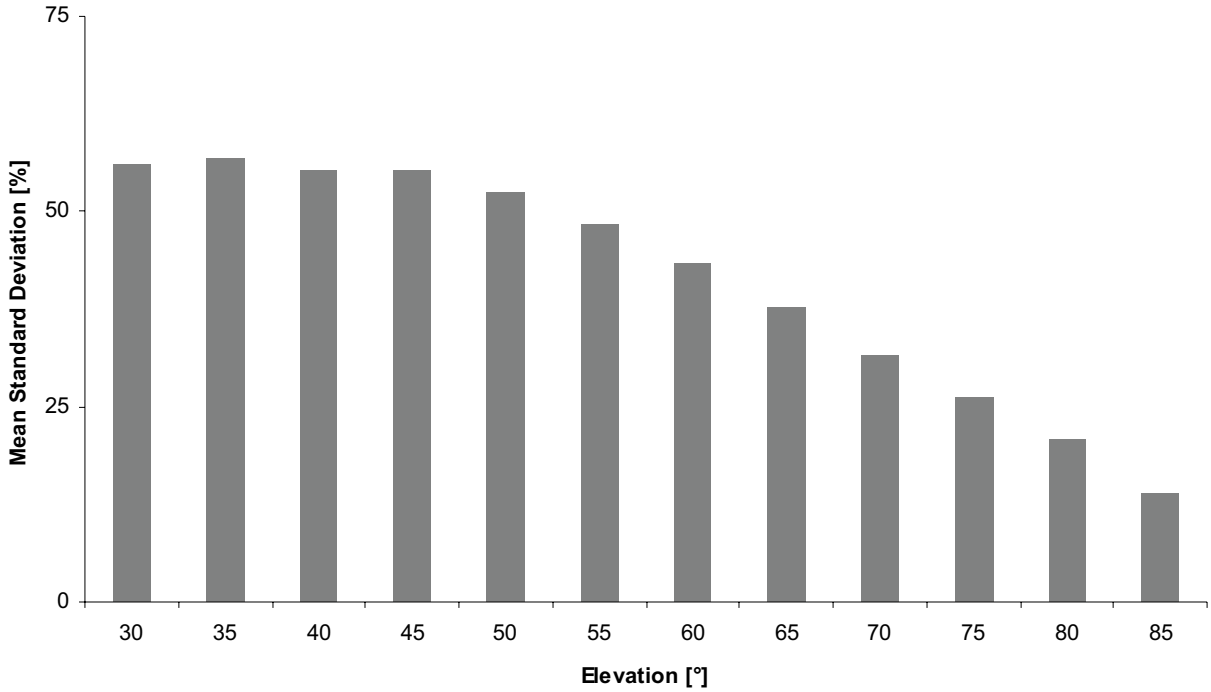



Fig. 24 Mean standard deviation of elevation levels in all analyzed samples. Examination of the entire samples shows peak variability at 35° and a minimum at 85°.

## 1.4 Discussion

### Measuring geometry

Bright reflections are needed in order to obtain an optimal signal-to-noise ratio. These are mainly found in clusters of rotation sectors around 60°-120° and 270°-300°. Although the highest reflecting angles are inconsistent within iridescent, structural and pigment-based colored feathers, these 2 groups are clearly distinguishable. The combined analysis of all samples shows that a rotation sector of 270° results most frequently in the brightest reflections, followed by 300° and 90°. There is a significant gap at 150°-210°. This sector should therefore never be used for gathering spectral data from avian plumage. The sector of 45° which in my study is represented by surrounding 30° and 60° is also not the most suitable angle and should also be avoided.

Measurements were obtained from the outer web of the left side of the bird's body. Reflection integrals of R90° and R270° should be high due to this part of the feather being directed towards a possible perceiver. These angles are usually situated near the 90° and 270° rotation sectors, whereas R90 is closest to the 270° angle and R270° around 90°. It is surprising that these rotation sectors which are directed towards the rami do exhibit good reflectance properties. This could be result of the fact that not only the feather barbs but the barbules too are involved in color generation. Moreover, the maximal reflections seem to correlate with the angle relative to the entire feather and not with an angle relative to the barbs. The latter is variable as the barbs' orientation is different in diverse feathers. It is important to note, that these results are generalized and do not correspond to any one feather or plumage part. There are various feathers, bearing superior reflection properties under different conditions which could be involved in specific signaling. Moreover, coincident illumination and viewing is far from any natural setting.

With regards to elevation levels, the analysis of reflection geometry produced a number of significant results. In no samples, did measurements produce the best results at the commonly used perpendicular angle. Even although the mean brightness of elevation levels of 80°, 85° and actually 90° are at the highest stage. The widely used elevation level of 45° produces top-ten scores of brightest

reflections, 69 times in all chromatic feathers. These cases include Trochilidae (13) and Psittacidae (10).

Nonetheless, analyzing elevation levels reveals a significant result in favor of 80°, 85° and 90°. In all cases, an elevation of 85° produced the best results. The frequently used perpendicular angle is in line with these findings and therefore still highly recommendable.

Variability

Reproducibility of measurement is limited by the variability within one single feather patch or plumage part. Variability does not affect data as long as the highest degree of accuracy can be guaranteed when selecting solid angles for measuring. Slightest alterations of the desired position of the reflection probe will lead to variation in spectral reflections. Most studies involving series of specimens are conducted under difficult conditions and minor variations in measuring geometry have to be accepted. In general, museum bird skins are analyzed and hence it is complicated to exactly position the reflection probe head. Even when using a spacer tube with an angular top, elevation levels might vary due to the flexible surface. Therefore, variability in reflections should be as low as possible in order to keep alterations under control. Many publications dealing with reflection spectrophotometry provide information about the elevation level of respective measurements. In only some cases the rotation sector is also indicated. However, this information is crucial, as spectral variability between different sectors exceeds appropriate rates. Variability in rotation sectors, exemplified at the elevation level of 45°, demonstrates clearly, the impact of orientation on the measuring geometry. Therefore the problem has to be dealt with that there might be no constancy even in data obtained from the same specimen. The total variability, represented by the mean standard deviation is unfavorably high at 51.95%. Hence, an accurately defined measuring geometry has to be perpetuated throughout an entire study. However, brightness alone does not provide explicit information about a certain specimen and, to make a comparison between different taxa necessitates a large number of measurements.

The total variability is as expected highest in iridescent plumage coloration. Since brightness changes along with hue, iridescence implies changes in hue in dependent

on the viewing angle. Variations in brightness in structural and pigment-based colors are lower than in iridescently colored samples. This was also expected, as to the human observer, most of these feathers appear equal, independent of the angle of observation. Since variability is still uncomfortably high, there is also a strong need for a high number of single measurements.

The alterations in dark feathers, like brown or dark blue feathers, which are not iridescent, can be referred to an overall background noise. This background noise consists of non chromatic brightness, caused by unaltered reflected light due to the glossy properties of a feather surface. It does not contain hue or chroma based on the chromophoric elements of the feather.

In terms of reliability only two sectors can be recommended for measurements. These are 90° and 270° where the mean standard deviations are minimal. Peak variability is reached at rotation sectors of 330°-0° and 150°-210°. These angles are unsuitable for gathering spectral data.

When dealing with elevation levels, development of variability is straightforward. Generally speaking, variability decreases analogous to increasing elevation levels. Iridescently colored feathers show peak variability at 45° which would make this popular elevation level the least recommendable. In structural and pigment-based colored plumage, a peak of mean standard deviation is reached at 35° and 30° respectively. In all samples, the mean standard deviation in elevation levels is lowest at 85°. The high variability at low elevation levels could be the result of the signaling properties of the respective feathers or plumage parts not necessarily designed to be viewed from the top.

The cluster analysis of suitable solid angles confirms these findings in this respect. Highest elevation levels are the most favorable, as well as certain rotation sectors as mentioned earlier. Measurements should never be obtained at elevation levels of 60°-70° and rotation sectors of 150°-210°.

Occasionally, an elevation level of 45° is recommended because specular glare is thought to be reduced at this elevation (e.g., Stein & Uy 2006). The brightness of

reflections at high elevation levels could therefore be a result of mirroring reflections and, hence, be a potential source of error relating to the actual hue or saturation. This property can easily be observed on screen and, if necessary, an alternative angle can be chosen. Moreover, feathers do not exclusively mirror at high elevation levels; in fact, this property depends on the surface structure of different feathers and is highly variable. Actually, further monitoring has indicated that certain feathers exhibit highly mirroring properties even at low illumination and observation levels, though this phenomenon has to be specifically tested individually.

The results of my study suggest using a measuring geometry with an elevation level of 85° and the rotation sector of 270°. On average this combination will ensure the best signal to noise ratio and minor variations in measurements. However, the popular procedure of using a perpendicular angle is the best alternative. This measuring geometry generally provides a highly reflecting setup without any variability. There is no need to be concerned about the rotation angle and hence, the latter is eliminated as potential source of failure. Thus, critical data can be consistently obtained at a high level of reproducibility.

Recommendation

It is advisable to use reflection spectrophotometry when studying plumage coloration. Data gathering based on photographs or drawings suffer from varieties in their reproduction. Any observation, bound by the limits of the human visual system suffers from the restrictions of perceivable spectral range. Moreover, inaccuracies due to variable background illumination are a major source of failure. Slight color variations cannot be quantified and, in the dim light of museum collections, they may easily elude the careful observer. Reflection spectrophotometry is indispensable due to the limitations inherent in other ways of analyzing spectral data.

A spacer tube should be attached to the standard reflection probe head to facilitate reflection spectrophotometric measurements. This spacer should perpetuate as accurately as possible the distance to the surface and the elevation angle. The latter can be ensured via a beveled tip of the spacer tube. Furthermore, a spacer tube protects the analyzed spot from ambient light, making it unnecessary to relate to a darkened place.

To define a procedure suitable for the particular investigation, preliminary observations should be made, assuming the needed information can actually be obtained. Dealing with taxonomy, it is unnecessary to mimic natural illumination and viewing conditions, as data are based on accuracy, reproducibility and objectiveness. In terms of ecological or behavioral studies, the respective measuring geometry has to be specifically selected. However, as long as reflection probes with coincident illumination and reading fibers are used, it is not possible to cope with natural conditions. For any application, it is mandatory to control spectra on the screen during measurements. This option will provide reliable information and is more important than the accuracy of other aspects relating to preparing and constructing spectrophotometers.

## 1.5 Abstract

Plumage coloration of museum bird skins provides significant morphometrical data. Besides different methods for analyzing coloration, reflection- spectrophotometry is the most effective way to gather such data, coping with the reflection of UV light by numerous feathers. Measuring geometry dramatically affects the quality of the obtained data. When using coincident illumination and reading fibers of a conventional reflection-spectrophotometer, I would advice positioning the latter at a perpendicular angle to the surface.

## 1.6 Technical terms used

| | |
|---|---|
| Measuring geometry: | The entire arrangement used to position illumination and reading fibers of a reflection spectrophotometer |
| Elevation: | Vertical angle |
| Elevation level: | Sum of possible positions with a given vertical angle |
| Rotation: | Horizontal angle |
| Rotation sector: | Sum of possible positions for a given horizontal angel |
| Reflectance integral: | Area of a spectrum; representing overall brightness |

## 1.7 References


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

Amundsen, T., Forsgren, E. & Hansen, L. T. T. 1997. On the function of female ornaments: male bluethroats prefer colourful females. *Proc. R. Soc. Lond. B* 264: 1579-1586.

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

Andersson, S. & Prager, M. 2006. Quantifying Colors. In Hill, G. E. & McGraw, K. J. (Eds) Bird Coloration (pp. 41-89). Cambridge, Massachusetts: Harvard University Press.

Arnold, K. E., Owens, I. P. & Marshall, N. J. 2002. Fluorescent signaling in parrots. *Science* 295: 92.

Auber, L. 1956. The distribution of structural colours and unusual pigments in the class Aves. *Ibis* 99: 463-476.

Badyaev, A. V. & Young, R. L. 2004. Complexity and integration in sexual ornamentation: an example with carotenoid and melanin plumage pigmentation. *J. Evol. Biol.* 17: 1317-27.

Bailey, S. F. 1978. Latitudinal gradients in colors and patterns of passerine birds. *Condor* 80: 372-381.

Bancroft, W. D., Chamot, E. M., Merritt, E. & Mason, C. W. 1923. Blue feathers. *Auk* 40: 275-300.

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

Bennett, A. T. D., Cuthill, I. C., Partridge, J. C. & Lunau, K. 1997. Ultraviolet plumage colors predict mate preferences in starlings. *PNAS* 94: 8618-21.

Berthold, P. 1965. Über nicht durch Pigment bedingte Rostfärbung bei Vögeln. *Naturwissenschaften* 52: 400-401.

Berthold, P. 1967. Über Haftfarben bei Vögeln: Rostfärbung durch Eisenoxid beim Bartgeier (*Gypaetus barbatus*) und bei anderen Arten. *Zool. Jb. Syst.* 93: 507-595.

Berthold, P. 1968. Haftfarben bei Vögeln. *Umschau in Wissenschaft und Technik* 14: 438-439.

Bleiweiss, R. 1994. Behavioural and evolutionary implications of ultraviolet reflectance by gorgets of sunangel hummingbirds. *Anim. Behav.* 48: 978–981.

Bleiweiss, R. 2004. Ultraviolet plumage reflectance distinguishes sibling bird species. *PNAS* 101: 16561-4.

Brush, A. H. 1978. Avian pigmentation. New York.

Brush, A. H. 1990. Metabolism of carotenoid pigments in birds. *Faseb J.* 4: 2969-77.

Brush, A. H. & Power, D. 1976. House finch pigmentation: carotenoid metabolism and the effect of diet. *Auk* 93: 725-739.

Burkhardt, D. 1989. UV vision: a bird's eye view of feathers. *J. Comp. Physiol. A:* 164: 787-796.

Burkhardt, D. 1996. Die Ultraviolett-Tüchtigkeit des Vogelauges und einige Konsequenzen. *Naturwissenschaften* 83: 492-497.

Burkhardt, D. & Finger, E. 1991. Black, White and UV: how birds see birds. *Naturwissenschaften* 78: 279-280.

Burtt, E. H. J. 1986. An anlysis of physical, physiological, and optical aspects of avian coloration with emphasis on wood-warblers. *Ornithol. Monogr.* 38: 1-126.

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

Cuthill, I. C., Bennett, A. T. D., Partridge, J. & Maier, E. J. 1999. Plumage reflectance and the objective assessment of avian sexual dichromatism. *Am. nat.* 153: 183-200.

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

Doucet, S., Shawkey, M., Rathburn, M., Mays Jr, H. & Montgomerie, R. 2004. Concordant evolution of plumage colour, feather microstructure and a melanocortin receptor gene between mainland and island populations of a fairy-wren. *Proc. R. Soc. Lond. B* 271: 1663-1670.

Durrer, H. 1965. Bau und Bildung der Augfeder des Pfaus ( *Pavo cristatus* L.). *Rev. Suisse de Zool.* 72: 263-409.

Durrer, H. & Villiger, W. 1962. Schillerfarben der Nektarvögel (Nectariniidae). *Rev. Suisse de Zool.* 69: 801-814.

Durrer, H. & Villiger, W. 1966. Schillerfarben der Trogoniden. *J. Ornithol.* 107: 1-26.

Durrer, H. & Villiger, W. 1975. Schillerstruktur des Kongopfaus (*Afropavo congensis* Chapin, 1936) im Elektronenmikroskop. *J. Ornithol.* 116: 94-102.

Dyck, J. 1966. Determination of plumage colours, feather pigments and - structures by means of reflection spectrophotometry. *Dansk Ornith. Foren. Tidsskr.* 49-76.

Dyck, J. 1987. Structure and light reflection of green feathers of fruit doves (*Ptilinopus* spp.) and an Imperial Pigeon (*Ducula concinna*). *Biologiske Skrifter* 30: 1-31.

Dyck, J. 1992. Reflectance spectra of plumage area colored by green feather pigments. *Auk* 109: 293-301.

Eaton, M. D. 2005. Human vision fails to distinguish widespread sexual dichromatism among sexually "monochromatic" birds. *PNAS* 102: 10942-10946.

Eaton, M. D. & Lanyon, S. M. 2003. The ubiquity of avian ultraviolet plumage reflectance. *Proc. R. Soc. Lond. B* 270: 1721-1726.

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

Finger, E. & Burkhardt, D. 1994. Biological aspects of bird colouration and avian colour vision including ultraviolet range. *Vision Res.* 34: 1509-14.

Fitzpatrick, S. 1998. Colour schemes for birds: structural coloration and signals of quality in feathers. *Annales Zoologici Fennici* 35: 67-77.

Fox, D. L. 1976. Animal biochromes and structural colours. Berkley, Cal.: Univ. of Cal. Pr.

Frank, F. 1939. Die Färbung der Vogelfeder durch Pigment und Struktur. *J. Ornithol.* 87: 426-523.

Giersberg, H. & Stadie, R. 1932. Zur Entstehung der gelben und roten Gefiederfarben der Vögel. *Z. f. Vergl. Physiol.* 18: 696-708.

Goldsmith, T. H. 1980. Hummingbirds see near ultraviolet light. *Science* 207: 786-788.

Gomez, D. & Voisin, J. F. 2002. Spectrometry validates subspeciation in the Kerguelen Tern (*Sterna virgata*). *Marine Ornithology* 30: 19-24.

Grill, C. P. & Rush, V. N. 2000. Analysing spectral data: comparison and application of two techniques. *Biol. J. Linn. Soc.* 69: 121-138.

Hausmann, F., Arnold, K. E., Marshall, N. J. & Owens, I. P. F. 2003. Ultraviolet signals in birds are special. *Proc. R. Soc. Lond. B* 270: 61-67.

Hill, G. H. 1998. An easy, inexpensive means to quantify plumage coloration. *J. Field Ornithol.* 69: 353-363.

Hofmann, C. M., Cronin, T. W. & Omland, K. E. 2006. Using spectral data to reconstruct evolutionary changes in coloration: carotenoid color evolution in New World orioles. *Evolution* 60: 1680–1691.

Hudon, J. 2005. Considerations in the conservation of feathers and hair, particularly their pigments. *CAC / ACCR 31st Annual Conference,* pp. 127-148.

Huth, H. H. & Burkhardt, D. 1972. Der spektrale Sehbereich eines Violettohr-Kolibris. *Naturwissenschaften* 59: 650.

Inouye, C. Y., Hill, G. E., Stradi, R. D. & Montgomerie, C. R. 2001. Carotenoid pigments in male House Finch plumage in relation to age, subspecies, and ornamental coloration. *Auk* 118: 900–915.

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

Jacobs, G. H. 1993. The distribution and nature of colour vision among the mammals. *Biol. Rev. Camb. Philos. Soc.* 68: 413-71.

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

Kniprath, E. 1967. Die Bestimmung der Helmholtzkoordinaten von Feder- und Haarfarben im ICI. *Bonn. Zool. Beitr.* 3: 297-307.

Land, M. F. 1972. The physics and biology of animal reflectors. *Prog. Biophys. Molec. Biol.* 24: 77-106.

Lubnow, E. 1963. Melanine bei Vögeln und Säugetieren. *J. Ornithol.* 104: 69-81.

Lubnow, E. & Niethammer, G. 1964. Zur Methodik von Farbmessungen für taxonomische Untersuchungen. *Verh. d. Dtsch. Ges. München* 646-663.

Mahler, B., Araujo, L. S. & Tubaro, P. L. 2003. Dietary and sexual correlates of carotenoid pigment expression in dove plumage. *Condor* 105: 258-267.

Maier, E. J. 1993. To deal with the "Invisible". *Naturwissenschaften* 80: 476-478.

Massaro, M., Davis, L. & Darby, J. 2003. Carotenoid-derived ornaments reflect parental quality in male and female Yellow-eyed Penguins (*Megadyptes antipodes*). *Behav. Ecol. Sociobiol.* 55: 169-175.

McGraw, K. J. & Nogare, M. C. 2004. Carotenoid pigments and the selectivity of psittacofulvin-based coloration systems in parrots. *Comp. Biochem. Physiol. B* 138: 229-33.

McGraw, K. J. & Nogare, M. C. 2005. Distribution of unique red feather pigments in parrots. *Biol. Lett.* 1: 38-43.

McGraw, K. J., Wakamatsu, K., Ito, S., Nolan, P. M., Jouventin, P., Dobson, S., Austic, R. E., Safran, R. J., Siefferman, L. M., Hill, G. H. & Parker, A. R. 2004. You can't judge a pigment by its color: carotenoid and melanin content of yellow and brown feathers in swallows, bluebirds, penguins, and domestic chickens. *Condor* 106: 390–395.

McNaught, M. K. & Owens, I. P. F. 2002. Interspecific variation in plumage colour among birds: species recognition or light environment? *Evol. Biol.* 15: 505-514.

Osorio, D. & Ham, A. D. 2002. Spectral reflectance and directional properties of structural coloration in bird plumage. *J. Exp. Biol.* 205: 2017-27.

Parker, A. R. 2000. 515 million years of structural colour. *J.Opt.A: Pure Appl. Opt.* 2: 1433-1446.

Pearn, S. M., Bennett, A. T. D. & Cuthill, I. C. 2001. Ultraviolet vision, fluorescence and mate choice in a parrot, the Budgerigar *Melopsittacus undulatus*. *Proc. R. Soc. Lond. B* 268: 2273-9.

Prum, R. O. 2006. Anatomy, physics, and evolution of structural colors. In Hill, G. E. & McGraw, K. J. (Eds) Bird coloration (pp. 295-353). Cambridge, Massachusetts: Harvard University Press.

Prum, R. O., Andersson, M. & Torres, R. 2002. Coherent scattering of ultraviolet light by avian feather barbs. *Auk* 120: 163–170.

Prum, R. O., Torres, R., Kovach, C., Williamson, S. & Goodman, S. 1999. Coherent light scattering by nanostructured collagen arrays in the caruncles of the malagasy asities (Eurylaimidae: aves). *J. Exp. Biol.* 202: 3507-3522.

Prum, R. O., Torres, R. H., Williamson, S. & Dyck, J. 1998. Coherent light scattering by blue feather barbs. *Nature* 396: 28-29.

Prum, R. O., Torres, R. H., Williamson, S. & Dyck, J. 1999. Two-dimensional Fourier analysis of the spongy medullary keratin of structurally coloured feather barbs. *Proc. R. Soc. Lond. B* 266: 13.

Prum, R. O. & Williamson, S. 2002. Reaction-diffusion models of within-feather pigmentation patterning. *Proc. R. Soc. Lond. B* 269: 781-792.

Raman, C. V. 1935. The origin of colours in the plumage of birds. *Proc. Ind. Nat. Acad. Sci. A* 1: 1-7.

Reneerkens, J. & Korsten, P. 2004. Plumage reflectance is not affected by preen wax composition in Red Knots *Calidris canutus*. *Journal of Avian Biology* 35: 405-409.

Schmitz-Ornés, A. 2006. Using colour spectral data in studies of geographic variation and taxonomy of birds: examples with two hummingbird genera, *Anthracothorax* and *Eulampis*. *J. Ornithol.*

Selander, R. K., Johnston, R. F. & Hamilton, T. H. 1964. Colorimetric methods in ornithology. *Condor* 66: 491-495.

Shawkey, M. D., Estes, A. M., Siefferman, L. M. & Hill, G. E. 2003. Nanostructure predicts intraspecific variation in ultraviolet-blue plumage colour. *Proc. R. Soc. Lond. B* 270: 1455-1460.

Shawkey, M. & Hill, G. E. 2005. Carotenoids need structural colours to shine. *Biol. Lett.* 1: 121-124.

Shi, Y. & Yokoyama, S. 2003. Molecular analysis of the evolutionary significance of ultraviolet vision in vertebrates. *PNAS* 100: 8308-8313.

Smithe, F. B. 1975. Naturalist's color guide. New York.

Stein, A. C. & Uy, J. A. C. 2006. Plumage brightness predicts male mating success in the lekking Golden-Collared Manakin, *Manacus vitellinus*. *Behav. Ecol.* 17: 41-47.

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

Villafuerte, R. & Negro, J. J. 1998. Digital imaging for colour measurement in ecological research. *Ecol. Lett.* 1: 151-154.

Völker, O. 1947. Über die Struktur der bei Vögeln vorkommenden Porphyrine. *Zeitschrift für Naturforschung* 2b: 316-317.

Völker, O. 1955. Die Pigmentfarben der Vögel. *Naturwissenschaftliche Rundschau* 7: 265-269.

Völker, O. 1961a. Die chemische Charakterisierung roter Lipochrome im Gefieder der Vögel. *J. Ornithol.* 102: 430-438.

Völker, O. 1961b. Bemerkungen über ein grünes, nicht carotinoides Pigment im Kleingefieder von *Rollulus roulroul* (Galli). *J. Ornithol.* 102: 270-272.

Völker, O. 1962. Experimentelle Untersuchungen zur Frage der Entstehung roter Lipochrome in Vogelfedern. *J. Ornithol.* 103: 276-286.

Völker, O. 1963. Gefiederfarben der Vögel und Carotinoide. *J. Ornithol.* 104: 288-289.

Völker, O. 1964. Federn die am Licht ausbleichen. *Natur und Museum* 94: 10-14.

Völker, O. 1965. Stoffliche Grundlagen der Gefiederfarben der Vögel. *Mitteilungen der Naturforschenden Gesellschaft in Bern* 22: 201-223.

Weber, H. 1961. Über die Ursache des Verlustes der roten Federfarbe bei gekäfigten Birkenzeisigen. *J. Ornithol.* 102: 158-163.

With, T. K. 1967. Freie Porphyrine in Federn. *J. Ornithol.* 108: 480-483.

Zuk, M. & Decruyenaere, J. G. 1994. Measuring individual variation in colour: a comparison of two techniques. *Biol. J. Linn. Soc.* 53: 165-173.

# 2 Color changes in museum bird skins

Implications of storage time and conditions on the spectral properties of plumage in avian specimens

## 2.1 Introduction

Plumage coloration is - compared to the skin, beak or eye - fairly stable when stored. Unlike the latter, feathers do not tend to fade immediately after the bird's death. Nevertheless, in certain cases, coloration in museum bird skins does not correspond to the pristine chromatic information. The spectral quality of specimens varies between species, plumage parts, museum collections and specific individuals. Bird evolution produced a natural means to prevent the negative effects of wear, bleaching or other age dependent damage or a change in plumage. A frequent molt, perpetuated even in adult stages of a bird's ontogenesis, provides a clean unspoiled plumage in periodical repeats. Additionally, feathers are maintained by daily preening and bathing for which the birds devote a certain proportion of their time (Cottgreave & Clayton 1994). However, a bird's plumage is exposed to continuous wear, fading and dirt. Their effects increase successively in between molts. Hence, it is mandatory to consider disadvantageous variability in spectral data when analyzing avian coloration. Moreover, this variability does not necessarily represent actual differences within a population. Under certain circumstances, it is administrable to clean feathers, in order to obtain more reliable data (Montgomery 2006).

### Inappropriate specimens

Certain specimens are inappropriate for spectral analysis in the first place. These include species with a naturally, highly variable plumage coloration or color deviations.

Pigmentary abnormalities occur incidentally in different species. Hypochromatism, i.e., the lack of pigments, gives rise to Albinism (all pigments are lacking), Leucism (feather pigments are lacking but beak, skin and eyes are normally pigmented), Schizochroism (one chromophoric element is not developed) and Chloroism (pigments are less densely distributed).

In contrast, Hyperchromatism, i.e., over production of pigments, gives rise to Melanism (excessive production of melanins) and Lipochromatism (excessive production of lipochromes, e.g., carotenoids) (Rutschke 1964). Spectral data obtained from specimens of these types does not allow you to draw conclusions about the spectral properties of the respective population.

My preliminary observations confirmed conspicuous spectral variances in a number of birds, clearly observable even without technical aids. Amongst others, dietary dependent variations in plumage coloration were the most obvious. These findings are in line with the observations of Völker (1964) and include well-recognized species such as flamingos (Phoenicopteridae), Orange Bishop *(Euplectes franciscanus),* Scarlet Ibis (*Eudocimus rubber),* Roseate Spoonbill (*Ajaia ajaja),* and the Great White Pelican (*Pelecanus onocrotalus)*. Furthermore, McNett & Marchetti (2005) analyzed 10 species of wood-warblers (Parulidae) from museum collections and reported uneven decreases in brightness compared to individuals from natural populations.

Some adventitious colors are applied from uropygial gland secretions, e.g., the seasonally occurring red color of the Black-headed Gull (*Larus ridibundus*), Great Black-headed Gull (*Larus ichthyaetus*) and the White Pelican (*Pelecanus onocrotalus*) (Stegmann 1956). These colors are uncomfortably volatile and thus, inappropriate for spectral analysis. Other adventitious colors taken up from the environment depend highly on the availability. Thus their application to the plumage is inhomogeneous, e.g., Bearded Vulture (*Gypaetus barbatus*) (Berthold 1965, 1967).

Natural variations

Besides the cases in which specimens are inappropriate in the first place, further difficulties involving spectral inaccuracies occur frequently. Ornamental coloration, sometimes developed exclusively for courtship, is not evident in regular plumage. Seasonal changes can lead to misinterpretations. Highly polymorphic species (Galeotti *et al.* 2003) are not suitable for spectral analysis, unless polymorphism itself is the subject of the intended study. Thus, naturally occurring alterations of coloration due to subspecies, nutritional condition, molt, age, season, availability of precursors for pigmentation has to be taken into account when dealing with chromatic information and the spectral properties of bird populations.

Plumage color has also been reported to be subject to alterations under natural conditions during a bird's lifecycle. These can be result of UV damage, abrasion or bacterial degradation. Progressively decreasing brightness after molt might not be significant but is still present. Seasonal changes, including slight shifts in hue, might be almost unnoticeable without technical aids (Örnborg *et al*. 2002). Nevertheless, seasonal color shifts can result entirely from plumage abrasion and fading. These changes are correlated with the periods between molts (Barrowclough & Sibley 1980, McGraw & Hill 2004).

Color changes

Structural colors are in general more aging resistant than most pigment based colors. Structural colors of different organisms can still be visible in fossil specimen including a 49 million year old beetle with iridescent wing coverts (Parker 1998, 2000, 2005). If based on non-pigment structures, chromophoric elements cannot become washed out by any agent. Nevertheless, even coloration based on nanostructure keratin that produces UV reflectance might be damaged by exposure to the sun (Prum *et al*. 1999) and even nutritional stress can affect structurally based iridescent plumage (McGraw *et al*. 2002). Nonetheless, melanins have been controversially discussed as potential abrasion or degradation protective in avian plumage (Bancroft 1924, Barrowclough & Sibley 1980, Bonser 1995, Burtt & Ichida 2004, Goldstein *et al*. 2004, McGraw & Hill 2004, but q.v. Butler and Johnson 2004). However, the possible ecological significance remains uncertain.

Carotenoids are generally resistant to the negative effects of light exposure and the latter are generally undetectable even in old skins (Völker 1964). Some time ago, Canthaxanthin has been proven to resist bleaching and to have enormous age stability. Völker (1963) demonstrated this phenomenon in a 100 year old specimen of the Scarlet Ibis (*Guara rubra*). However, the same pigment in the Resplendent Quetzal (*Pharomachrus mocinno*) turned out to be highly soluble to alcohol and to fade dramatically when exposed to light (Völker 1964). Furthermore, carotenoids in feathers differ crucially with regard to the ease with which they are released to organic solvents (Hudon 2005). Feathers of other species containing Lutein, proved to be resistant to light-induced decay and, above all, bleaching of carotenoid pigmented feathers appears to be a rare occurrence (Völker 1964).

Carotenoids can contribute to all colors except blue in feathers (McGraw *et al*. 2004, McGraw 2006). As carotenoids occasionally serve as fitness indicators (Hamilton & Zuk 1982, Zuk *et al.* 1990, Stein & Uy 2006), color variations have to be anticipated.

Another chromophoric element employed in feather coloration, but a less frequently distributed pigment, is porphyrin which occasionally induces problems for spectral analysis. While the widespread Kopoporphyrin is degraded by light, the copper binding Turacin is stable to light (Völker 1947, 1961, 1964, 1965; With 1967). Turacin is highly soluble in alkaline solutions and therefore, the intensely red colored feathers of the Turacos (Musophagidae) are frequently subject to loss of coloration (Krumbiegel 1925). This is a serious matter for living birds as well as museum specimens exposed to any, even slightly, alkaline substances.

Museum skins

Museums skins have been collected for over a hundred years. Spectral data is subject to occasional age-dependant color changes in feathers (Cuthil *et al*. 1999, 2000; Hausmann *et al*. 2003). Accordingly, hummingbirds are an interesting avian group since their coloration is predominantly based on structural colors (Auber 1956, Greenewalt *et al*. 1960, Dyck 1976). It is expected that no negative effects occur from differently aged color pigments. Taking this data into consideration, it will be possible to contribute to an evaluation of color measurements involving old and even very old bird skins in natural history museums. This investigation is particularly beneficial for research in systematics and taxonomy based on color comparisons of bird skins as the age dependent effects can be taken into account.

Study goals:

Implications of wear and aging processes in feathers are to be examined.

Potential age dependent color changes in museum bird skins are to be observed.

Effects of different storage conditions are to be taken into consideration.

The reliability of spectral data obtained from stored specimens is to be analyzed.

## 2.2 Material and methods

Reflectance spectra were taken using an Ocean Optics USB 2000 spectrometer, with a Xenon pulse light source, generating wavelengths of visible spectrum and ultraviolet light. A compressed pill of barium sulphate ($BaSO_4$) was used as a white reference standard, a black velvet cloth was being used as a dark reference. Measurements were taken in the absence of ambient light. A black PVC tube was used to maintain the proper distance and angle. The spectra were observed on the screen during measurements to enable reliable measurements of the analyzed plumage parts. This tube was used for reflection probe, protecting it from ambient light. The reflection probe was held in the direction of the distal end of the feathers. The reflection probe is part of the bifurcated cable UV/VIS 400UM from World Precision Instruments, illuminating a field of approximately 2 - 3 $mm^2$. The summation time for each measurement was 10 ms. All reflectance data were measured between the wavelengths 300 and 750 nm. Reflection spectra of each specimen were calculated based on average percentage reflectance values from 50 measurements. The data were processed using the spectrometer software SpectraWin® 5.0.

Photos haven been shot, using a Nikon D70s SLR. To obtain UV-images the UV-Nikkor 105/4.5 lens was employed. A Heliopan BG 23 and a Hoya U 360 filter were combined, to exclude visible and infrared spectra. A Metz CT 45 Flashlight was used as light source. In order to exploit maximal UV-radiation, the diffusion filter was removed from the flashlight.

Age stability in iridescent colors

To demonstrate age stability in structural colors, specimens were chosen based on long term collection and storage. The specimens represent different storage times, and cover about one hundred years. Regarding correctly stored museum bird skins, specimens of the Emerald-bellied Woodnymph (*Thalurania hypochlora*), Tschud's Woodnymph (*Thalurania furcata jelskii*), Green-headed Woodnymph (*Thalurania fannyi verticeps*), Fork-tailed Woodnymph (*Thalurania furcata boliviana*), and Violet-capped Woodnymph (*Thalurania glaucopis*) have been analyzed.

All of the latter were housed in the American Museum of Natural History (AMNH), New York, N.Y., USA. The collection of the AMNH contains a fair profile of specimens constantly collected over more than a century.

Color changes in aged feathers held under different storage conditions

In another analysis, selected examples of insufficiently stored specimen were selected from a series of separate investigations to demonstrate noteworthy effects on plumage coloration in museum bird skins and their implications for spectral data analysis.

The two analog specimens of the Streaked Bowerbird (*Amblyornis subalaris*) are both about 50 years old. One was held in a public exhibition, protected from dust but exposed to intense light on a daily basis. The other specimen was held in a scientific collection and therefore typically protected from light.

Tail feathers of a Glossy Black-Cockatoo (*Calyptorhynchus latami*) have been analyzed according storage time and exposure to environmental hazards. In a 102 year old specimen, covered parts as well as uncovered parts of the same tail feathers were spectrally analyzed. The covered parts had been protected by other plumage parts overlapping the feather. For comparative purposes, the same feather of a two year old specimen was analyzed to obtain information about the pristine unaltered spectral characteristics.

To demonstrate the effects of soiling in plumage, two specimens of the Golden Parakeet (*Aratinga guarouba*) were studied. The soiling is visually distinguishable.

Effects of insect pests were tested in two specimen of the Chestnut-fronted Macaw (*Ara severa*). One of the samples had been damaged by insect pests and its feather structure corrupted.

Effects of changes in hue due to storage time are demonstrated in a specimen of the Red-winged Parrot (*Aprosmictus erythropterus*). The change of hue is especially interesting because changes are almost invisible to a human observer as it mainly occurs in the UV.

Color changes in an Australian King-Parrot (*Alisterus scapularis*)

Spectral data of the entire plumage in two different specimens of the Australian King-Parrot (*Alisterus scapularis*) have been generated to demonstrate the significance of occasional color changes. The most striking samples are shown. The specimens have been held in collection for about 40 years.

Color changes in the Golden Bowerbird (*Prionodura newtoniana*)

The same observations were made in two different specimens of the Golden Bowerbird (*Prionodura newtoniana*). The specimens had both been stored for approximately 50 years.

Color changes in an Eclectus Parrot (*Eclectus roratus*) from a museum exhibition

A unique specimen of the Eclectus Parrot (*Eclectus roratus*) has been studied and analyzed by means of UV-photography. This specimen has been exhibited and therefore been exposed to daylight for several years. Remarkably, only one side has been exposed while the other was turned to the wall, thus protecting it from light-induced damage. The change in hue of the exposed side is clearly visible.

## 2.3 Results

In order to compare the spectral data obtained from the analyzed specimens, the data are presented in a combined manner in the various figures.

Data, concerning age stability in specimens of *Thalurania* are accompanied with the average integral of the particular spectra as well as the percentage standard deviation. The integrals of the spectra represent the overall brightness of the entire color, encompassing the wavelengths from 300 nm to 750 nm. Each of the spectra contains significant color information. The throat and the crown of male *Thalurania* had been chosen due to their exhibiting the most conspicuous colors.

The reflectance spectra of coloration deviated specimens aim to demonstrate potential effects of storage and age on the plumage color. Spectra from the same plumage region are combined.

Age stability in iridescent colors

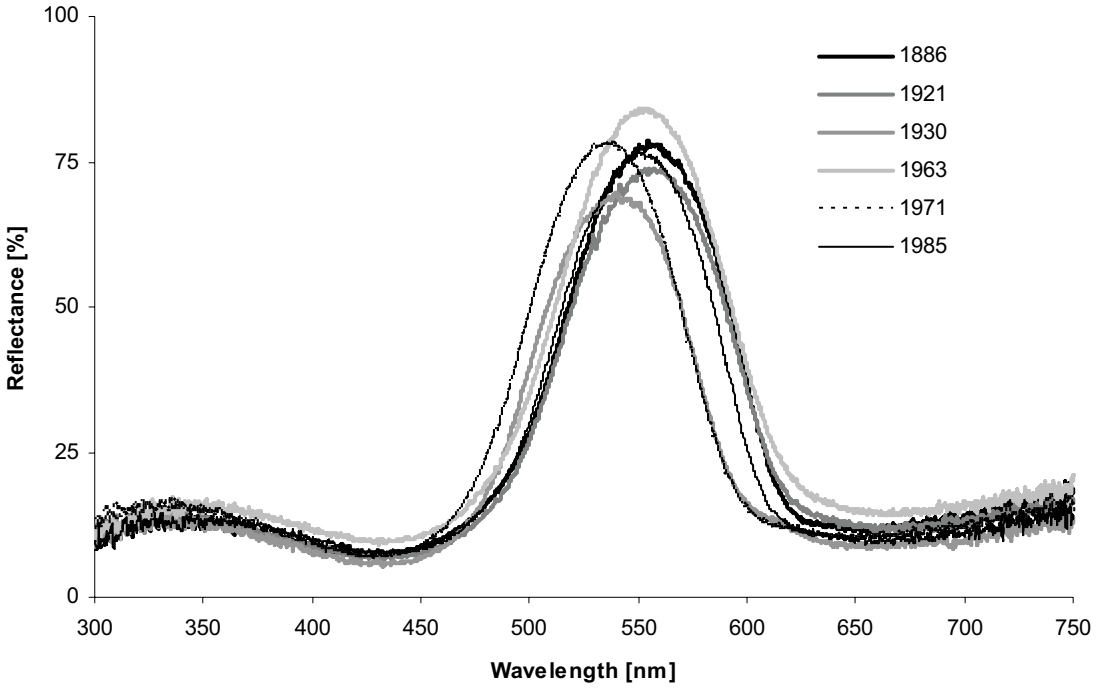



Fig. 25 Crown of an Emerald-bellied Woodnymph (*Thalurania hypochlora*).
Average Integral: 27003 Standard deviation [%]: 3.28

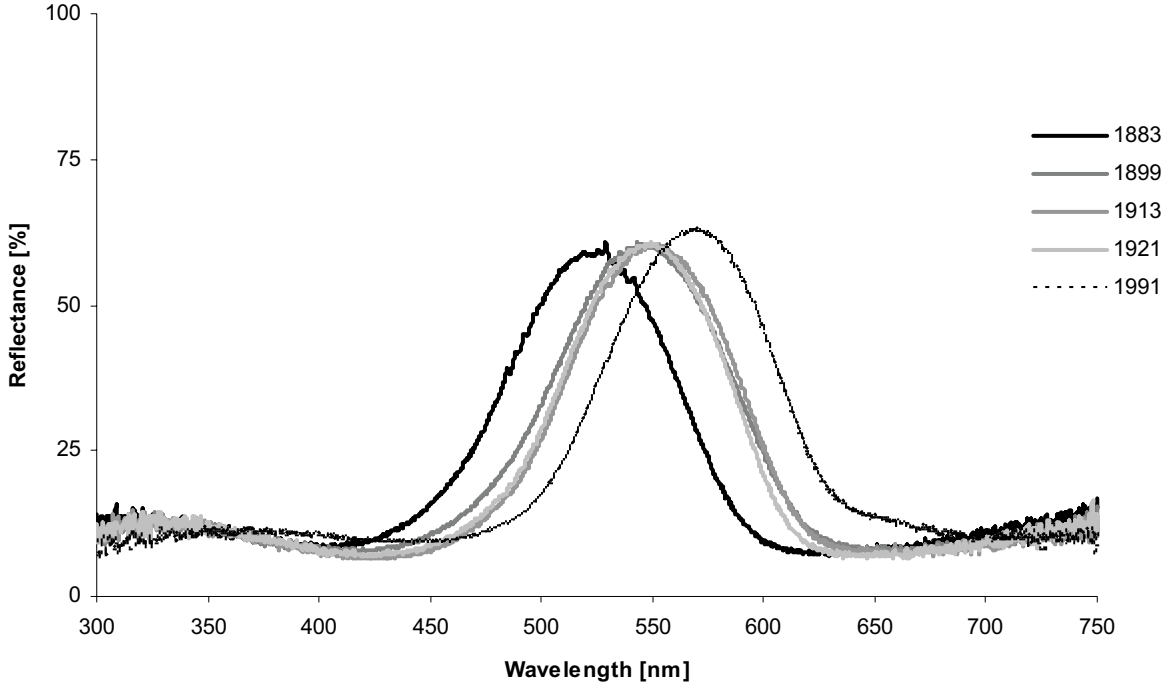



Fig. 26 Throat of a Tschud's Woodnymph (*Thalurania furcata jelskii*).
Average Integral: 32479 Standard deviation [%]: 9.12

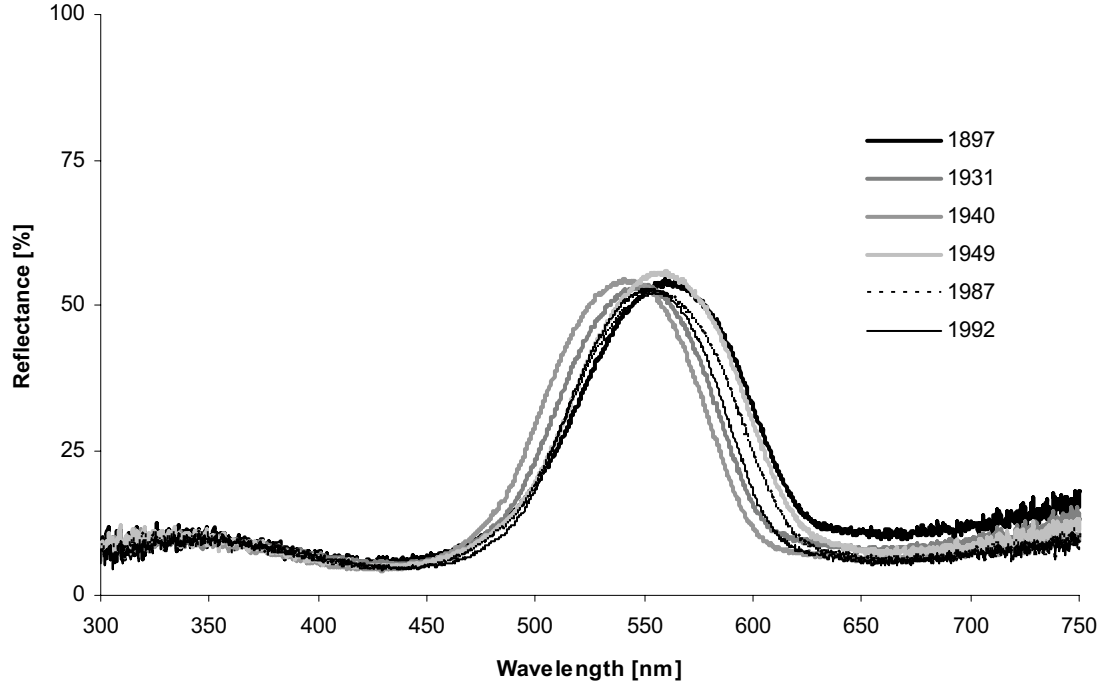



Fig. 27 Throat of a Green-headed Woodnymph (*Thalurania fannyi verticeps*).
Average Integral: 22523 Standard deviation [%]: 6.71

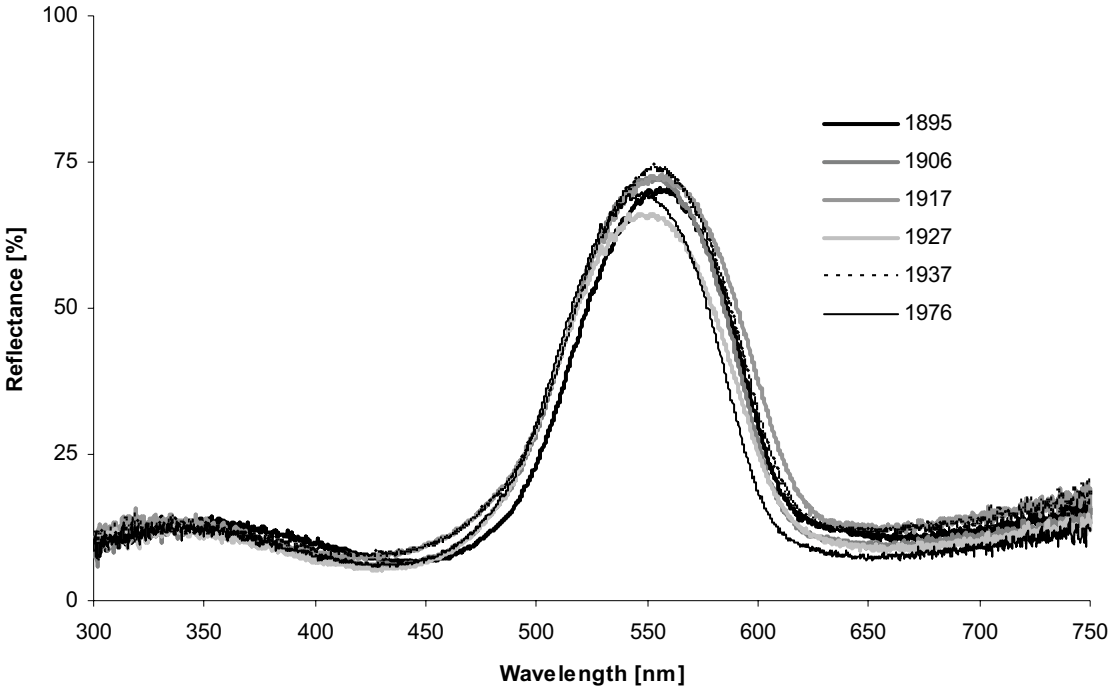



Fig. 28 Throat of a Fork-tailed Woodnymph (*Thalurania furcata boliviana*).
Average Integral: 29970 Standard deviation [%]: 6.98

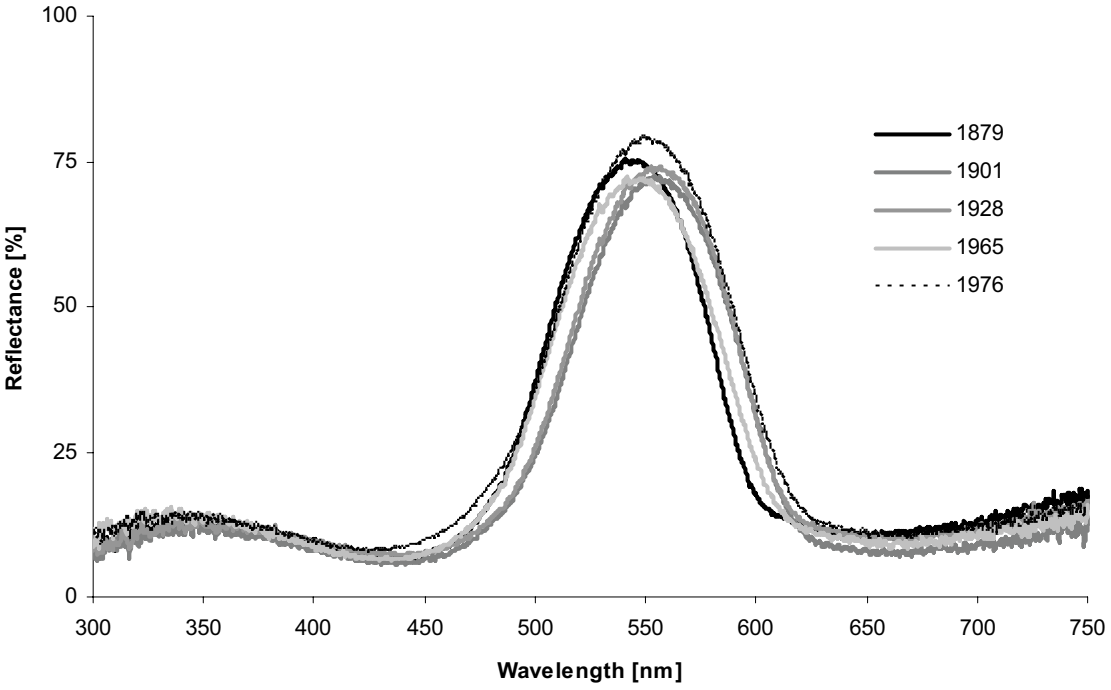



Fig. 29 Throat of a Violet-capped Woodnymph (*Thalurania glaucopis*).
Average Integral: 30692 Standard deviation [%]: 6.1

The spectra of the *Thalurania hypochlora* (Fig. 25) do not exhibit alterations in overall brightness although the hue is slightly shifted. However, both cannot be related to the age of the specimen since the eldest as well as the youngest specimen possess average value. The standard deviation is remarkably low although the analyzed specimens cover a period of about one hundred years.

*Thalurania furcata jelskii* (Fig. 26) alters just as little in total reflectance integral but the hue is shifted in two specimens. Nevertheless there is neither a gradual nor a discrete change which can be related to storage time.

*Thalurania fannyi verticeps* (Fig. 27) shows an even presentation of reflectance spectra, independent of the storage time which encompasses 95 years.

The reflection spectra obtained from *Thalurania furcata boliviana* (Fig. 28) appear to be consistent. This is also confirmed by the low standard deviation of total brightness.

In line with the previous specimens, *Thalurania glaucopis* (Fig. 29), exhibits reflectance spectra which are not affected by age.

In none of the analyzed cases can any shift in brightness or hue be related to the storage time, though neither the eldest nor the most recently collected specimens are assigned to the brightest or least reflecting samples.

Color changes in aged feathers held under different storage conditions

The reflectance spectra of the aged specimens exhibit severe changes in hue, brightness and chroma in comparison to the pristine plumage coloration.

In the Crown of the *Amblyornis subalaris* (Fig. 30) and the Alula of *Ara severa* (Fig. 35) the variations are obvious and easily detectable by the human observer. The spectral changes are accompanied by a noticeably different coloration, actually unnecessary to prove by spectrophotometry. In the other cases, alterations of reflectance spectra are more cryptic. Brightness is slightly changed which is not notable at first observation. Hue remains unaltered as long as UV is not involved. The most dramatic changes are found in the ultraviolet region, where chroma is reduced to zero in some cases. This causes a profound change in hue, however invisible to the human eye. In the feathers of the *Aratinga guarouba* (Fig. 32 & 33), a dramatic decrease of UV-reflection is evident which can be demonstrated by means of UV-photography (Fig. 46 – 48). The images reveal a strong contrast in the ultraviolet due to soiling.

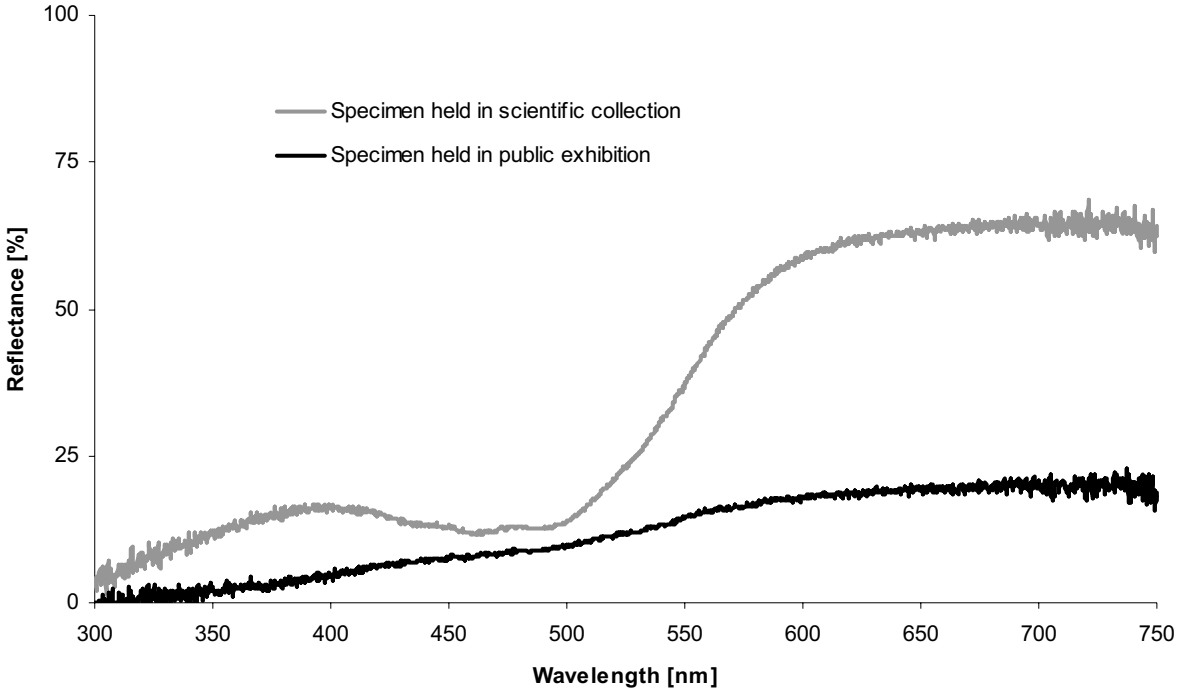



Fig. 30 Crown of a Streaked Bowerbird (*Amblyornis subalaris*).
The plumage of the exposed specimen is bleached and does not exhibit any of its original spectral properties. The skin held in a scientific collection, was protected from any hazardous impact and hence, its coloration is properly maintained.

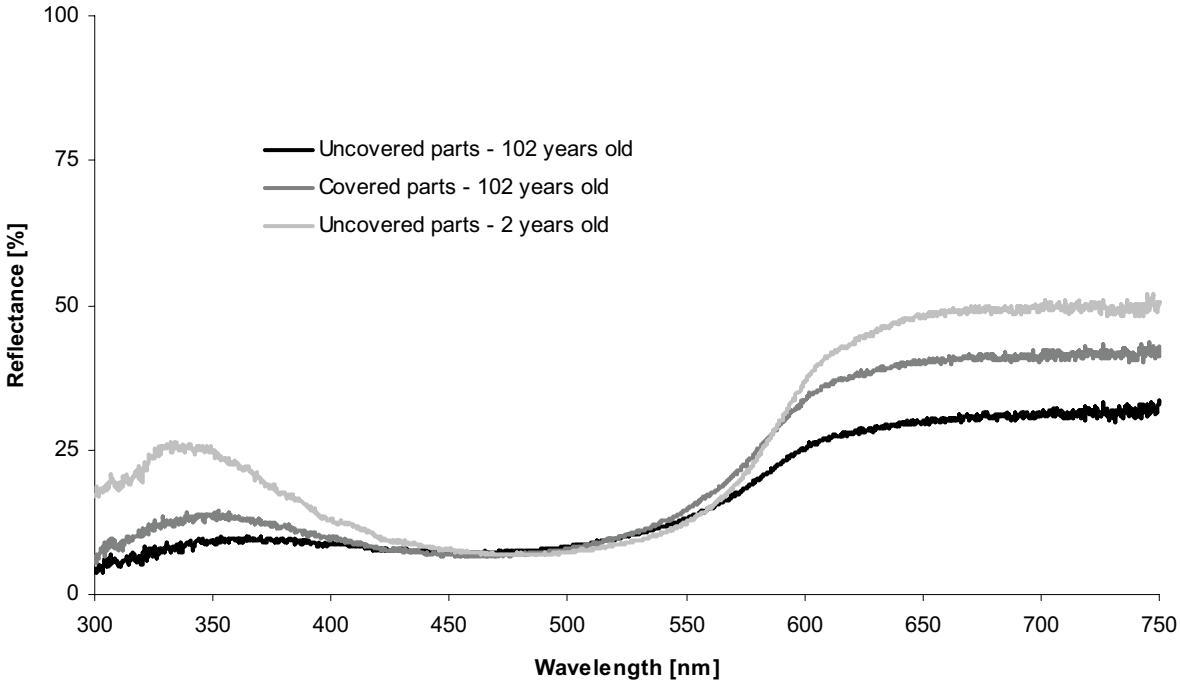



Fig. 31 Tail feathers of a Glossy Black-Cockatoo (*Calyptorhynchus latami*).
The 102 year old feather parts, directly exposed to environmental conditions are bleached and lack UV-reflections. The covered parts of the same age show a reduced overall brightness but, nevertheless, all characteristics of the coloration are present. The UV-reflections in the two year old specimen are distinctive.

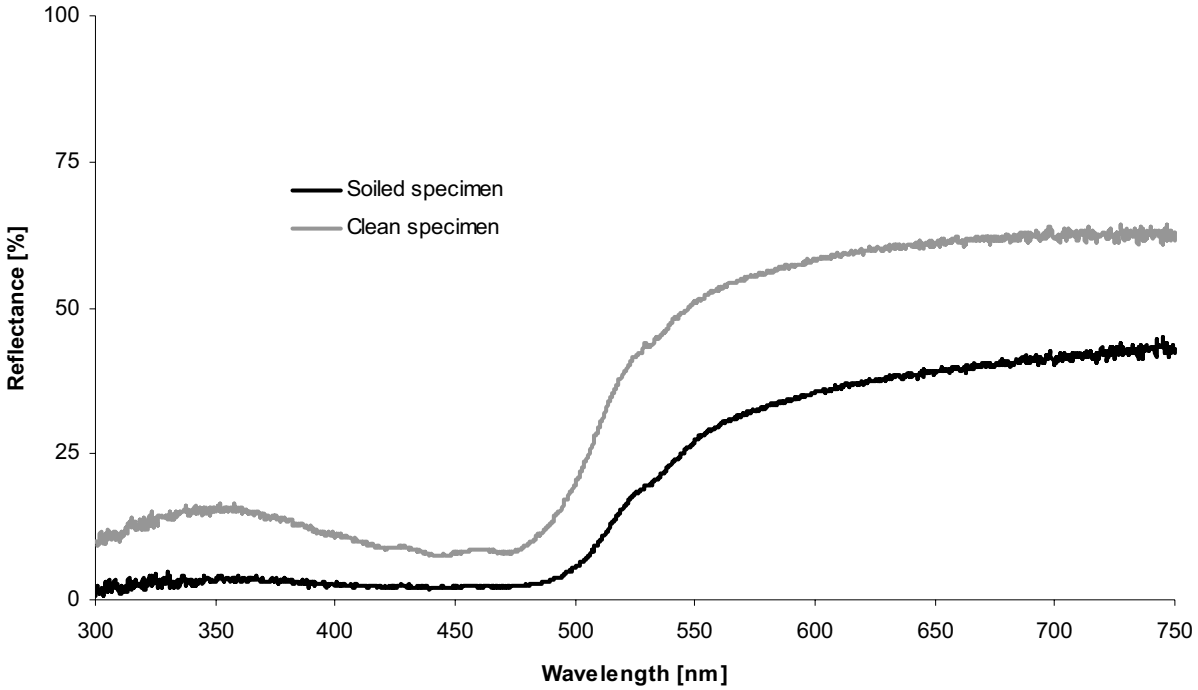



Fig. 32 Wing coverts of a Golden Parakeet (*Aratinga guarouba*).
The plumage soiled with dust due to inadequate storage conditions has decreased brightness and lacks any UV-reflections which are conspicuous in the clean specimen.

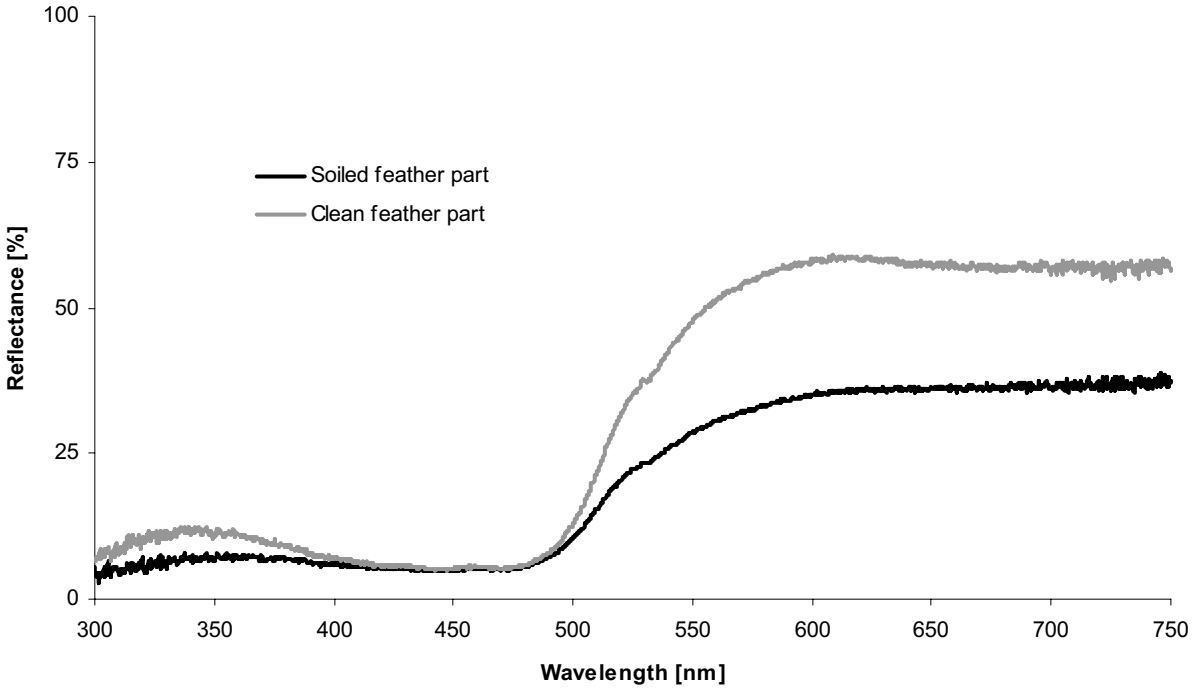



Fig. 33 Tail feathers of a Golden Parakeet (*Aratinga guarouba*).
In these specimens, the clean feather part is bright in the long wavelengths and displays a slight peak in the ultraviolet. Contrary to that, the spectrum of the soiled part is reduced in the long wavelengths and lacks a UV peak.

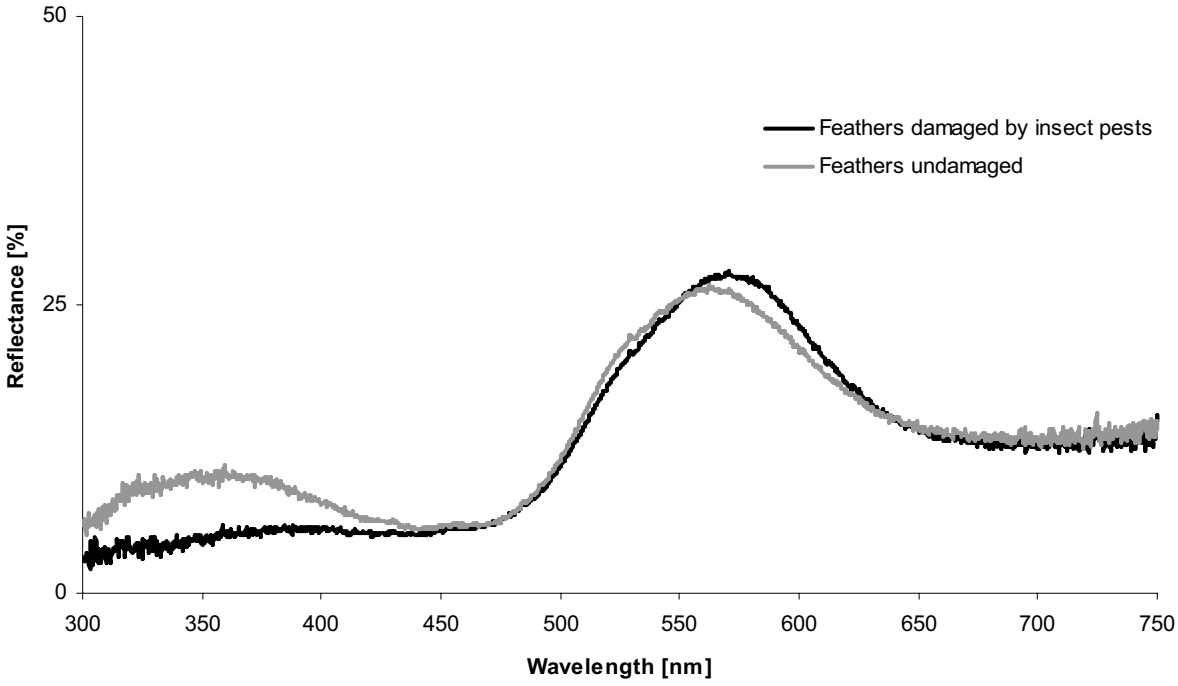



Fig. 34 Belly coverts of a Chestnut-fronted Macaw (*Ara severa*).
The damaged feathers do not show a notable change in the visible range (400 nm – 750 nm) but the effects in the ultraviolet are severe.

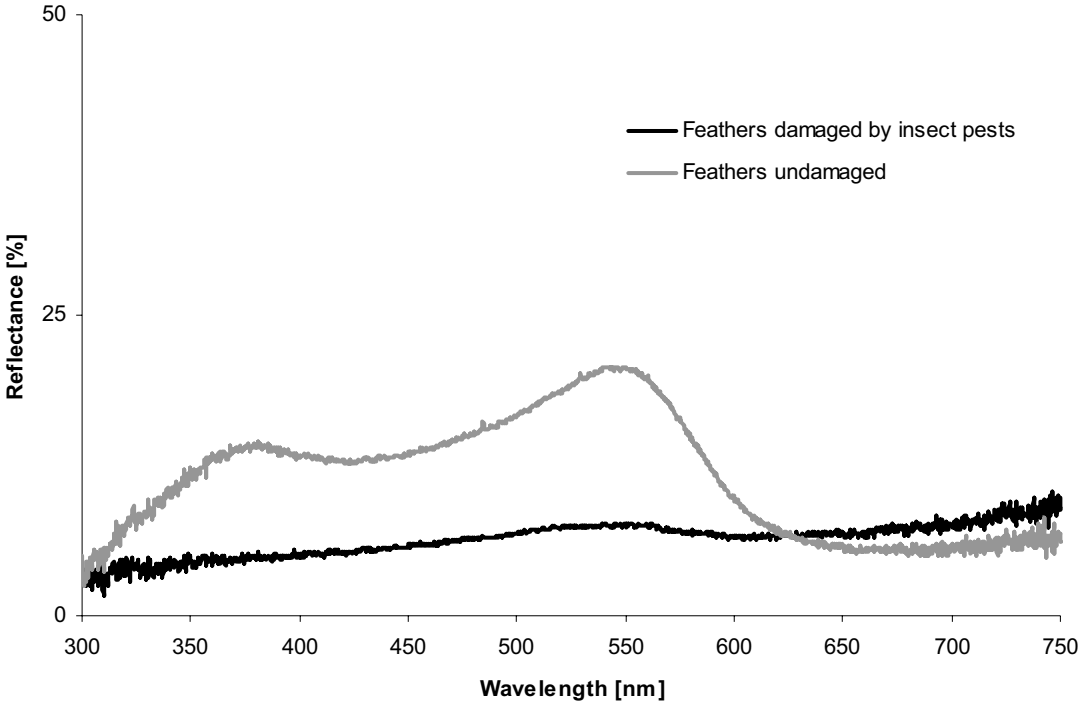



Fig. 35 Alula of a Chestnut-fronted Macaw (*Ara severa*).
In this case, the spectral change induced by insects caused feather damage which annihilates the entire coloration attributes of the affected specimen.

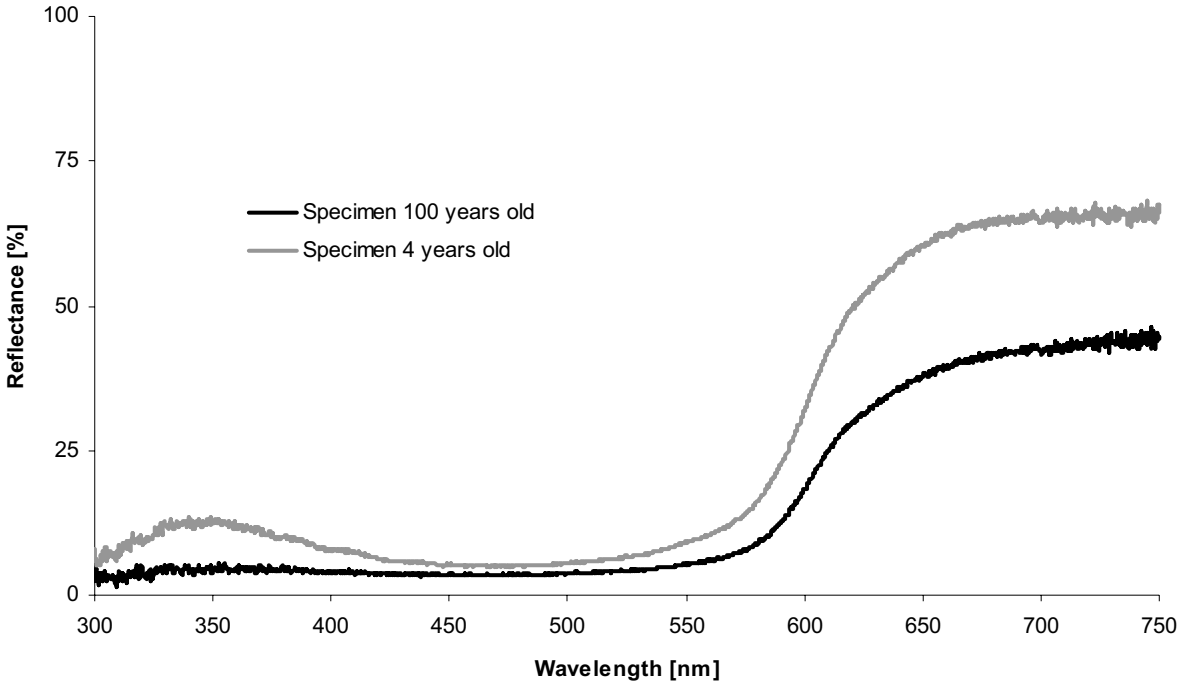



Fig. 36 Upper wing coverts of a Red-winged Parrot (*Aprosmictus erythropterus*).
The 4 year old specimen exhibits a clear peak reflectance in the ultraviolet range. This is completely absent in the 100 year old specimen which is decreased in overall brightness.

Color changes in an Australian King-Parrot (*Alisterus scapularis*)

In *Alisterus scapularis* variations between affected and pristine specimens are most notable in the ultraviolet. In almost the same manner as the previous cases, alterations in the UV remain inconspicuous to the investigator as long as spectrophotometry is not involved.

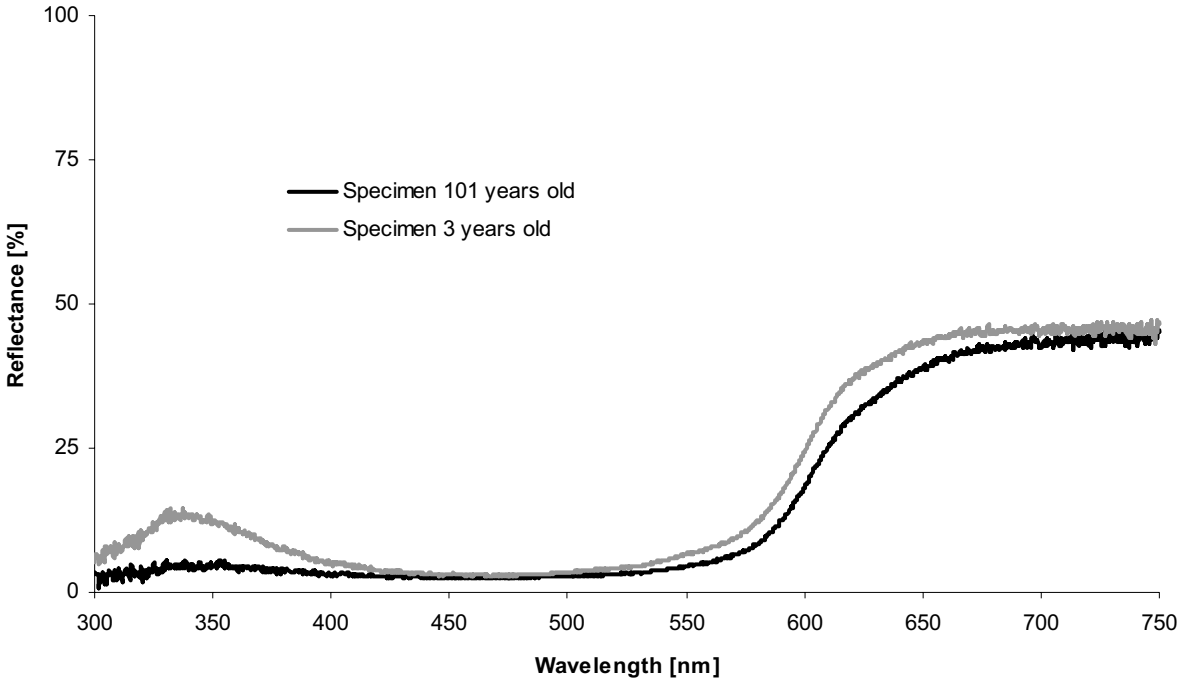



Fig. 37 Nape coverts.
Even though the entire visible range (400 nm - 750 nm) is unaffected there is a dramatic aberration in the ultraviolet.

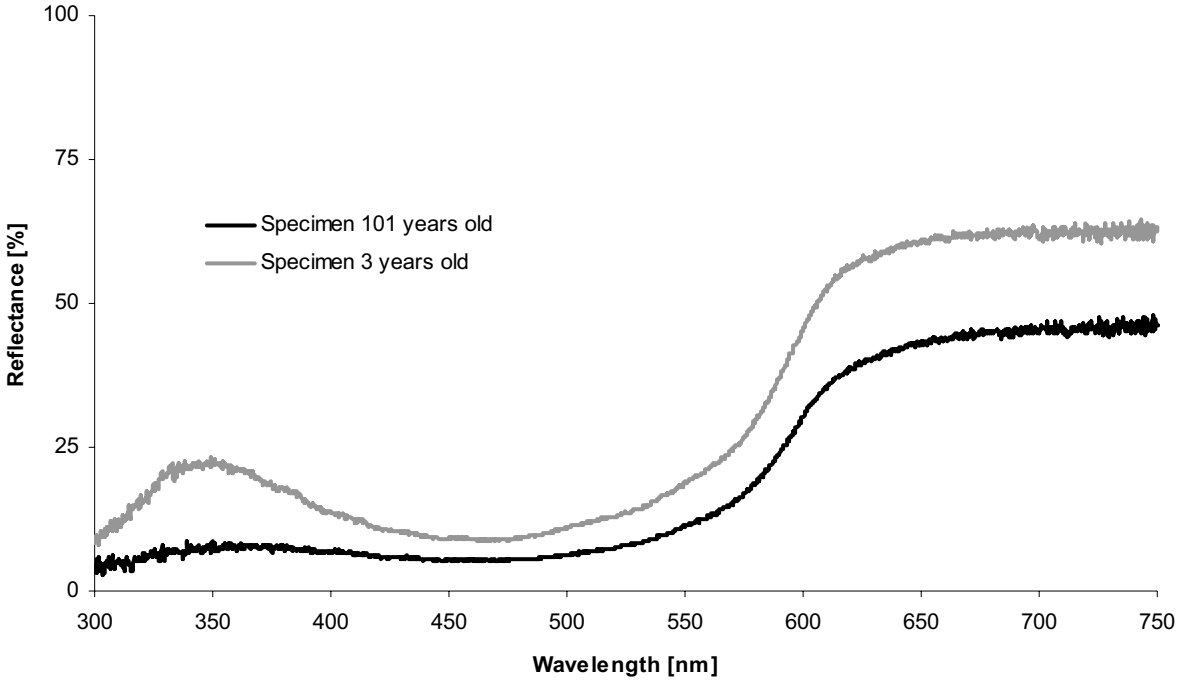



Fig. 38 Throat.
As in the visible range (400 nm -750 nm), only brightness is reduced, the ultraviolet is severely affected in the 101 years old specimen.

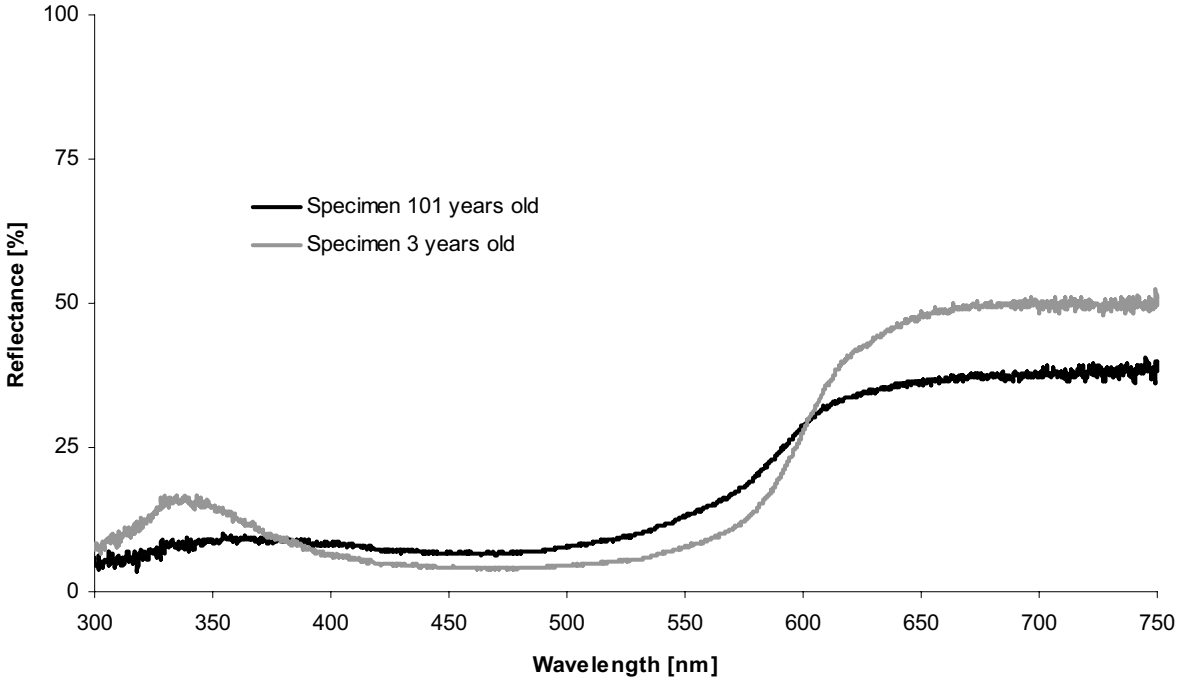



Fig. 39 Brest coverts.
The hue of the elder specimen has turned to grayish, characterized by a smoothed graph. The naturally well elaborated UV-reflection is missing.

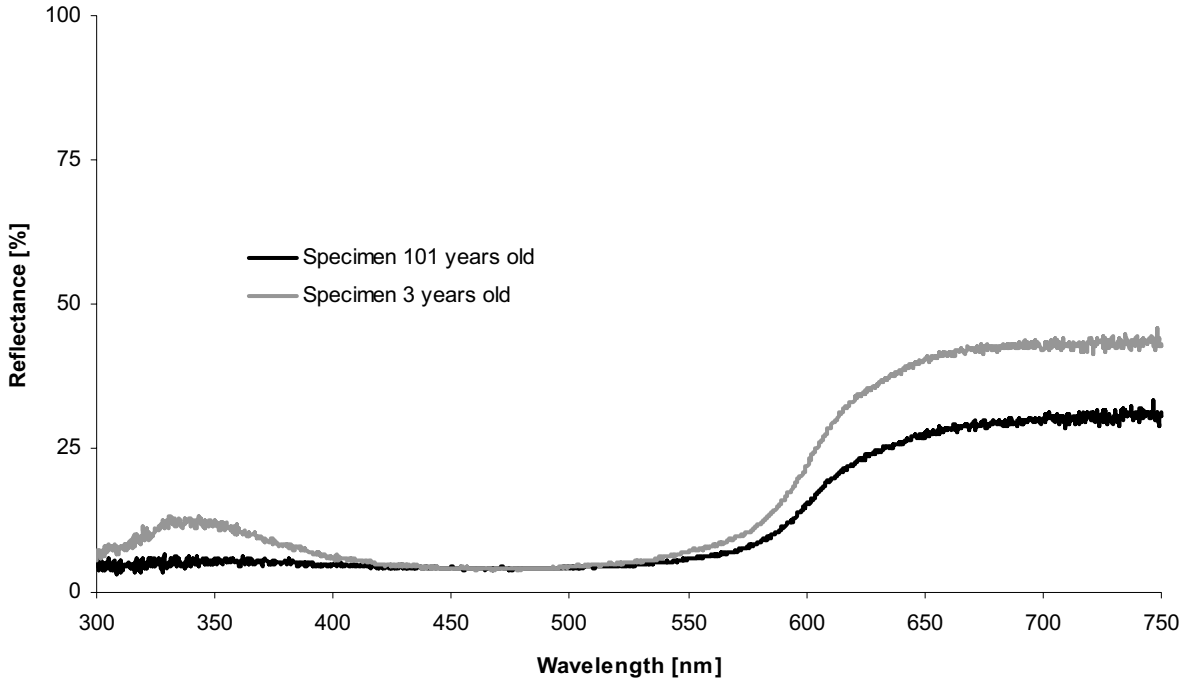



Fig. 40 Under wing coverts.
The entire reflection is reduced in the elder specimen. Nevertheless, most major alterations are to be found in the ultraviolet, as the hue has changed, even though it is not observable with the human eye.

Color changes in a Golden Bowerbird (*Prionodura newtoniana*)

In *Prionodura newtoniana*, color changes are obvious to the observer. The entire plumage of the publicly exhibited specimen is bleached. The color has faded to grayish or brownish hues. Interestingly, brightness is increased in certain parts of the spectrum, mainly between 400 and 550 nm. The entire spectrum of the Alula (Fig. 45) is significantly enhanced in brightness.

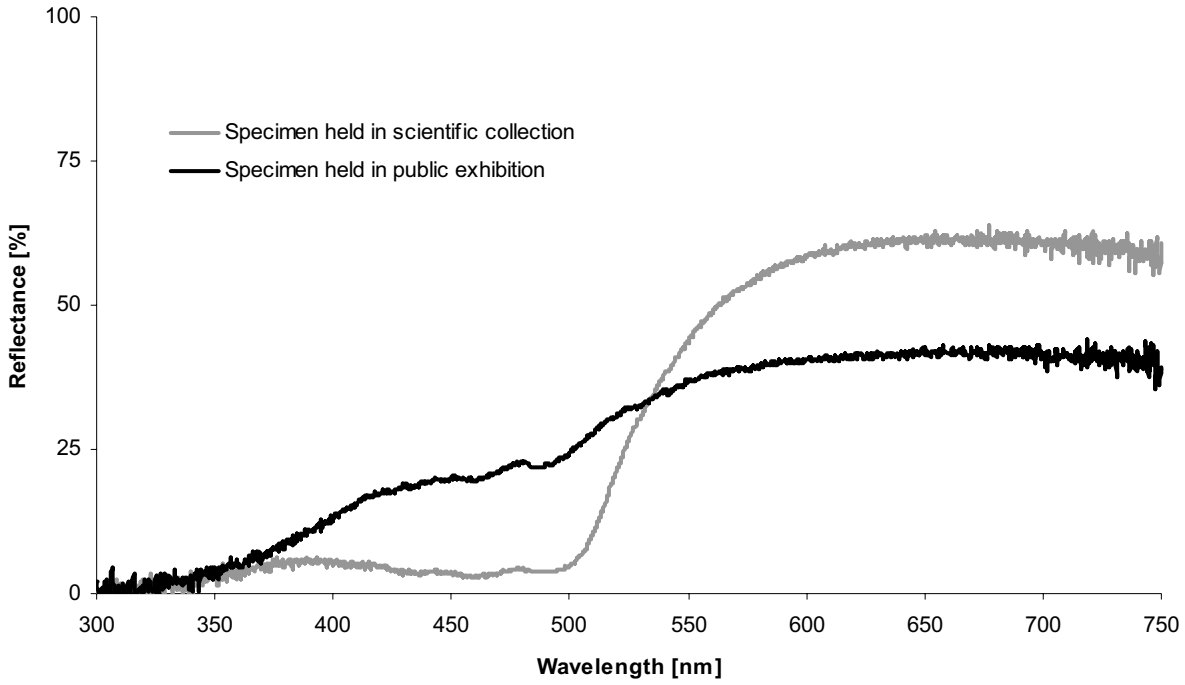



Fig. 41 Crown.
The coloration has changed from a bright yellow to a dull brownish tint. Interestingly, some parts of the spectrum gain brightness while it is reduced in other parts.

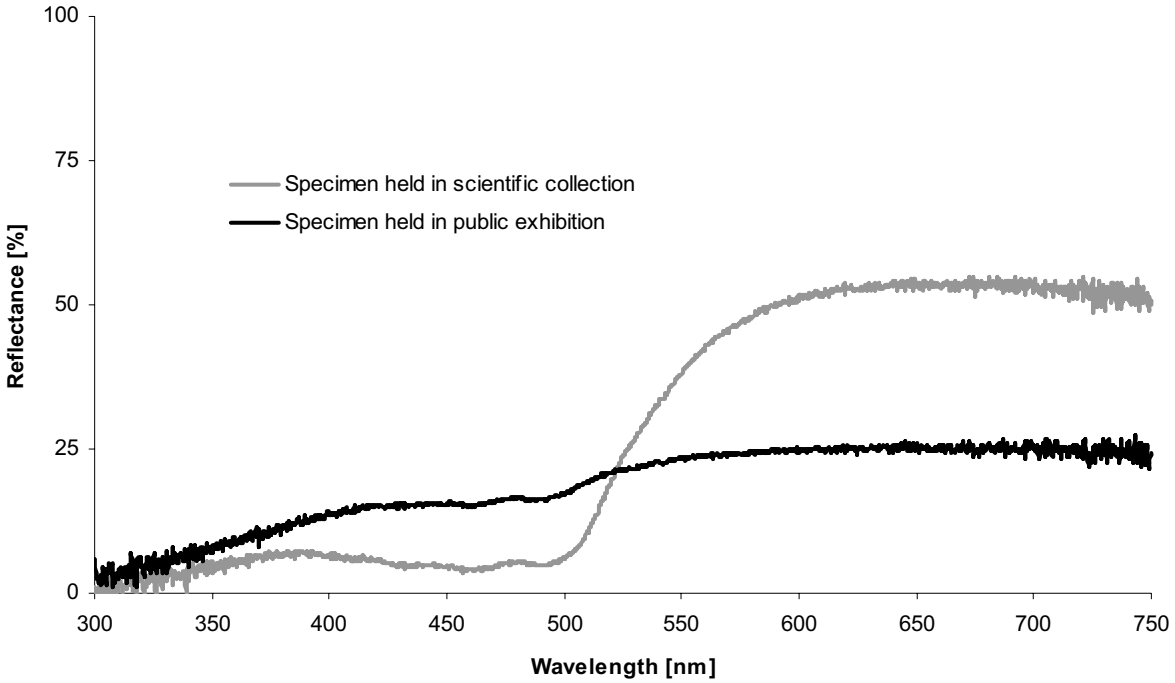



Fig. 42 Nape.
Plumage coloration has faded to grey in the exhibition specimen. Naturally occurring characteristics have vanished which are still present in the specimen from the scientific collection.

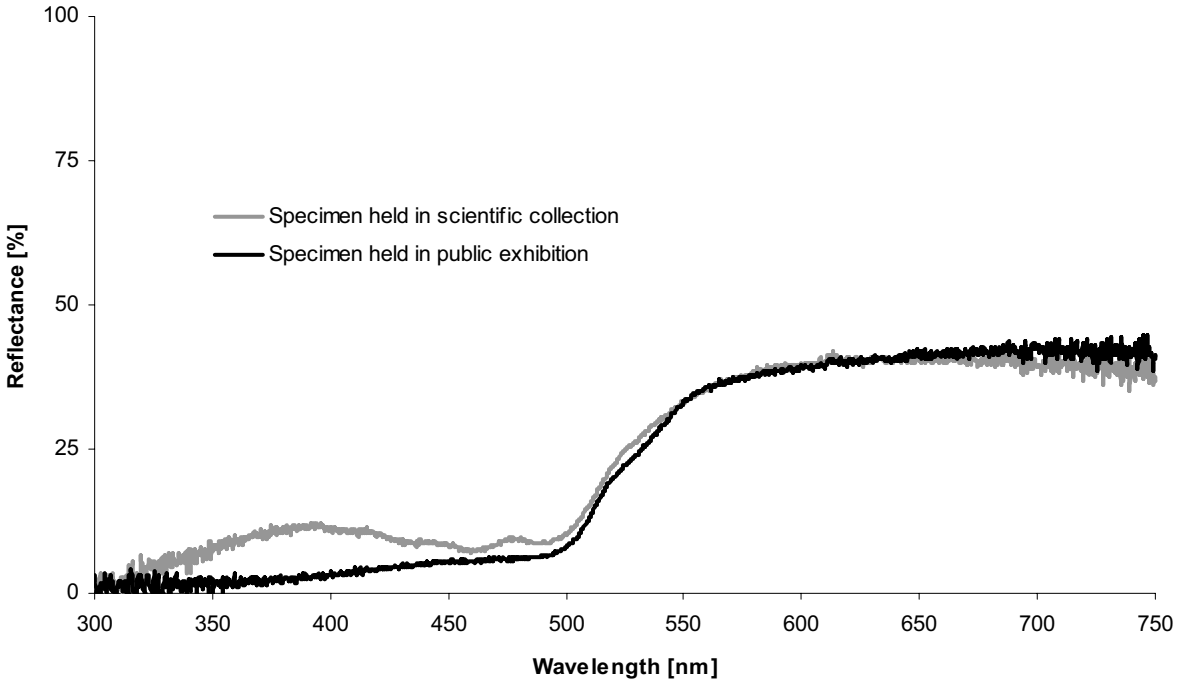



Fig. 43 Tail feather.
With regard to the wavelengths visible to a human observer, no obvious change in hue or brightness can be detected. The ultraviolet range shows a noteworthy spectral deficiency.

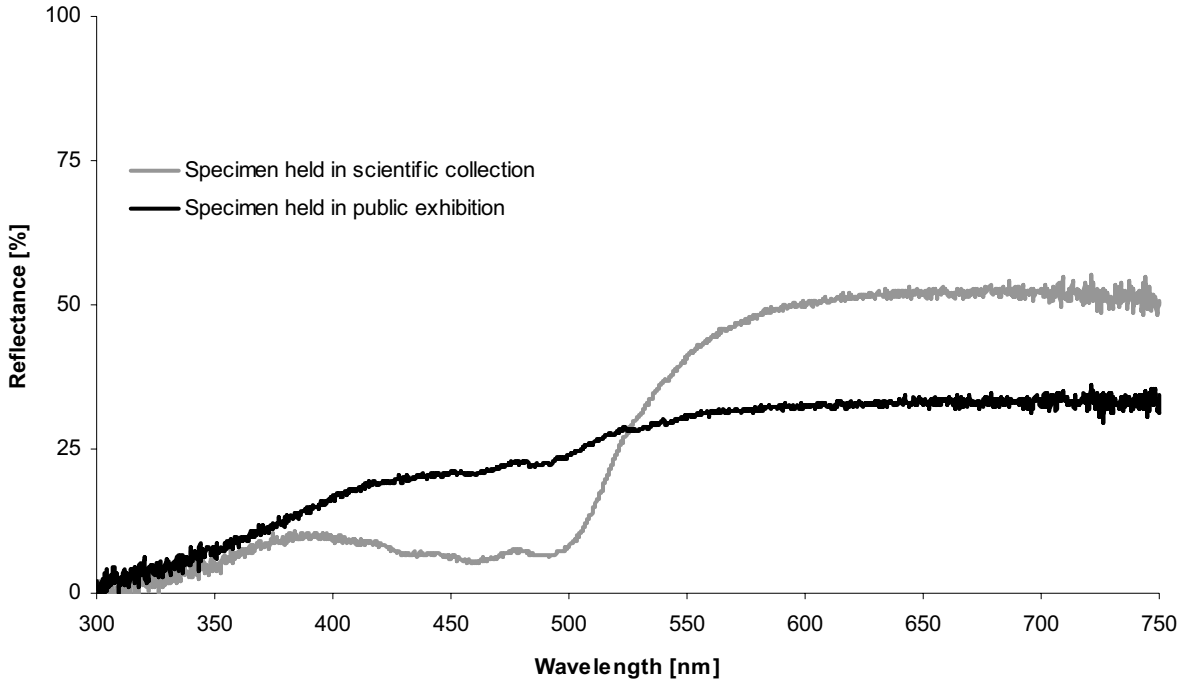



Fig. 44 Throat.
The entire spectrum changed from a natural yellow coloration, including an additional peak in the near UV, to a brown hue. It is noteworthy that the blue and green range of the spectrum is conspicuously brightened, while the red is dimmed.

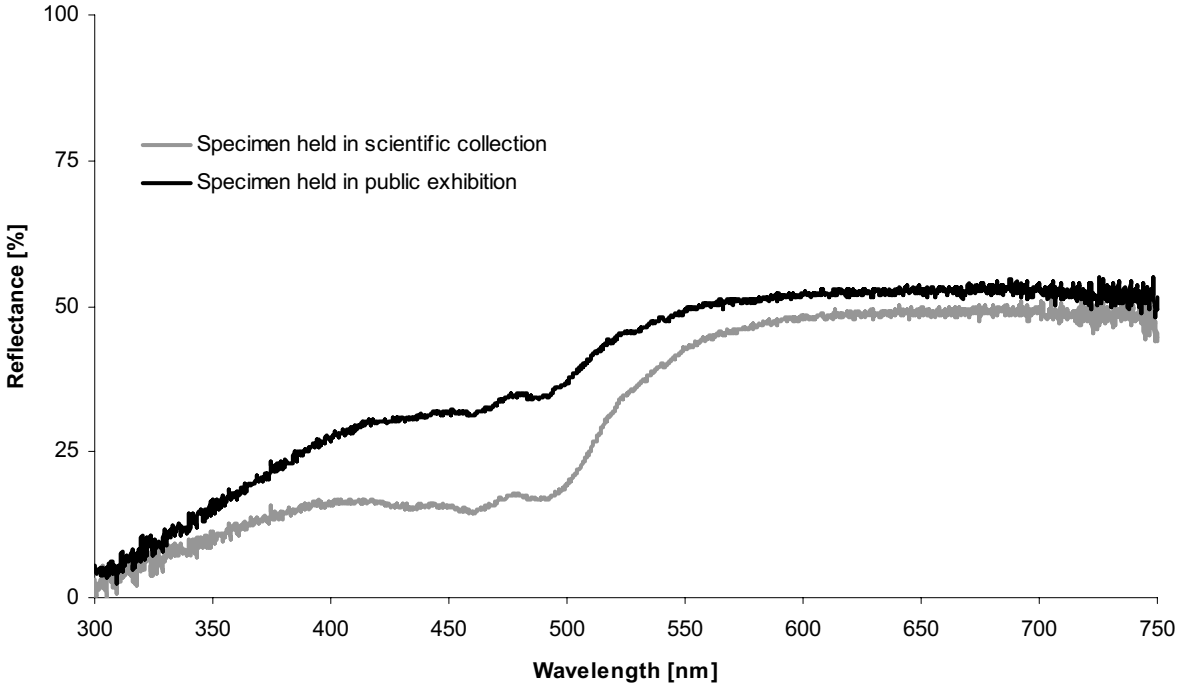



Fig. 45 Alula.
Interestingly the spectrum of the specimen held in public exhibition is completely brightened in comparison to the properly stored one. However, spectral information is lost, even though the original characteristics can still be anticipated. This is a typical example for the increase in overall brightness associated with the loss of quality.

Color changes in an Eclectus Parrot (*Eclectus roratus*) from a museum exhibition

In this remarkable case, one side of the specimen has been entirely bleached due to daylight exposure (Fig. 49). The other side remained pristinely colored (Fig. 51). The color of the faded plumage parts is shifted in the visible range from green to turquoise, indicating the loss of yellow chromophoric elements. The structure is still in good order and thus perpetuating reflections depending on it. This difference is significantly demonstrated in the ultraviolet. The unaltered side lacks almost any UV-reflection (Fig. 50). Conversely, the faded plumage parts exhibit bright UV-reflections (Fig. 52). The loss of the absorbing elements leads to an increase of structurally originated ultraviolet reflections which otherwise would be eliminated.

Fig. 46 Golden Parakeet (*Aratinga guarouba*) dirt on tail feathers.

Fig. 47 Golden Parakeet (*Aratinga guarouba*) tail feathers in B&W.

Fig. 48 Golden Parakeet (*Aratinga guarouba*) tail feathers in UV.

Fig. 49 Eclectus Parrot, male (*Eclectus roratus*).

Fig. 50 Eclectus Parrot, male (*Eclectus roratus*) in UV light.

Fig. 51 Eclectus Parrot, male (*Eclectus roratus*) having been exposed to the sun.

Fig. 52 Eclectus Parrot, male (*Eclectus roratus*) having been exposed to the sun in UV-light.

## 2.4 Discussion

My study reveals the inconsistent occurrence of age- or storage-related alterations in the spectral properties of museum bird skins. The observed color changes occur regularly but they are not a common phenomenon. All of these findings can be related to storage conditions and not to natural decay. Certain species are unsuitable for spectral analysis. If plumage coloration strongly depends on the dietary uptake of pigments, spectral data is a priory not reliable, e.g. particularly colors which are not subject to sexual selection and hence highly variable.

### Age stability in iridescent colors

The analysis of hummingbirds, collected over a period of about hundred years, strikingly demonstrates the stability of the structural iridescent colors. Iridescent coloration, particularly in hummingbirds, is exceptionally directional. The reflected color depends dramatically on the angle of illumination and observation (see chapter 1). Hence, peak shifts are likely to occur by slight variance in the surface structure of a feather patch. If some feathers are not arranged evenly, the color deviates from the reference. Even though the surface of flamboyant body regions like crown or throat can be easily estimated by the investigator, variations in the orientation of some exiguous feathers might remain undetected. The arrangement of plumage could also be affected by contact with the light protection tube of the reflection probe. However, none of the observed color deviations could be related to the age of respective specimen. The coloration of hummingbirds is based on the structural arrangement of the keratin and the melanin structures in the feather. Neither has been affected by age. The specimens were stored properly and damage was prevented. As a result, we can have confidence in the bird collections in natural history and research museums.

### Color changes

My study provides evidence that UV studies of plumage reflections are frequently affected most significantly by age, wear and contamination with dust or other soil. This might result from the frequency dependency of light scattering and diffusion which increase dramatically at shorter wavelengths to the fourth power of λ. Hence,

as dust covers the feather or the structural integrity is impaired, light of short wavelengths is likely to be diffracted or scattered.

Ultraviolet colors are a result of the structural properties of chromophoric elements in the feather. The ultraviolet part of a color should therefore not be affected by aging processes even though pigments, producing colors in the visible range, are noticeably faded. This is proven by observations of the partially faded *Eclectus roratus* specimen. But there is something to consider. The UV is sometimes the least intensely reflecting part of the plumage coloration. Hence, it could be eliminated completely by fouling without the visible spectrum being significantly affected (Fig. 37 & 43). Moreover, in the dim light prevalent in museum collections, color changes may easily elude the observer's perception. In particular, small reflectance peaks can easily be ignored. At low levels of overall brightness and chroma in both, naturally dull feathers or bleached specimens, slight variations in the reflectance spectrum might well be insignificant. However, they might contain valuable information concerning hue and therefore may be involved in avian signaling. Hence, with behavioral or ecological studies, only unaltered feathers are suitable for analysis.

In other cases, aged feathers gain overall brightness, i.e. integrals of the entire reflectance spectrum. This seemingly irrational characteristic may be a result of different changes in the chromophoric elements in avian plumage. Dust on the feather can lead to a diffuse reflection thus brightening dark parts, while bright parts become duller. Destruction of feather structure or loss of pigments caused by wear, mechanical abrasion, chemical decay, or fading under ultraviolet light will decrease the reflection effects in almost the same manner as those of absorption. The *Eclectus roratus* specimen clearly demonstrates this effect. Pigments are lost, thus only structural coloration remains. Absorbing elements do not function any more and hence, light of the particular wavelength cannot be absorbed but reflected within the remaining keratin and residues of the destructed pigments. With a decreasing distribution of pigments, the refractive and reflective effect of feather keratin is on the rise. Therefore, those specimens, in particular - bleached as a result of long-time exposure to ambient light, - are most frequently brightened up and exhibit a slightly brownish hue which is typical for pure keratin.

Dust itself does not just cover the feather and therefore prevent regular reflectance properties, it also contributes with its own spectral properties to the resulting spectral data. Environmental dust in a museum collection contains small particles of broken feathers, preservation agents, remains of cloth, paper, minerals, feces of insect pests and mites as well as any imaginable component of the surrounding atmosphere. Some of these components have distinctive colors and others are, in addition, fluorescent. Due to these properties, dust diminishes the reflectance spectra but not homogeneously. Certain parts of the spectrum are occasionally stronger than others affected by a dust covering (see Chapter 3).

In cases of feather damage due to insect pests, destruction is usually so severe, that the affected plumage part is useless for spectral analysis studies. In those cases, where the effects are apparently minor, the potential influence of insect feces has to be taken into account.

In most colors there is no evidence for age dependent loss of saturation, hue or brightness. The reliability of plumage coloration can be estimated by observing color changes, perceivable with the human eye. As usually several specimen of one type are stored in museum collections, coloration differences can be compared between them. This appears to especially inevitable in studies, dealing with pigment based plumage coloration, even though, in most cases, the latter is fairly reliable as well as structural coloration. In most cases in which pigments fade, they are observable in advance and can be separated along with those specimens judged as inappropriate in the first place.

## 2.5 Abstract

In my study, the plumage coloration of museum bird skins has been evaluated based on spectral data and its reliability for such work. Under appropriate storage conditions, the structural iridescent coloration of hummingbirds can be maintained unaltered for more than a hundred years. Specimens exposed to light, dust or insect pests are in danger of alteration to their spectral properties. Some specimens are unsuitable for spectral analysis, either in from the outset or due to acquired color changes.

## 2.6 References


Auber, L. 1956. The distribution of structural colours and unusual pigments in the class Aves. *Ibis* 99: 463-476.

Bancroft, W. D. 1924. Preliminary experiments on feather pigments. *J. Phys. Chem.* 1:1.

Berthold, P. 1965. Über nicht durch Pigment bedingte Rostfärbung bei Vögeln. *Naturwissenschaften* 52: 400-401.

Berthold, P. 1967. Über Haftfarben bei Vögeln: Rostfärbung durch Eisenoxid beim Bartgeier (*Gypaetus barbatus*) und bei anderen Arten. *Zool. Jb. Syst.* 93: 507-595.

Bonser, R. H. C. 1995. Melanin and the abrasion resistance of feathers. *Condor* 97: 590-591.

Burtt, E. H. & Ichida, J. M. 2004. Gloger's rule, feather-degrading bacteria, and color variation among song sparrows. *Condor* 106: 681-686.

Butler, M. & Johnson, A. S. 2004. Are melanized feather barbs stronger? *J. Exp. Biol.* 207: 285-293.

Cotgreave, P. & Clayton, D. H. 1994. Comparative analysis of the time spent grooming by birds in relation to parasite load. *Behaviour* 131: 171-187.

Cuthill, I. C., Bennett, A. T. D., Partridge, J. & Maier, E. J. 1999. Plumage reflectance and the objective assessment of avian sexual dichromatism. *Am. nat.* 153: 183-200.

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

Dyck, J. 1976. Structural colours. *Proc.16th Int. Ornithol. Congr.,* pp.426-437.

Galeotti, P., Rubolini, D., Dunn, P. O. & Fasola, M. 2003. Colour polymorphism in birds: causes and functions. *Evol. Biol.* 16: 635-646.

Goldstein, G., Flory, K. R., Browne, B. A., Majid, S., Ichida, J. M. & Burtt, E. H. 2004. Bacterial degradation of black and white feathers. *Auk* 121: 656-659.

Greenewalt, C. H., Brandt, W. & Friel, D. D. 1960. Iridescent colors of hummingbird feathers. *J. Opt. Soc. Am.* 50: 1005-1013.

Hamilton, W. D. & Zuk, M. 1982. Heritable true fitness and bright birds: A role for parasites? *Science* 218: 384-387.

Hausmann, F., Arnold, K. E., Marshall, N. J. & Owens, I. P. F. 2003. Ultraviolet signals in birds are special. *Proc. R. Soc. Lond. B* 270: 61-67.

Hofmann, C. M., Cronin, T. W. & Omland, K. E. 2006. Using spectral data to reconstruct evolutionary changes in coloration: carotenoid color evolution in New World orioles. *Evolution* 60: 1680–1691.

Hudon, J. 2005. Considerations in the conservation of feathers and hair, particularly their pigments. *CAC / ACCR 31st Annual Conference,* pp. 127-148.

Krumbiegel, I. 1925. Versuche über das Abfärben des Turacins. *J. Ornithol.* 73: 440-446.

McGraw, K. J. 2006. Mechanics of carotenoid-based coloration. In Hill, G. E. & McGraw, K. J. (Eds.) Bird Coloration (pp. 177-242). Cambridge, Massachusetts: Harvard University Press.

McGraw, K. J. & Hill, G. E. 2004. Plumage color as a dynamic trait: carotenoid pigmentation of male house finches (*Carpodacus mexicanus*) fades during the breeding season. *Can. J. Zool.* 82: 734–738.

McGraw, K. J., Mackillop, E. A., Dale, J. & Hauber, M. E. 2002. Different colors reveal different information: how nutritional stress affects the expression of melanin- and structurally based ornamental plumage. *J. Exp. Biol.* 205: 3747-55.

McGraw, K. J., Wakamatsu, K., Ito, S., Nolan, P. M., Jouventin, P., Dobson, S., Austic, R. E., Safran, R. J., Siefferman, L. M., Hill, G. H. & Parker, A. R. 2004. You can't judge a pigment by its color: carotenoid and melanin content of yellow and brown feathers in swallows, bluebirds, penguins, and domestic chickens. *Condor* 106: 390–395.

McNett, G. D. & Marchetti, K. 2005. Ultraviolet degradation in carotenoid patches: live versus museum specimens of wood warblers (Parulidae). *Auk* 122: 793–802.

Montgomerie, R. 2006. Analyzing colors. In Hill, G. E. & McGraw, K. J. (Eds) Bird Coloration (pp. 90-147). Cambridge, Massachusetts: Harvard University Press.

Ornborg, J., Andersson, S., Griffith, S. C. & Sheldon, B. C. 2002. Seasonal changes in an ultraviolet structural colour signal in Blue Tits, *Parus caeruleus*. *Biol. J. Linn. Soc.* 76: 237-245.

Parker, A. R. 1998. Colour in Burgess Shale animals and the effect of light on evolution in the Cambrian. *Proc. R. Soc. Lond. B* 265: 967-972.

Parker, A. R. 2000. 515 million years of structural colour. *J. Opt. A: Pure Appl. Opt.* 2: 1433-1446.

Parker, A. R. 2005. Review. A geological history of reflecting optics. *J. R. Soc. Interface* 2: 1-17.

Prum, R. O. 1999. Development and evolutionary origin of feathers. *J. Exp. Biol.* 285: 291-306.

Rutschke, E. 1964. Grundsätzliches über abweichend gefärbte Vögel. *Der Falke* 6: 195-199.

Stein, A. C. & Uy, J. A. C. 2006. Plumage brightness predicts male mating success in the lekking golden-collared manakin, *Manacus vitellinus*. *Behav. Ecol.* 17: 41-47.

Völker, O. 1947. Über die Struktur der bei Vögeln vorkommenden Porphyrine. *Zeitschrift für Naturforschung* 2b: 316-317.

Völker, O. 1963. Gefiederfarben der Vögel und Carotinoide. *J. Ornithol.* 104: 288-289.

Völker, O. 1964. Federn die am Licht ausbleichen. *Natur und Museum* 94: 10-14.

Völker, O. 1965. Stoffliche Grundlagen der Gefiederfarben der Vögel. *Mitteilungen der Naturforschenden Gesellschaft in Bern* 22: 201-223.

Völker, O. 1961. Bemerkungen über ein grünes, nicht carotinoides Pigment im Kleingefieder von Rollulus roulroul (Galli). *J. Ornithol.* 102: 270-272.

With, T. K. 1967. Freie Porphyrine in Federn. *J. Ornithol.* 108: 480-483.

Zuk, M., Johnson, K., Thornhill, R. & Ligon, J. D. 1990. Parasites and male ornaments in free-ranging and captive Red Jungle Fowl. *Behaviour* 114: 232-248.

# 3 Fluorescence in Avian Plumage

## 3.1 Introduction

Avian coloration has been in the focus of many research projects over the last decades. Many of these studies suffer from the failure to meet practical requirements and are limited in their reliability (see Chapter 1). Recent studies make increasing use of reflection spectrophotometric techniques. The latter provide adequate data relating to the “true colors” of avian plumage, expanding the range of spectral observation. The entire range of avian color vision can now be taken into account.

Behavioral studies, as well as anatomical and physiological experiments have shown that avian visual perception differs completely from human vision (Burkhardt 1989, Cuthill *et al.* 2000). Numerous studies have been conducted, contributing data in favor of the bird’s capability to see ultraviolet light (300 - 400 nm) (Huth & Burkhardt 1972; Maier 1992, 1993, 1994; Bennett & Cuthill 1994; Bennett *et al.* 1997). Thus, great attention has been devoted to the ultraviolet (UV) range of avian color patterns, invisible to the human eye, but easily detectible with modern measurement devices. Hence, the significance of these short wavelength colors for signaling ecology is feasible. The major role of UV-light perception for foraging success in birds, but especially for their courtship behavior, is supported by studies conducted over the last decade (Andersson & Amundson 1997; Andersson *et al.* 1998; Church *et al.* 1998, 2001; Cuthill *et al.* 2000). In addition to ultraviolet reflections in many birds’ plumages, another exceptional mechanism of feather coloration exists: fluorescent pigmentation.

Fluorescence itself is a natural property of different substances. It occurs when light is absorbed and immediately reemitted at the same or, more frequent, at longer wavelengths. In the most general cases, UV-light is used as excitation and light of the visible spectrum is reemitted. Under normal light conditions, this phenomenon will usually remain undiscovered by the human observer due to the strong, overriding effect of ambient light. Fluorescence is known from both non-organic and organic substances, with the vast majority of organic materials glowing under UV-illumination

(Römp 1996). In the living world, fluorescence is a fairly widespread phenomenon occurring in different groups of organisms. It is known from chlorophyll in plants and the shells of certain sea dwelling mollusks. In corals, it is used for color production and acts as a photo-protective means to avoid bleaching from sunlight (Salih *et al.* 2000, Mazel & Fuchs 2003). In addition, fluorescence is widespread in some crustaceans (Mazel *et al.* 2004). Famous, but not yet well understood, is the intense glowing of scorpions as a result of fluorescing compounds in their exoskeleton (Stahnke 1972, Stachel *et al.* 1999, Frost *et al.* 2001, Lowe *et al.* 2003, Wankhede 2004). Insects also contain fluorescing pigments as recently reported for a butterfly (*Papilio nireus*) (Vukusic & Hooper 2005) and a euglossine bee (*Eulaema niveofasciata*) (Nemésio 2005). Examples of the histochemical and biotechnological use of fluorescence derived from living organisms are the green fluorescing protein (GFP) as a marker (Kummer 2003, Biron 2003) and the detection of micro-organisms (Bhatta *et al.* 2005) based on their fluorescent properties.

Natural fluorescent plumage

Bird-related fluorescence was already shown in 1932 by Schönwetter in a study dealing with the coloration of avian eggshells which frequently contain porphyrins - a fluorescent class of pigments (Völker 1947). In plumage coloration, unlike UV-reflections, the existence of this phenomenon is well known since it was first reported by Völker 1936. He found a fluorescing pigment in the Budgerigar (*Melopsittacus undulatus*) and subsequently in other Australian parrot species (Völker 1937). Fluorescence, as a part of avian coloration, has been intermittently reported by several researchers, but exclusively dealing with Australian parrots (Driesen 1953, Völker 1955, Schmidt 1961).

In 1964, Völker introduced fluorescing plumage patterns in other bird orders. Furthermore, he studied fluorescence in the different feather parts. He identified a red fluorescing porphyrin which is rapidly destroyed under light. Neck feathers of the Red-crested Bustard (*Eupodotis ruficristata*) contain porphyrins as well as Turacos (Musophagidae), but they have to be treated with sulfuric acid to generate fluorescence (Schmidt & Ruska 1965). Also, the plumage parts of bustards (Otididae) and owls (Strigidae) and the entire poults of tits (*Parus* sp.) were found to be red fluorescing unless they were exposed to daylight.

Red fluorescing feathers are commonly found in plumage parts which are protected from daylight exposure. At least 13 orders of birds are known to exhibit this kind of coloration although they were not specially reported (Völker 1965).

Völker (1965) classified three different types of fluorescence:

Type 1 *Cacatua* - gold-yellowish fluorescence
Type 2 *Melopsittacus* - sulfur-yellowish fluorescence
Type 3: *Palaeornis* - greenish fluorescence

Due to the present state of knowledge in vision ecology, researchers dealing mainly with ecological or behavioral questions have had to expand their studies of plumages to encompass the UV waveband. This encompasses fluorescence as a natural counterpart. Fluorescing plumage parts do not exhibit proper UV-reflections because the paramount part of UV is transmitted to longer wavelengths.

The exact identification of the feather pigments responsible for fluorescence is still poorly understood but recent studies have been conducted on this unique coloration. They are mainly dealing with fluorescing parrot species (Boles 1990, 1991; Nemésio 2001; Pearn *et al.* 2001, 2003; Parker 2002, 2005; Arnold *et al.* 2002; Hausmann *et al.* 2003). It was shown, that the alteration of UV-reflecting and fluorescent non-UV-reflecting plumage parts influence courtship behavior (Pearn *et al.* 2001, Parker 2002, Arnold *et al.* 2002, Hausmann *et al.* 2003, Pearn *et al.* 2003, Parker 2005). Pigments not yet identified, such as fluorescent biochromes also color the downy natal plumage of many birds. More fluorescing colors have been found in the natal down of Domestic Chicks (*Gallus domesticus*), Japanese Quail (*Coturnix japonica*) and Wood Ducks (*Aix sponsa*) (McGraw 2006). The poults of Wild Turkey (*Meleagris gallopavo*) also exhibit yellow fluorescence (Sherwin & Devereux 1999). Furthermore, fluorescent colors are known from different species, e.g., in Anseriformes, Charadriiformes and Galliformes (McGraw 2006). Penguins also bear fluorescing colors and use them as sexual signals (Massaro *et al.* 2003). Their feathers do not contain carotenoids but fluorescing pigments (McGraw *et al* 2004). Contrary to these findings the fluorescing yellow plumage color of Big Tit's (*Parus major*) chicks is based on its carotenoid containing diet (Fitze *et al.* 2003).

The well known fluorescence in eggs could relate to Riboflavin which has been identified in chicken eggs where it acts as a vitamin (McGraw 2006).

Fluorescence in avian plumage provides two major effects: the absorption of short wavelengths, especially UV and the emission of longer wavelengths. Based on this assumption, two main hypothesizes can be derived.

1. Fluorescence is somehow an integral part of signaling.
2. Fluorescence occurs as an incidental effect of feather coloration.

There is controversy about these concepts. Many authors favor the significance of fluorescence in signaling (Arnold *et al.* 2002; Parker 2002, 2005; Hausmann *et al.* 2003). Nemésio (2003) and Pearn *et al*. (2003) disagree with this thesis because of the misattribution of fluorescence's possible relevance. Parker (2005) presumes that the irregular distribution of fluorescence in parrot plumage caused by their biogeographical history. Thus, their distributional centre lies in Australia, with numbers decreasing from there to Africa and further to South-America. However, Parker (2005) solely considers parrots and hence the integration of fluorescent pigments can be assumed to be a plesiomorphic character of this taxon as well as an integral part of signaling. If fluorescence is an integral part of signaling, it can act in two different ways:

A. Producing brighter plumage parts and a more saturated color.
B. The avoidance of UV-reflection in these plumage parts in order to enhance the contrast with juxtaposed UV-reflecting patches.

Implications of the entire coloration of one species is based upon a mosaic, consisting of light environment, patches varying in color, brightness, size, shape and position in both the body and visual background (Endler & Mielke 2005). Environmental light conditions are subject to great variability depending on geography, geomorphology, climate, vegetation, season, and time of the day (Henderson & Hodgekiss 1963, Henderson 1970). Ambient light plays a crucial role in the evolution of coloration (Slagsvold & Lifjeld 1985, Endler 1993, Marchetti 1993, Heindl 2002, McNaught & Owens 2002) and therefore implication and visibility of

colors varies under different light conditions (Bailey 1978, Endler 1990, Chiao *et al*. 2000, Gomez & Théry 2004). Furthermore, actual coloration in combination with ambient light affects courtship behavior (Endler & Théry 1996; Maddocks *et al.* 2002a, 2002b). Hence, a male's display is often connected with the choice of distinct light conditions in order to enhance the contrast against the background (Endler 1995, Endler & Théry 1996, Théry 2001, Heindl & Winkler 2003, Uy & Endler 2004). However, the difference between conspicuousness and camouflage of one color is dependent on the quality and quantity of light respectively. In this way, success in foraging can depend on ambient light conditions (Merilaita & Lind 2005) as well as enabling predation and predation avoidance (Endler 1978, Håstad *et al*. 2005).

Artificial fluorescent plumage in museum bird skins

In addition to naturally occurring fluorescence phenomena, another phenomenon has to be taken into account. Artificially applied fluorescing agents sometimes unintentionally influence the spectral appearance of museum specimens. Today, the use of reflection spectrophotometry is the most commonly used technique to objectively study plumage coloration. While examining some thousand reflection spectra of different bird species in several research projects an unexpected alteration of spectral data was obtained under certain circumstances. In these cases, the spectra showed deficiencies in their UV-reflections unlike specimen of the same population. The studies included representatives of all bird orders and almost all bird families, as well as 300 parrot species.

Avian taxidermy has been used for a considerable time for the conservation of specimens in both art and science. Preparation techniques are known to have been used in bird collections at least since the middle ages and taxidermic conservation measures themselves have a tradition going back to prehistory (Schulze-Hagen *et al.* 2003). Traditional taxonomic and phylogenetic research is often conducted with museum skins. Many different preservation agents have been employed to prevent the skins from being damaged by decomposition, fungal attack or insects. In the nineteenth century, and in the first decades of the twentieth century, recipes with arsenic salts and mercuric chloride in the form of liquids and powders dominated (Hawks & Williams 1986, Hawks & Von Endt 1990, Goldberg 1996, Sirois 2001).

The number of available preservation agents increased in the twentieth century due to greater efficiency and less toxic side effects to humans. In the last decades, different mixtures of a number of organic and non-organic compounds became pre-eminent and the use of preservation agents varied in different collections and countries (Goldberg 1996). Preservation agents were usually applied on the inner side of the bird's skin. However, sometimes, part of the plumage was contaminated. The resulting stains, when dried, are almost invisible and cause no obvious change in feather coloration to the human eye under sunlight conditions. Such skins have been regarded as a reliable source for gathering morphometric data.

Despite the known age-dependent color changes in some museum bird skins (Endler and Théry 1996; Hausmann *et al.* 2003), for centuries this data has been regarded as being reliable. Today, as far as spectrophotometric techniques are concerned, their reliability must be questioned. This is because some preservation agents contain fluorescent components. Undetectable to the human eye, stains of these agents annihilate UV-reflection and prevent accurate data collection on plumage colors. Measuring a plumage part which has accidentally been stained, may lead to an underestimation of UV reflection compared to clean feathers. This might cause problems in interpreting data and may produce variations not apparent to the human eye. Next to preservation agents, there are further possible sources of fluorescence accidentally applied to the plumage of bird skins. Fluorescence appears regularly in decomposition processes. When ultraviolet illumination is used on dead animals this often reveals fluorescence in most body parts. Remains of body fluids and lipids contain fluorescent components, e.g., pigments, Lipofuscin in particular (Eldred *et al*. 1982, Tsuchida *et al*. 1985, Schnell *et al*. 1999, Porta 2002). Even if birds had been preserved properly, the remains of lipids or proteins still contaminate the specimen. These natural body liquids can result in the artificial fluorescence of bird feathers if accidentally spilled over the plumage, even although preservation agents are not involved at all. Thus, fluorescent stains are predominantly found on the ventral part of the skin where the body had been opened. Moreover, fluorescence can frequently be found on the legs, the eye cavities and the origin of the beak. All these areas are likely to be contaminated with preservation agents or body fluids as well as with tissue remains.

My investigation of the above was carried out in addition to gathering avian plumage reflectance spectra for further studies. Thus spectral properties of some 10 000 bird skins have been studied. Different museum collections have been screened in order to get an insight into the abundance of fluorescent stains in bird skins.

Study goals:

In my study a possible correlation between light habitat and fluorescent plumage is discussed.

A diversified analysis of fluorescence properties of avian plumage is conducted.

The role of biogeographical regions is taken into account, and possible implications of fluorescence in avian coloration are discussed.

For the first time, the role of preservation agents and related methods has been taken into consideration.

## 3.2 Material and methods

To detect fluorescent plumage regions on bird skins, initially a portable UV-lamp was used, originally designed for the detection of fluorescence in banknotes, stamps or documents. These lamps provide UV-light with a peak intensity of 366 nm. Using this lamp in a darkened environment immediately revealed the fluorescing parts of a bird skin. In studies dealing with different aspects of avian plumage coloration, over 10,000 bird skins held in different collections of the A. Koenig Zoological Research Museum in Bonn, Germany, the Senckenberg Research Institute and Natural History Museum in Frankfurt, Germany, the Natural History Museum in Tring, United Kingdom, the Australian Museum in Sydney, Australia, the Queensland Museum in Brisbane, Australia, the Academy of Natural Sciences in Philadelphia, USA and the American Museum of Natural History in New York, USA were used for data collection. The studies were carried out over the last 4 years.

Reflectance spectra were obtained using an Ocean Optics USB 2000 spectrometer, with a Xenon pulse light source, providing wavelengths of the visible spectrum and ultraviolet light. A compressed pill of barium sulphate ($BaSO_4$) was used as a white reference standard, a black velvet cloth being used as a dark reference. Measurements were taken in the absence of ambient light in 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 evaluated between the wavelengths 300 nm and 750 nm. Reflection spectra for each distinctly colored area on a feather of each specimen were calculated based on the average percentage reflectance values from 10 measurements.

UV- photos were taken with a Nikon D70s digital SLR-camera body and a 105 / 4.5 UV-Nikkor lens. In order to exclude the visible spectra, a Hoya U 360 ultraviolet pass filter was used. The filter was additionally combined with a Heliopan BG 23 in order to exclude any infrared transmission. For illumination, a Metz CT 45 Flashlight was employed. The diffusion filter of the flashlight was removed, ensuring a maximal ultraviolet radiation source.

Natural fluorescent plumage

In my study, habitats and geographical distribution are classified according to Sibley and Monroe's bird list (1990). The biogeographical regions are defined by Newton (2003).

The exact classification of light habitats depends on the composition of harbored organisms and its implication for the different avian observers. In any case, birds living in a particular environment use different places for specific activities. Sites visited for courtship may well be different from those used for foraging. Nesting sites vary from resting places. Thus, it appears that distinct light habitats, within a seemingly consistent ambient light habitat, may be quite divergent (e.g., Endler 1993, Gomez & Théry 2004). It is still not clear in which context, i.e., micro light habitats, the fluorescence is used by its bearers. Therefore it is inadvisable to distinguish the spectral properties of these micro light habitats according to a possible role of fluorescence. Furthermore, there are many sources of inaccuracy when classifying micro light habitats. In this respect, spectral conditions were roughly simplified to the assumed brightness of ambient light, taking into account the vegetation in the areas of distribution of each species under study.

It is highly likely, that in some specific cases, the supposed spectral conditions differ dramatically from those under which the plumage is displayed. Despite this, the canopy inhabiting species were not assigned to bright habitats. Nevertheless, basic ideas about the distribution of fluorescent plumage could be derived from my study. A habitat was classified as bright if the particular population inhabits for example - a desert, savannah, open woodland, eucalyptus forest, open country, grassland, acacia scrub, scrub, arid areas, or is pelagic. It was classified as dark if the particular population exclusively inhabits forest, humid forest or other apparently dense and shady places. If a realistic classification was not feasible the habitat was specified as non- distinguishable.

Statistics used:

For the purpose of statistically confirming the relationship between fluorescent plumage and light habitat, the non-parametric Chi-square test was used. Level of significance: 5%.

$H_0$: Fluorescent species/families are homogenously distributed in all light habitats
$H_1$: Fluorescent species/families are predominately living in bright habitats

Artificial fluorescent plumage in museum bird skins

In order to find the cause of artificial fluorescence in bird skins, different commonly used and seldom used preservation agents were studied for their fluorescence properties. The following compounds were examined: arsenic, mercuric chloride, ethanol, borax, sulfur, camphor, formaldehyde, naphthalene, and Seibokal ES. Furthermore, untreated, partly decomposed and naturally dried birds were studied under UV-light. Each bird skin analyzed by means of reflection spectrophotometry was studied in advance using a black light lamp. In cases where artificial fluorescence was detected, the applied preservation agents have been cited, provided that this data was available.

## 3.3 Results

### Natural fluorescent plumage

In my study, 181 bird species in 14 families with fluorescent plumage parts have been found (Table 2). The vast majority are parrots (114 species). The biogeographical distribution and light habitat preferences are shown in Table 3 & 4 and Fig. 66.

In most cases the fluorescent plumage parts do not exhibit any distinguishable color changes according to human perception. To a greater extend than the three fluorescence types classified by Völker (1965), my study revealed that fluorescence includes even red and blue colors, however greenish and yellowish fluorescence dominates. Nevertheless, reflectance spectra show striking differences between fluorescent and non-fluorescent plumage parts seemingly equal for the human observer. The breast feathers of the strongly fluorescing Edwards' Fig-Parrot (*Psittaculirostris edwardsii*) reveal a high reflectance in the green range but low reflectance in the ultraviolet (Fig. 53) In contrast, the green non-fluorescing breast feathers of the Eclectus Parrot (*Eclectus roratus*) are not as bright in the green part of the spectrum though brighter in the ultraviolet (Fig. 53).

Another major instance of UV-annihilation in favor of fluorescence is reported in Fig. 54. The yellow ear feathers of the Edwards's Fig-Parrot are strikingly fluorescent and lack any ultraviolet reflection. The yellow part of the spectrum is strongly enhanced. The seemingly equally colored wing coverts of the Scarlet Macaw (*Ara macao*) show a typical spectrum of an ultraviolet-yellow color in parrots with a reflection peak also in the UV.

Figs. 59-61 clearly demonstrate the effect of fluorescence in the plumage of Edwards' Fig-Parrot. This species fluoresces strongly in different colors almost over its entire body. The ultraviolet is almost completely annihilated.

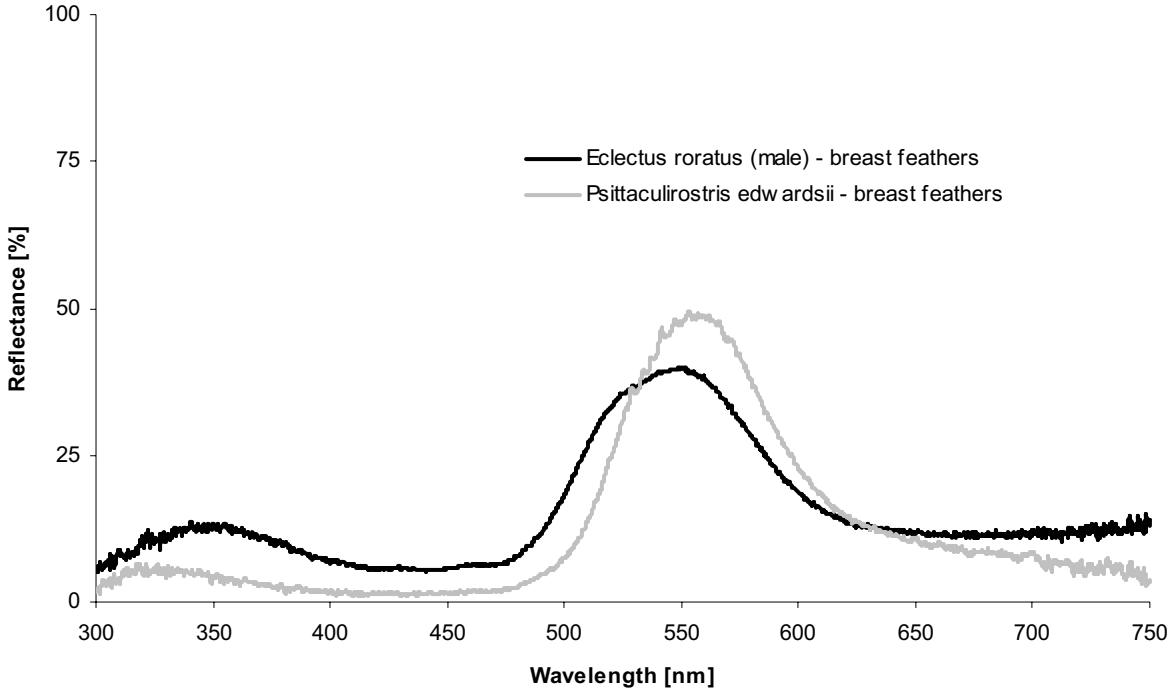



Fig. 53 Fluorescent green breast coverts of an Edwards' Fig-Parrot (*Psittaculirostris edwardsii*) and non-fluorescent green breast coverts of an Eclectus Parrot (*Eclectus roratus*).

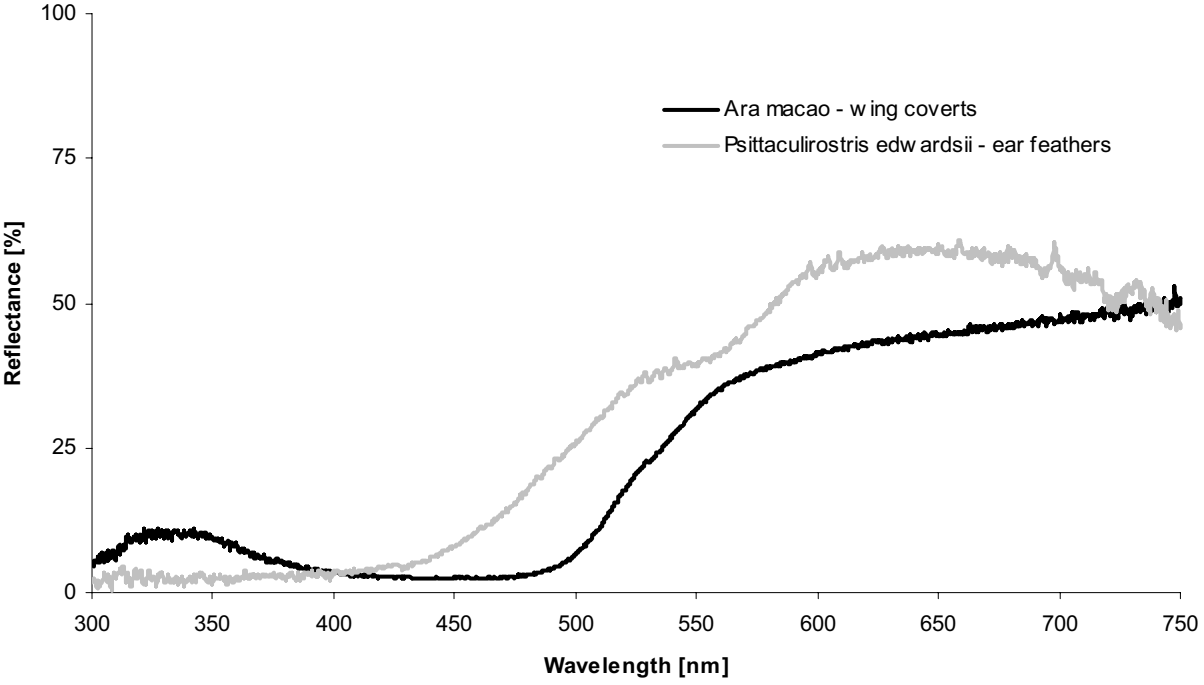



Fig. 54 Fluorescent yellow ear feathers of an Edwards' Fig-Parrot (*Psittaculirostris edwardsii*) and non fluorescent yellow wing coverts of a Scarlet Macaw (*Ara macao*).

The Figures 55-58 demonstrate the frequently investigated (Völker 1936, Driesen 1953, Schmidt 1961, Pearn *et al.* 2001, Arnold *et al*. 2002, Pearn *et al.* 2003) fluorescent properties of the Budgerigar (*Melopsittacus undulatus*). Under sunlight conditions, the Budgerigar displays its normal appearance (Fig. 55). When illuminated with ultraviolet light, fluorescent parts of the plumage glow brightly. In particular, the crown and parts of the face fluoresce conspicuously (Fig. 56). The black and white image of the same specimen, taken under normal light conditions, has a contrasting pattern, as it is to be expected from its color pattern (Fig. 57). On the other hand, the black and white image - reproducing exclusively ultraviolet wavelengths - exhibits a different contrasting pattern (Fig. 58). The crown and the fluorescing parts of the face are dark. This is due to the UV-light removing property of the fluorescence itself, whereby the ultraviolet is transmitted to longer wavelength. Thus, both wavelengths are influenced, the visible spectrum as well as the ultraviolet. The contrast between UV-reflecting and fluorescing non-UV-reflecting plumage parts is enhanced.

In the Colasisi (*Loriculus philippensis*) (Fig 62 & 63), the throat in particular fluoresces strongly, a phenomenon, frequently found in Hanging-Parrots (*Loriculus* sp.) (Figs. 64 & 65).

Fig. 55 Budgerigar (*Melopsittacus undulatus*).

Fig. 56 Fluorescing plumage of the Budgerigar (*Melopsittacus undulatus*).

Fig. 57 Budgerigar (*Melopsittacus undulatus*) in B&W.

Fig. 58 Budgerigar (*Melopsittacus undulatus*) in UV-light.

Fig. 59 Edwards' Fig-Parrot (*Psittaculirostris edwardsii*).

Fig. 60 Edwards' Fig-Parrot, fluo**res**cing (*Psittaculirostris edwardsii*).

Fig. 61 Edwards' Fig-Parrot (*Psittaculirostris edwardsii*) in UV.

Fig. 62 Portrait of a Philippine Hanging-Parrot (*Loriculus philippensis*).

Fig. 63 Fluorescing plumage of the Philippine Hanging Parrot (*Loriculus philippensis*).

Fig. 64 Four Hanging-Parrot species (*Loriculus* spp.).

Fig. 65 Fluorescing plumage of four Hanging-Parrot species (*Loriculus* spp.).

Abbreviations used in Table 2:

N (north), E (east), S (south), W (west), n (northern), e (eastern), s (southern), w (western), c (central), ne (north-eastern), se (south-eastern), sw (south-western), nw (north-western), nc (north-central), ec (east-central), cs (central-southern), cw (central-western), Is. (islands), Mt. (mountain), Mts. (mountains).

Table 2 Birds with fluorescent plumage parts.
* According to Sibley and Monroe (1990)

| Species | Distribution* | Habitat* |
|---|---|---|
| PICIFORMES | | |
| Picidae | | |
| Melanerpes candidus (Otto, 1796) | e S. America | Forest edge, open woodland, savannah farmlands. Lowlands and Mts. to 2200 m. |
| Melanerpes formicivorus (Swainson, 1827) | w N. and n Central America | Oak woodland, mixed oak-coniferous forest |
| Melanerpes cactorum (Orbigny, 1840) | sc S. America | Scrubby woodland, palms, arid scrub Lowlands and Foothills to 2500 m |
| Melanerpes aurifrons (Wagler, 1829) | cs U.S. and Central America | Open woodland, scrub, second growth |
| Dendropicos elliotii (Cassin, 1863) | wc Africa | Humid forest, second growth. Mts., 1000-2300 m |
| Piculus leucolaemus (Natterer & Malherbe, 1845) | w S. America | Humid forest edge, open woodland second growth |
| Piculus aurulentus (Temminck, 1821) | se S. America | Moist woodland edge, second growth |
| Piculus rivolii (Boissonneau, 1840) | w S. America | Humid forest. Mts., 1800-3700 m |
| Colaptes punctigula (Boddaert, 1783) | s c. and n,c S. America | Open woodland, second growth, mangroves, palm savannah, forest edge. Lowlands to 1500 m |
| Colaptes campestris (Vieillot, 1818) | nc,c,e S. America | Grassland, savannah, farmlands. |
| Celeus flavus (Statius Muller, 1776) | S. America | Riverine forest, savannah, mangroves woodland, generally near water. Lowlands to 750 m |
| Picus vittatus (Vieillot, 1818) | se Asia | Forest, mangroves, coastal scrub |
| Picus squamatus (Vigors, 1831) | s Asia | Forest edge, juniper woodland, orchards. Hills and Mts., 100-3700 m |
| Picus awokera (Temminck, 1836) | Japan | Woodland. Hills and Mts., 300-2000 m |
| Picus viridis (Linnaeus, 1758) | w Eurasia | Forest edge, second growth, woodland. Lowland and Mts. to 2750 m |
| Picus erythropygius (Elliot, 1865) | se Asia | Dry forest, scrub woodland. Lowlands to 825 m |
| Picus canus (Gmelin, 1788) | Eurasia | Mixed forest edge, dry woodland, farmlands. Hills and Mts., 1200-3650 m |
| Dinopium benghalense (Linnaeus, 1758) | s Asia | Dry woodland, scrub. Lowlands to 1700 m |

| Species | Distribution* | Habitat* |
|---|---|---|
| Ramphastidae | | |
| Pteroglossus inscriptus (Swainson, 1822) | wc S. America | Humid forest, edge, palm groves, often near water. Lowlands to 500 m |
| Pteroglossus viridis (Linnaeus, 1766) | n S. America | Humid forest. Lowlands to 600 m |
| Pteroglossus azara (Vieillot, 1819) | wc S. America | Humid forest, edge, woodland, generally near streams. Lowlands to 500 m |
| Pteroglossus castanotis (Gould, 1834) | c S. America | Riverine forest, second growth, gallery forest. |
| Pteroglossus aracari (Linnaeus, 1758) | e S. America | Humid forest, edge, open woodland, second growth, savannah, usually near water |
| Pteroglossus torquatus (Gmelin, 1788) | nw S. America | Humid forest, edge, second growth, woodland. Lowlands to 1500 m |
| Pteroglossus beauharnaesii (Wagler, 1832) | wc S. America | Humid forest. Lowlands |
| Selenidera reinwardtii (Wagler, 1827) | w S. America | Humid forest. Lowlands to 1200 m |
| Selenidera culik (Wagler, 1827) | n S. America | Humid forest. Lowlands to 900 m |
| Ramphastos sulfuratus (Lesson, 1830) | Central and nw S. America | Humid forest, edge, woodland. Lowlands to 1600 m |
| Ramphastos vitellinus (Lichtenstein, 1823) | e S. America | Humid forest, usually near water |
| Ramphastos dicolorus (Linnaeus, 1766) | se S. America | Humid forest. Lowlands |
| Ramphastos tucanus (Linnaeus, 1758) | wc S. America | Humid forest, edge, usually along rivers. Lowlands to 1100 m |
| Ramphastos toco (Statius Muller, 1776) | sc,e S. America | Woodland, second growth, Lowlands |
| TROGONIFORMES | | |
| Trogonidae | | |
| Trogon viridis (Linnaeus, 1766) | s c. and w S. America | Humid forest, edge, second growth, woodland. Lowlands to 1300 m |
| Trogon melanocephalus (Gould, 1836) | Central America | Open woodland, scrub, bushes. Lowlands |
| CORACIIFORMES | | |
| Meropidae | | |
| Nyctyornis amictus (Temminck, 1824) | se Asia | Forest. Lowlands to 1700 m |
| Merops oreobates (Sharpe, 1892) | e Africa | Forest edge, open scrub, grassy areas, farmlands. Highlands to 2600 m |
| Merops orientalis (Latham, 1802) | Subsaharan Africa | Arid steppe, thorn bush, dense second growth, swamps |
| Merops superciliosus (Linnaeus, 1766) | sw,e,se Africa | Open country, swamps, farmlands |
| Merops apiaster (Linnaeus, 1758) | s Palearctic | Open country, woodland, orchards, desert oases, farmlands |

| Species | Distribution* | Habitat* |
|---|---|---|
| PSITTACIFORMES | | |
| Psittacidae | | |
| Charmosyna multistriata (Rothschild, 1911) | w New Guinea | Forest. Mts., 200-1800 m |
| Calyptorhynchus funereus (Shaw, 1794) | e Australia | drier areas |
| Calyptorhynchus banksii (Latham, 1790) | Australia | Open forest, woodland, scrub, riverine forest |
| Callocephalon fimbriatum (Grant,JB, 1803) | se Australia | Forest, woodland. Lowlands to to 2000 m |
| Cacatua leadbeateri (Vigors, 1831) | Coastal Australia | Grasslands, scrub, riverine forest |
| Cacatua sulphurea (Gmelin, 1788) | Sulawesi, is. In Java Sea, Lesser Sunda Is. | Forest edge, woodland, farmlands |
| Cacatua galerita (Latham, 1790) | Austral-asian region | Forest, savannah, swamp, palm and eucalyptus forest, mangroves, farmlands |
| Cacatua ophthalmica (Sclater,PL, 1864) | Bismarck Ach. | Forest. Lowlands to 1000 m |
| Cacatua moluccensis (Gmelin, 1788) | s. Mollucas | Forest, Woodland |
| Cacatua alba (Statius Muller, 1776) | c,n Mollucas | Forest |
| Cacatua haematuropygia (Statius Muller, 1776) | Philippines | Forest edge, second growth, farmlands |
| Cacatua goffini (Finsch, 1863) | Tanimbar Is. | Forest, woodland, scattered trees |
| Cacatua sanguinea (Gould, 1843) | sw, w, n, int. e Australia | Riverine Woodland, savannah, farmlands |
| Cacatua gymnopsis (Sclater,PL, 1871) | sw, w, n, int. e Australia | Riverine Woodland, savannah, farmlands |
| Cacatua pastinator (Gould, 1841) | sw W. Australia | Woodland, farmlands |
| Cacatua tenuirostris (Kuhl, 1820) | Extreme se S. Australia | Open forest, woodland, riverine forest, farmlands |
| Cacatua ducorpsii (Pucheran, 1853) | e Solomon Is. | Forest edge, second growth, farmlands |
| Nymphicus hollandicus (Kerr, 1792) | Australia | Open woodland, riverine forests, scrub, farmlands |
| Micropsitta keiensis (Salvadori, 1876) | New Guinea region | Forest |
| Micropsitta geelvinkiana (Schlegel, 1871) | Is. w of New Guinea | Forest |
| Micropsitta pusio (Sclater,PL, 1866) | New Guinea region | Forest, Lowlands to 850 m |
| Micropsitta meeki (Rothschild & Hartert, 1914) | Bismarck Arch. | Forest |
| Micropsitta finschii (Ramsay,EP, 1881) | Bismarck Arch. | Forest |
| Micropsitta bruijnii (Salvadori, 1875) | New Guinea region | Forest. Mts., 1000-2300 m |
| Cyclopsitta gulielmiterti (Schlegel, 1866) | New Guinea | Forest, savannah. Lowlands to 800 m |
| Cyclopsitta diophthalma (Hombron 1841) | Austral-asian region | Humid forest, second growth, riverine forest, farmlands |
| Psittaculirostris desmarestii (Desmarest, 1826) | New Guinea | Forest, savannah. Lowlands to 1500 m |
| Psittaculirostris edwardsii (Oustalet, 1885) | New Guinea | Humid forest. Lowlands to 800 m |
| Psittaculirostris salvadorii (Oustalet, 1880) | New Guinea | Forests. Costal lowlands to 400 m |
| Bolbopsittacus lunulatus (Scopoli, 1786) | Philippines | Open woodland, forest edge, savannah, farmlands |
| Geoffroyus geoffroyi (Bechstein, 1811) | e Indonesia and Austral -asian region | Forest, savannah woodland, mangroves, farmlands. Lowlands to 1400 m |

| Species | Distribution* | Habitat* |
|---|---|---|
| Geoffroyus simplex (Meyer,AB, 1874) | New Guinea | Humid forest. Mts., 800-2300 m |
| Prioniturus montanus (Ogilvie-Grant, 1895) | n Philippines | Humid forest. Mts., 850-1700 m |
| Prioniturus discurus (Vieillot, 1822) | Philippines | Humid forest. Lowlands to 1750 m |
| Prioniturus flavicans (Cassin, 1853) | n Sulawesi | Humid forest edge. Lowlands to 1000 m |
| Prioniturus platurus (Vieillot, 1818) | Sulawesi | Humid forest edge, woodland. Lowlands to 2000 m |
| Tanygnathus megalorhynchos (Boddaert, 1783) | c,e Indonesia | Humid forest edge, woodland, farmland |
| Tanygnathus lucionensis (Linnaeus, 1766) | ne Malay Arch. | Forest, farmlands |
| Alisterus scapularis (Lichtenstein, 1816) | e Australia | Forest, eucalyptus woodland, scrub |
| Aprosmictus jonquillaceus (Vieillot, 1818) | Lesser Sunda Is. | Woodland. Lowlands to 2600 m |
| Aprosmictus erythropterus (Gmelin, 1788) | Australian region | Forest edge, woodland riverine forest, acacia scrub savannah, mangroves, farmlands |
| Polytelis swainsonii (Desmarest, 1826) | se Australia | Riverine eucalyptus forest, woodland |
| Polytelis anthopeplus (Lear, 1831) | sw,se Australia | Riverine eucalyptus forest, woodland, scrub |
| Polytelis alexandrae (Gould, 1863) | w,c Australia | Dry riverine eucalyptus forest, woodland, acacia scrub |
| Purpureicephalus spurious (Kuhl, 1820) | sw Australia | Riverine forest, woodland, farmlands |
| Platycercus zonarius (Shaw, 1805) | s,c Australia | Humid costal forest, Woodland, desert scrub |
| Platycercus barnardi (Vigors & Horsfield, 1827) | e Australia | eucalyptus woodland, riverine woodland, scrub |
| Platycercus caledonicus (Gmelin, 1788) | Tasmania | Humid forest, open woodland, riverine woodland, scrub, farmland |
| Platycercus elegans (Gmelin, 1788) | E.,se Australia | Humid forest, woodland |
| Platycercus adelaidae (Gmelin, 1788) | e,s Australia | |
| Platycercus flaveolus (Gould, 1837) | se Australia | Riverine forest, woodland, farmlands |
| Platycercus venustus (Kuhl, 1820) | N. Australia | Open woodland, riverine woodland, scrub, farmlands |
| Platycercus adscitus (Latham, 1790) | ne,e Australia | Open woodland, riverine woodland, scrub, farmlands |
| Platycercus eximius (Shaw, 1792) | se Australia | Open forest, riverine woodland, scrub, farmlands |
| Platycercus icterotis (Temminck & Kuhl, 1820) | sw Australia | Open forest, riverine woodland, farmlands |
| Northiella haematogaster (Gould, 1838) | se W. Australia | Open woodland, riverine woodland, scrub, farmlands |
| Psephotus haematonotus (Gould, 1838) | se Australia | Open woodland, scrub, farmlands |
| Psephotus varius (Clark,AH, 1910) | s Australia | Riverine woodland, scrub |
| Psephotus dissimilis (Collett, 1898) | nc Australia | Dry open woodland, eucalyptus woodland |
| Psephotus chrysopterygius (Gould, 1858) | Extreme ne Australia | Open eucalyptus woodland, scrub, mangroves |
| Psephotus pulcherrimus† (Gould, 1845) | Formerly ec Australia | Grassy eucalyptus woodland, grassy scrub |
| Cyanoramphus unicolor (Lear, 1831) | Antipodes Is. | Dense tall Poa tussocks, open scrub |
| Cyanoramphus auriceps (Kuhl, 1820) | New Zealand region | Forest, subalpine scrubs. Lowlands and Mts. |
| Neophema chrysostoma (Kuhl, 1820) | se Australia | Open woodland, heath, forest, scrub, grassland, farmlands |
| Neophema elegans (Gould, 1837) | sw,se Australia | Open woodland, scrub, grassland, farmlands, salt marshes |
| Neophema chrysogaster (Latham, 1790) | sw Tasmania | Open grasslands, salt marshes, sandy areas, tidal beaches |

| Species | Distribution* | Habitat* |
|---|---|---|
| Neophema pulchella (Shaw, 1792) | se Australia | Open woodland, heath, scrub, grassland |
| Neophema splendida (Gould, 1841) | sw,sc Australia | Open eucalyptus woodland, scrub |
| Melopsittacus undulatus (Shaw, 1805) | Drier parts of Australia | Grasslands, spinifex, riverine woodland, farmlands |
| Pezoporus occidentalis (Gould, 1861) | Australia | Spinifex in stony or sandy area |
| Agapornis canus (Gmelin, 1788) | Madagascar | Forest edge, brush, grassland, farmlands |
| Agapornis pullarius (Linnaeus, 1758) | w,c Africa | Second growth, open woodland, savannah, farmlands |
| Agapornis taranta (Stanley, 1814) | n,c,w Ethiopia | Forest. Highlands, 1300-3200 m |
| Agapornis swindernianus (Kuhl, 1820) | w,c Afrika | Humid forest. Lowlands to 1800 m |
| Agapornis roseicollis (Vieillot, 1818) | sw Africa | Dry open country, savannah. Lowlands to 1600 m |
| Agapornis fischeri (Reichenow, 1887) | ec Africa | Acacia grassland, savannah, farmlands. Highlands 1100-1700 m |
| Agapornis personatus (Reichenow, 1887) | ec Africa | Acacia grassland, savannah. Highlands 1100-1700 m |
| Agapornis lilianae (Shelley, 1894) | se Africa | Mopane and acacia woodland. Lowlands, 600-1000 m |
| Agapornis nigrigenis (Sclater,WL, 1906) | sc Africa | Mopane woodland in river valleys. Lowlands to 1000 m |
| Loriculus vernalis (Sparrman, 1787) | S. Asia | Open forest, woodland, bamboo, jungle thickets. Lowlands and Mts. to 2000 m |
| Loriculus beryllinus (Forster,JR, 1781) | Ceylon | Woodland. Lowlands and Mts. to 1600 m |
| Loriculus philippensis (Statius Muller, 1776) | Philippines | Forest, second growth, bamboo, farmlands. Lowlands and Mts. to 2500 m |
| Loriculus galgulus (Linnaeus, 1758) | se Asia | Open woodland, bamboo, orchards. Lowlands to 1250 m |
| Loriculus stigmatus (Muller,S, 1843) | Sulawesi | Open country, woodland. Lowlands to 800 m |
| Loriculus amabilis (Wallace, 1862) | Wallacea | Forest edge, second growth |
| Loriculus sclateri (Wallace, 1863) | Indonesia | Forest edge, second growth |
| Loriculus aurantiifrons (Schlegel, 1871) | New Guinea region | Forest. Lowlands to 1200 m |
| Loriculus tener (Sclater,PL, 1877) | Bismarck Arch. | Forest |
| Loriculus exilis (Schlegel, 1866) | n,e,se Sulawesi | Forest, woodland, mangroves. Lowlands to 800 m |
| Loriculus pusillus (Gray,GR, 1859) | W Indonesia | Forest edge. Lowlands to 1850 m |
| Psittacula eupatria (Linnaeus, 1766) | S Asia | Forest, woodland, farmlands, mangroves |
| Psittacula krameri (Scopoli, 1769) | Subsaharan Africa | Open woodland, savannah, farmlands |
| Psittacula himalayana (Lesson, 1832) | se Asia | Forest, second growth. Himalayas to 2500 m |
| Psittacula finschi (Hume, 1874) | se Asia | Forest, second growth, orchards. Foothills and Mts. to 3600 m |
| Psittacula cyanocephala (Linnaeus, 1766) | s Asia | Open scrub, deciduous woodland, open forest, farmlands. Lowlands and Mts. to 1800 m |
| Psittacula roseate (Biswas, 1951) | se Asia | Forest, second growth, farmlands. Lowlands to 900 m |
| Psittacula columboides (Vigors, 1830) | sw India | Humid forest, woodland. Lowlands to 1500 m |
| Psittacula calthropae (Blyth, 1849) | Ceylon | Forest, woodland. Lowlands to 2000 m |
| Psittacula derbiana (Fraser, 1852) | sw China | Pine and rhododendron forest. Himalayas, 2800-4000 m |

| Species | Distribution* | Habitat* |
|---|---|---|
| Psittacula alexandri (Linnaeus, 1758) | s Asia | Forest, second growth, mangroves. Lowlands to 1500 m |
| Psittacula caniceps (Blyth, 1846) | Nicobar Is. | Forest, woodland |
| Psittacula longicauda (Boddaert, 1783) | se Asia | Forest, woodland, palm groves, second growth. Lowlands to 350 m |
| Aratinga guarouba (Gmelin, 1788) | ne Brazil | Humid forest. Lowlands |
| Bolborhynchus lineola (Cassin, 1853) | Central America | Humid forest, open woodland, savannah. Locally in highlands, 750-3000 m |
| Forpus sclateri (Gray,GR, 1859) | n,wc S. America | Riverine forest, second growth. Lowlands to 500 m |
| Brotogeris chiriri (Vieillot, 1818) | sc,se S. America | Open forest, woodland, scrub, savannah. Lowlands |
| Brotogeris jugularis (Statius Muller, 1776) | Central and nw S. America | Open woodland, second growth, forest edge, arid scrub. Lowlands to 1400 m |
| Brotogeris cyanoptera (Pelzeln, 1870) | wc S. America | Savannah, woodland. Lowlands to 500 m |
| Brotogeris chrysopterus (Linnaeus, 1766) | n,nc S. America | Forest, edge, savannah. Lowlands to 1200 m |
| Pionites melanocephala (Linnaeus, 1758) | nc S. America | Forest, savannah. Lowlands to 1100 m |
| Pionites leucogaster (Kuhl, 1820) | wc S. America | Forest. Lowlands |
| Amazona agilis (Linnaeus, 1758) | w Jamaica | Forest. Mts. and hills |
| Amazona tucumana (Cabanis, 1885) | s S. America | Alder forest. Mts., 1800-2000 m |
| Amazona guildingii (Vigors, 1837) | St. Vincent | Forest |
| COLUMBIFORMES | | |
| Columbidae | | |
| Treron calva (Temminck, 1811) | w,c,ne Africa | Open woodland, savannah, gallery forest |
| Treron sanctithomae (Gmelin, 1789) | Sao Tome | Tall forest |
| Ptilinopus occipitalis (Gray, GR, 1844) | n Philippines | Dense second growth, forest |
| Ptilinopus perousii (Peale, 1848) | S. Polynesia | Forest, grassland copses |
| CICONIIFORMES | | |
| Spheniscidae | | |
| Aptenodytes patagonica (Miller,JF, 1778) | Is. of s oceans | Pelagic |
| Aptenodytes forsteri (Gray,GR, 1844) | Coastal Antarctica | Pelagic |
| Eudyptes chrysocome (Forster, JR, 1781) | s S. America | Pelagic |
| Eudyptes chrysolophus (Brandt, 1837) | Is. of s oceans | Pelagic |
| Megadyptes antipodes (Hombron & Jacquinot, 1841) | New Zealand region | Pelagic |

| Species | Distribution* | Habitat* |
|---|---|---|
| GRUIFORMES | | |
| Otididae | | |
| Eupodotis senegalensis (Vieillot, 1820) | n,e Africa | Grassland, acacia veld, scrub, open woodland, dry plains |
| PASSERIFORMES | | |
| Pittidae | | |
| Pitta versicolor (Swainson, 1825) | E. Australia | Humid forest |
| Tyrannidae | | |
| Pipra fasciicauda (Hellmayr, 1906) | sc S. America | Forest. Lowlands |
| Pipra filicauda (Spix, 1825) | c S. America | Forest. Lowlands to 1000 m |
| Pipra erythrocephala (Linnaeus, 1758) | s c. and n,wc S. America | Humid forest undergrowth, edge, second growth. Lowlands to 2000 m |
| Pipra rubrocapilla (Temminck, 1821) | c,e S. America | Humid forest, edge. Lowlands |
| Pipra pipra (Linnaeus, 1758) | s c. America | Undergrowth of forest and savannah |
| Meliphagidae | | |
| Anthochaera carunculata (Shaw, 1790) | s Australia | Open forest |
| Corvidae | | |
| Cicinnurus magnificus (Forster, JR, 1781) | New Guinea region | Forest. Mts., 575-1600 m |
| Cicinnurus respublica (Bonaparte, 1850) | w Papuan is. | Forest. Int. hills above 300 m |
| Paradisaea apoda (Linnaeus, 1758) | New Guinea region | Forest. Lowlands to 1000 m |
| Paradisaea guilielmi (Cabanis, 1888) | se New Guinea | Forest. Mts., 500-1800 m |
| Passeridae | | |
| Chloebia gouldiae (Gould, 1844) | N. Australia | Savannah, mangroves, near water |
| Fringillidae | | |
| Carduelis carduelis (Linnaeus, 1758) | w Palearctic | Open country, woodland, farmlands, weedy areas |
| Buthraupis Montana (d'Orbigny & Lafresnaye, 1837) | w S. America | Humid forest, second growth, woodland |
| Tangara icterocephala (Bonaparte, 1851) | s c. and nw S. America | Humid forest, edge, second growth. Mts., 400-2600 m |
| Tangara xanthocephala (Tschudi, 1844) | S. America | Humid forest, edge, open woodland, second growth. Mts., 750-3100 m |
| Gymnostinops Montezuma (Lesson, 1830) | Central America | Clearings with large trees, humid forest |

The observed species are grouped into biogeographical regions according to their distribution shown in Table 2.

Table 3 Fluorescing species with respect to the biogeographical region.

| Biogeographical Region | # Species | # Family |
|---|---|---|
| Palaearctic Region | 5 | 3 |
| Indomalayan Region | 28 | 4 |
| Afrotropical (Ethiopian) Region | 18 | 5 |
| Australasian Region | 79 | 6 |
| Nearctic Region | 2 | 1 |
| Neotropical Region | 44 | 6 |
| Oceania | 1 | 1 |
| Antarctica | 3 | 1 |

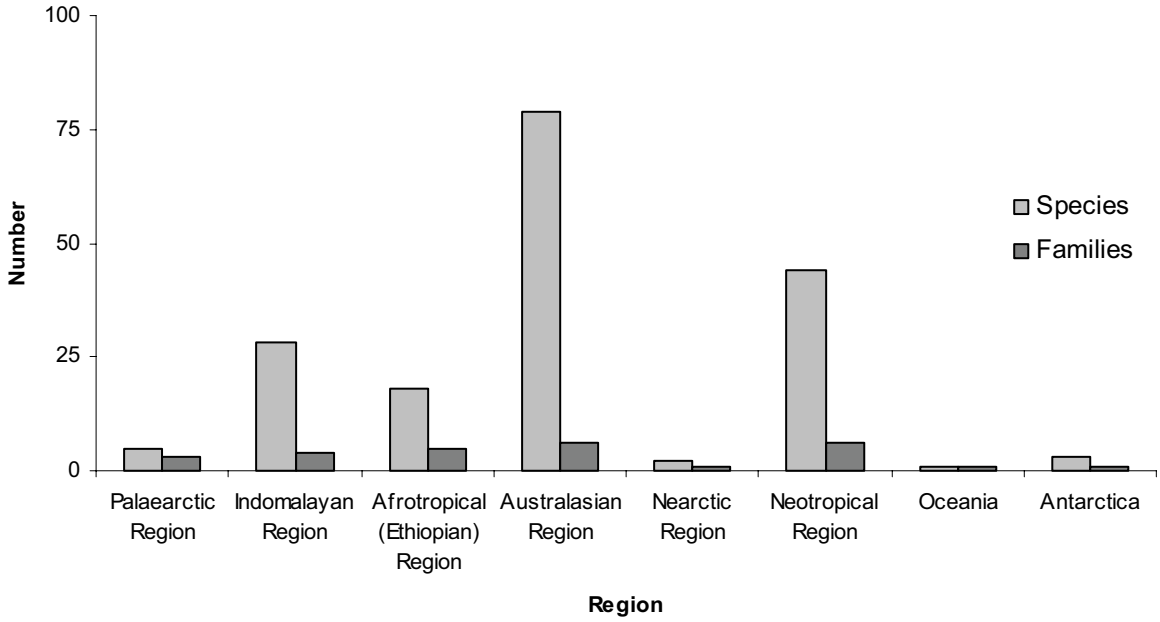



Fig. 66 Biogeographical Distribution of Fluorescent Plumage Pattern.
There is an obvious tendency for the Australasian Region being the “hot spot” of fluorescing species, though this position can not be perpetuated on the family level.

Light habitats are derived from the habitats, presented in Table 2.

Table 4 Fluorescing species with respect to the simplified Light Habitats.

| Light Habitat | # Species | # Family |
|---|---|---|
| Open | 99 | 10 |
| Shady | 61 | 9 |
| Non-distinguishable | 20 | 5 |

$Chi^2$ species: p = 0.0026

$Chi^2$ families: p = 0.8185

Regarding species level only, there is a clear significance for birds exhibiting fluorescent plumage, living in open habitats. However, on integrating the results to family level, no preference for any light environment is evident.

Artificial fluorescent plumage in museum bird skins

Plumage parts, contaminated with any kind of fluorescent substance, show a substantial decrease in their ultraviolet reflections. Other parts of the reflectance spectrum are enhanced. This effect is demonstrated in Fig. 67. Uncontaminated breast coverts show a peak reflectance in the green range, as well as another peak in the UV. Breast coverts of the same species, contaminated with a fluorescing preservation agent (in this particular case, an older recipe of Seibokal ES), dramatically lack ultraviolet reflections while the green is irregularly brightened.

On using black light lamps on bird museum skins in a darkened environment, it is easy to detect all the fluorescent parts of a bird skin, both those which are naturally fluorescing and those which are accidentally fluorescing. Fluorescent stains will shine with a bright greenish or yellowish color when illuminated by UV-light.

Fluorescent stains of non-natural origin occurred in some 500 bird skins of varying ages (1913-2004) in different museum collections. The intensity of contamination of the plumage with fluorescent preservation agents varied within the different affected bird skins. In order to establish the cause, different commonly and seldom used preservation agents were checked for their fluorescent properties. Seibokal ES, a preservation agent produced by Heindl GmbH, Germany exhibited fluorescence.

Fluorescence did not occur in any of the frequently modified recipes of Seibokal ES. Mercurous chloride (HgCl) exhibits a fluorescing red a phenomenon, never observed in artificially fluorescing bird skins.

Some birds, prepared with obviously non-fluorescing preservation agents still exhibit fluorescing stains, occurring predominantly on breast coverts or ventral coverts of a bird skin. These parts of the skin are at highest risk of being contaminated with body fluids during taxidermy. Although most of the stains found in this body region are also invisible to a human observer, they nonetheless influence the UV reflectance spectra. Many of them can't be related to any preservation agent and are likely to consist of body fluids. Different oils and fats fluoresce under black light illumination. The naturally decomposing, non-preserved birds also exhibited fluorescence, predominately around the eyes, at the feet and at the base of the beak.

As an example, the effects of contamination due to preservation agents are demonstrated by means of the strongly contaminated green breast feathers of a Red-lored Parrot skin (*Amazona autumnalis*) held in the scientific collection of the Zoological Research Institute and Museum A. Koenig, Bonn, Germany. Uncontaminated breast feathers of the Red-lored Parrot strongly reflect UV light, with a remarkable UV-reflectance peak at 355 nm (Fig. 67). The same plumage parts of another specimen, stained with the preservation agent Seibokal ES, were measured to illustrate the effects of contamination. The UV-reflectance peak almost disappeared, while reflections in the visible spectrum were altered by the effects of the re-emitted light from fluorescence (Fig. 67). The artificial fluorescent plumage can easily be distinguished from natural fluorescent feathers: stains caused by some preparation agents have a dirt-like appearance similar to a dried milky liquid, while the naturally fluorescing parts can be ascribed to certain plumage regions without exhibiting such properties.

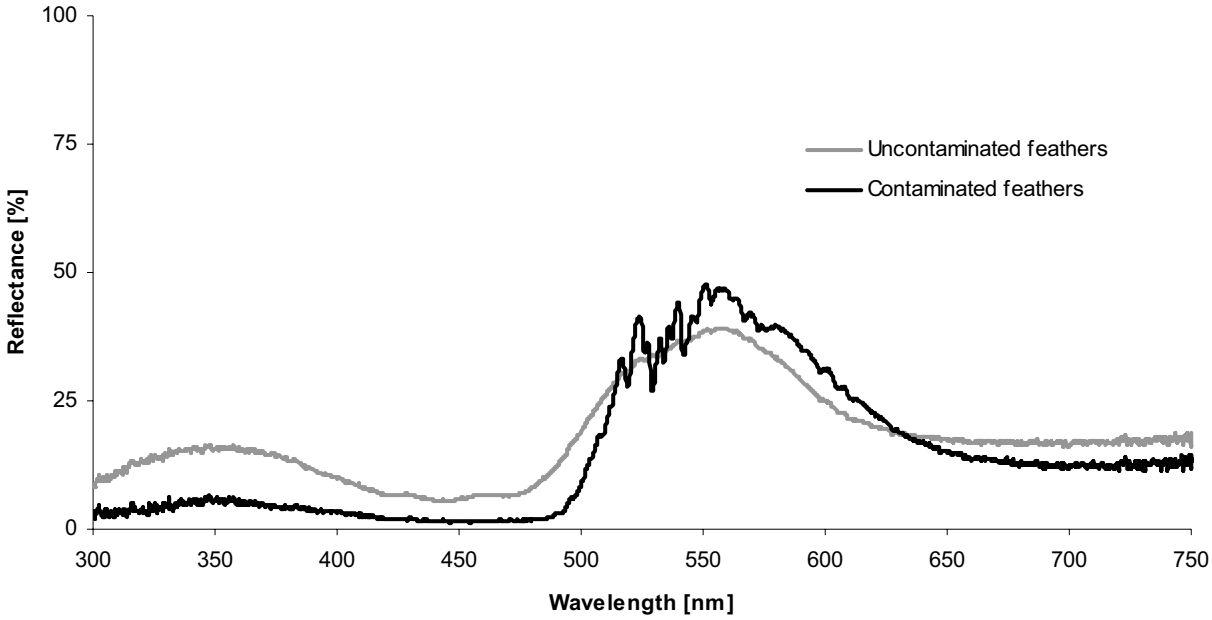



Fig. 67 Spectra of Contaminated and Uncontaminated Feather Patches in two museum held skins of the Red-lored Parrot (*Amazona autumnalis*).

## 3.4 Discussion

### Natural fluorescent plumage

Fluorescence can be assumed to be a widespread phenomenon among birds. In my study, 181 bird species in 14 families with fluorescent plumage parts have been confirmed. Fluorescence generates different effects on color and brightness. Though in many cases, neither the ultimate nor the proximate evolutional traits are conspicuous, still some characteristics are evident. One undisputable effect of fluorescence in avian plumage is the alteration in ultraviolet reflections. Whether fluorescence is involved in signaling, or an incidental side-effect of feather pigmentation, the optical appearance of the particular bird is substantially affected. This phenomenon can affect any color and the spectrum of fluorescence extends from blue to red, consistent with the overall color of the respective feather patch.

### Fluorescence brightens plumage coloration

Hausmann *et al.* (2003) reported a significant relationship between fluorescence and plumage presented in courtship. However, these findings alone do not allow any evaluation of its potential signal character. Light emissions based upon fluorescent pigments may contribute to the overall brightness and saturation of particular colors. Plumage brightness has already been reported to correlate positively with male mating success (Stein & Uy 2006). Even although fluorescence intensifies certain colors, it still leads to a reduction in the total amount of reflected light. According to the First Law of Thermodynamics and the Stoke's Law, energy can't be gained due to fluorescence; quite the contrary is the case, it will decrease. Nevertheless, some parts of the spectrum are brightened. A potential signal would benefit from radiation being transferred from wavelengths unsuitable for visual perception to those more suitable for ecological or physiological necessities. Light of a certain wavelength could be emitted, compatible with the maximal spectral sensitivity of the receiver. The additional enhancement of a certain color due to fluorescence could increase success in courtship, if biased by sexual selection. Fluorescence could also partly outshine the deficiency of pigments or defects in feather structure if alternately used

for color production. In accordance with the Hamilton-Zuk Hypothesis (1982), the existence of fitness indicating pigments (McGraw & Ardia 2003) could be mimicked. These pigments would usually advertise the male's quality with regard to being capable of fending off parasites and gathering high-grade food (Fitzpatrick 1998, McGraw 2005), as well as parental qualities (Massaro *et al.* 2003). Plumage coloration can be influenced by carotenoid contents in diet (Navara & Hill 2003). Although, if carotenoid pigments are not sufficiently available, proper feather coloration is at risk. This deficiency could probably be covered partly by fluorescence effects, according to the sensory trap hypotheses (Christie 1995), assuming that the fluorescent pigment is more readily available.

Fluorescence enhances contrast in plumage patterns

The fact, that Budgerigars' plumage appears bright to humans, and fluoresces under UV light, does not imply that it is the yellow light, visible to humans, that is involved in bird signaling. The signal could possibly be the avoidance of UV-reflections in order to enhance the contrast between fluorescing and ultraviolet reflecting feathers. Different studies reported the importance of UV reflections of feathers when females choose a mate. The females prefer UV-reflecting males to non-UV-reflecting males (e.g., Bennett *et al*. 1997, Andersson *et al*. 1998, Hunt *et al*. 1999). Evidence that fluorescence itself acts as a signal is still to be found. Further information can be derived from the parrots. This study indicates that the occurrence of fluorescence is most widespread in parrots, likewise UV reflections (Mullen & Pohland, unpublished data). About 300 parrot species were analyzed and the findings indicate that there is no other group of birds exhibiting such a remarkable amount of UV-phenomena in their plumage. Unlike the findings of other authors (Arnold *et al*. 2002, Hausmann *et al*. 2003), it was demonstrated that UV signals are not special, in line with the findings of Eaton & Lanyon (2003). Many parrot feathers, such as the blue cheek patches of the Budgerigar, reflect strongly in the ultraviolet (Fig. 58). If the generation of UV reflections is a common plesiomorphic feature of all parrots, then there might be a need for the avoidance of such. The avoidance of UV reflections via fluorescence provides two different scenarios. Many birds calculate colors from four types of cone receptors in their retina. Hence, the lack of information from one type, due to absence of UV components in a color, might create a different color.

Another effect is the enhancement of contrast, especially in courtship-relevant plumage patterns. Therefore, in specific cases, it would be appropriate to avoid UV reflections by using the short wavelength energy for fluorescence. This applies particularly for parrots, where the abundance of UV reflections reaches its peak level. Contrast enhancement functions in any light environment involving ultraviolet rays. It is independent of species, region and the overall brightness of a scene.

Fluorescence influences courtship behavior

Different authors proposed a crucial role of fluorescence as well as ultraviolet reflections in avian mate choice (Pearn *et al.* 2001, Parker 2002, Arnold *et al.* 2002, Hausmann *et al.* 2003, Pearn *et al.* 2003, Parker 2005). Males lacking certain characteristics related to UV reflections and fluorescent plumage parts were reported to be less successful than regularly colored conspecifics. It is likely, that any alteration in plumage coloration leads to a reduced success in mate choice, because coloration can act as a major criterion in advertising male quality (Hamilton & Zuk 1982, Fitzpatrick 1998, Massaro *et al.* 2003, McGraw & Ardia 2003, Navara & Hill 2003, McGraw *et al.* 2004).

These findings reasonably concur with theories concerning female selection in sexually dimorphic birds. Parrots are not the best example for sexual dimorphisms in birds. Actually most species are not sexually dimorphic at all. Males and females of many parrot taxa share the same properties in both ultraviolet and fluorescent plumage parts. Nevertheless, amongst all bird orders, these properties are the most widespread in parrots. The fact, that fluorescence and ultraviolet reflecting plumage predominates in a taxon in which sexual dimorphism is not or only scarcely elaborated leads to the conclusion, that there is no special role for these properties in avian mate choice. Hence, when these colors are altered it might cause reduction in courtship success, as well as in the alteration of any other color component.

## Taxon dependency of fluorescence

Even though my study demonstrates, to a large extent that parrots are fluorescent, 13 more bird families with fluorescent plumage were taken into account. It is likely, that more families with fluorescent species exist. In relation to the species level, parrots are in the clear majority. The high number of fluorescent parrots is probably biased by the fact that this taxon, as far as fluorescence is concerned, is the best explored. Nevertheless, it is notable, that more than a third of all parrot species exhibit fluorescent plumage parts. Fluorescence occurs frequently in connection with colorful feathers. Parrots are predominantly rich in coloration. Many different pigments have been found in parrot feathers. Fluorescence is based on the physical properties of certain pigments. Hence, as colorful pigments are involved, there might be a probability for fluorescence. Above all, parrots might depend on fluorescence to suppress UV reflection as mentioned above.

Regarding the family level, the exclusiveness of fluorescent plumage for certain taxa seems to be invalid and thus, a phylogenetic correlation would appear to be questionable. It is most probable that many more bird families include species with fluorescent plumage parts. To my knowledge, as far as fluorescence is concerned, this study is by far the most fundamental. More than 1 500 species have been studied for their fluorescent properties. However, more species could fluoresce. Some type of fluorescence cannot be reliably detected with a black light lamp. Further analyses including fluorescence spectrophotometry will be essential to confirm fluorescence in other specimens. Based on current data, there is no evidence for a taxon dependency of avian plumage fluorescence. Hence, it may be a plesiomorphic character of some group.

## Biogeographical relations in fluorescence phenomena

The most naturally fluorescing bird species seem to live in Australia. Different studies from other authors support this finding. However, these studies mainly focused on Australian parrot species. There has never been a broad screening of fluorescence phenomena involving different taxa from other regions. The predominance of Australian species is likely to be biased by the high number of closely related parrot

species analyzed in this study as well. With regard to bird families, the assumption of a biogeographically originated distribution of fluorescence in avian plumage cannot be supported. Species exhibiting fluorescent plumage are found in every biogeographical region of the world. There is still a tendency for this phenomenon to be widely distributed in the tropics. This could be influenced by the selection of specimens, for the studies on which this analysis is based, as I have mainly dealt with tropical birds. Moreover, tropical birds are, in many cases, more colorful. Since fluorescence is usually attributed to vividly colored plumage parts, the increase in fluorescent species is as expected for tropical regions.

Fluorescence is attributed to light habitat

A possible explanation of heterogeneous distribution of fluorescing birds is given by Parker (2005). He hypothesized that many Australian parrots live in open habitats while South American species tend to inhabit forest and therefore are highly associated with shady habitats. In open habitats, UV light - necessary for fluorescence - is available in much higher amounts than in habitats of dense forests. Although, once again, only parrots are considered, light habitats could play a crucial role for the evolution of fluorescent colors. In my study, light habitats have been reduced to just two basic alternatives, i.e., open or shady habitats. This simplification, in some cases does not meet apparent behavior. Birds living in uniform light habitats might still make use of differences in micro light habitats, such as sunny spots or exposed perches. Moreover, light changes diurnally depending on weather conditions and the time of day. Annual changes in light habitats originate in the sun cycle, climatic changes and altering vegetation, the latter acting as a light filter as well as a contrasting background. However, the basic light habitat influences the evolution of plumage coloration, at least mediated by natural selection due to predation avoidance.

The results of my study provide evidence for a connection of light environment and fluorescent plumage coloration, when considered at species level. As mentioned above, the high number of parrots may influence these results. At family level, there is no significance for light habitats influencing the distribution of fluorescent plumage patterns, suggesting an ecological cause rather than plesiomorphy. Fluorescing birds

have been found living in both, open and shady environments. Actually, there seems to be no need to additionally brighten plumage in a bright environment where enough light is available for ordinary reflection. In contrast, in dark environments a brightening of certain patterns would have a greater effect, especially on organisms adapted to a dim environment. However, in dark habitats, UV light is sparsely available. Provided that the light environment influences the evolution of coloration, but does not at first govern the distribution of fluorescence, it appears likely that fluorescence of avian plumage plays an alternate role.

Fluorescence acts as a sun protection

Fluorescence has been discussed in the literature as acting as sun protectant in scorpions. It is reported to prevent bleaching in certain corals. In this context, it could be considered to act as a sun protection for birds as well. Fluorescent plumage could annihilate ultraviolet light without creating heat and protect its bearer against the potentially dangerous effects of UV radiation on the organism. However, on argument against the hypothesis of fluorescence acting as a kind of sun blocker is that a dense plumage is rather opaque. Furthermore, protection from ultraviolet light is easily acquired by just absorbing pigments, without any need for fluorescence. In addition to that, it has to be considered, that fluorescence annihilates only a certain part of the spectrum, i.e., the mandatory excitation wavelength. This does not include necessarily UV-B radiation, the most harmful for the organism.

Fluorescence is involved into signaling of cave breeding birds

Another possible implication of fluorescent signaling was proposed by Schuchmann (personal communication). He hypothesized, that fluorescent plumage could be a character of cave breeding birds. As a matter of fact, most birds exhibiting fluorescent plumage are cavity breeders. This finding correlates with the high number of parrots with fluorescent plumage which are predominately cavity-breeding. Also penguins breeding on a clear ground perpetuated this plesiomorphic feature from an ancestral cave breeding species. Beyond that, the relation between cave breeding and fluorescence is in line with the reported fluorescence in poults of various bird taxa. A potential benefit from this phenomenon could be bright advertising that a

cavern is already occupied. This signaling does not necessarily take place in the more or less complete darkness of the cavern but at the entrance. Either conspecifics or other birds would rapidly recognize the inhabitant and look for another place. On an intraspecific level this could optimize the exploitation of breeding holes when a closer observation of occupied places is dispensable. An a priori avoidance of both intraspecific and interspecific competition would support the evolution of this attribute.

However, in the dark environment of a nest-hole where light is sparsely available, the ultraviolet radiation needed for fluorescence would be very limited. Nonetheless, just a marginal increase in contrast could well be recognized against an entirely black background of a cave. If the communication takes place inside a breeding cavern, a dark adapted perceiver would likely be able to distinguish between slightly altered color signals. In this case, fluorescence would also act as a contrast enhancer in favor of one particular color channel, at the cost of overall brightness.

Fluorescent plumage colors are visible in crepuscular light.

Mating in birds frequently occurs early in the morning or the late evening when sunlight is not available. Crepuscular light is characterized by high amounts of short wavelengths which could be used for fluorescence. As well as reef dwelling organisms, a bird could benefit from exhibiting a colorful plumage in a monochromatic environment. Colors produced by fluorescence would be the first visible chromatic elements in the early morning before sunrise and the last visible chromatic elements in the late evening. Thus, a bird exhibiting fluorescent plumage parts could temporize for courtship behavior. However, even penguins spend several month of the year in the monochromatic crepuscular blue of the Antarctic winter. Their fluorescent plumage patches could therefore be the only additional color during this time and hence, would be a feasible element in signaling.

Fluorescence is just a side-effect of pigmentation

Unless there is no radical evidence for either an ecological or evolutionary implication of fluorescence in avian plumage, the possibility of it being just a side effect of pigmentation has to be seriously taken into consideration. Whenever pigments are

involved, there is the possibility of fluorescence. Fluorescence occurs unpredictably in molecules, especially of organic compounds. Different pigments fluoresce while UV reflections are based upon structural properties of a feather. However, feathers exclusively exhibiting structural colors never fluoresce. This is the reason for the lack of fluorescence in some taxa, otherwise known for their vivid coloration, e.g., hummingbirds. Parrots impressively demonstrate plumage coloration originating in both, pigments and feather structure. Anyway, fluorescent pigments as well as non-fluorescent pigments are found in this family and hence an evolutionary drive is likely to exist integrating fluorescent pigmentation at least in some feather parts. Moreover, in most cases, fluorescent pigmentation is found within the same individual as is non-fluorescent pigments, excluding food dependent biases. Under these circumstances an existence of fluorescence in avian plumage without any implication would not appear to be the most lucid explanation.

Artificial fluorescent plumage in museum bird skins

Museum bird skins stained with fluorescing agents do not occur markedly often, though regularly. The Red-lored Parrot skin, presented as an example in this study, was contaminated with Seibokal ES. As the recipe is confidential, neither the specific content nor the fluorescent component of the brownish liquid is obtainable. Data regarding the components of different preparation agents are rarely available due to the manufactures` policy of not revealing their trade secrets. Moreover, the composition of these agents is subject to change in order to improve efficiency.

Information on the components of preservation agents does not necessarily permit conclusions to be drawn on their effect on fluorescence. A slight change in its electronic configuration can alter a compound's ability to fluoresce. Hence, it is so far impossible to predict in advance a molecule's fluorescing properties. Consequently, an a priori assumption about potential fluorescence is virtually impossible to make. 50 % of the fluorescing skins were collected and prepared long before the Seibokal ES agent was invented 25 years ago (one fluorescent skin dates from 1913). Thus, we must assume that Seibokal ES is not the only fluorescing agent which has been used for preservation purposes.

Unfortunately, in many older bird skins it is impossible to find documentary evidence about the applied preservation agent. In most collections, birds had been gathered for at least one hundred years. Collections contain specimens, not only gathered by museum staff, but bought from different sources or seized from private origin.

Furthermore, another source of artificial fluorescence in museum bird skins was detected. Naturally decomposing birds, without any preservation agent involved, still exhibit fluorescence. This could be ascribed to body fats and proteins, e.g., Lipofuscin. Lipofuscin is cumulated in body cells with increasing age, producing so-called aging stains in different organs (Tsuchida 1985, Winterbourne & Weingast-Johnson 1994, Sharifzadeh *et al*. 2006). Lipofuscin has already been reported to complicate fluorescence microscopy due to its accumulation with age in the cytoplasm of cells and because of its broad excitation and emission spectra (Schnell *et al*. 1999).

Therefore, when museum skins are used for reflection spectrophotometric studies it is advisable to use an UV-light, as an essential item in the researcher's toolbox, to undertake a rapid pre-screening of the series of bird skins planned to be examined via spectrophotometry. The fluorescent stains are easily detectable to the human eye when illuminated with ultraviolet light in an otherwise darkened environment.

However, a contaminated skin can still be used to collect morphometric data with regard to plumage color as long as the artificial fluorescent parts are excluded. As many museums use different preservation agents, it will be mandatory to study their possible fluorescence properties and, where feasible, to change to non-fluorescent agents, e.g. one of the agents examined in my study (such as Borax). Today, the emphasis of conserving bird skins in natural history museums lies on appropriate environmental conditions and storage to keep pests at bay. A further change for the worse due to successively applied agents is therefore unlikely. Thus, using preparation agents with care and avoiding spilling body fluids during preparation process, as well as taking their possible influence on plumage color changes into consideration, will help avoid misinterpretation in the future when conducting spectrophotometric or related studies.

## 3.5 Abstract

In my study, to my knowledge, the most diversified analysis has been conducted involving the distribution of fluorescence in avian plumage. Fluorescent plumage occurs notably often in different bird taxa. In my study, 181 bird species in 14 families with fluorescent plumage parts have been confirmed. The ecological reasons cannot be ascribed to particular context, as yet. Evidence for a dependency of both, light environment and biogeographical region was obtained at species level but could not be perpetuated at family level, suggesting an ecological rather than a phylogenetic cause of fluorescence.

For the first time, the crucial significance of preservation agents for the spectral properties of museum bird skins has been demonstrated. Artificial fluorescence in museum bird skins originates from fluorescent compounds in preservation agents as well as the remains of body fats due to unsatisfactory preservation techniques. Although this affects the results of reflection spectrophotometric measurements, skins must be observed under black light illumination before collecting data.

## 3.6 References


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

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

Arnold, K. E., Owens, I. P. & Marshall, N. J. 2002. Fluorescent signaling in parrots. *Science* 295: 92.

Bailey, S. F. 1978. Latitudinal gradients in colors and patterns of passerine birds. *Condor* 80: 372-381.

Bennett, A. T. D. & Cuthill, I. C. 1994. Ultraviolet vision in birds: what is its function? *Vision Res.* 34: 1471-8.

Bennett, A. T. D., Cuthill, I. C., Partridge, J. C. & Lunau, K. 1997. Ultraviolet plumage colors predict mate preferences in starlings. *PNAS* 94: 8618-21.

Bhatta, H., Goldys, E. M. & Learmonth, R. 2005. Rapid identification of microorganisms by intrinsic fluorescence. *Imaging, Manipulation, and Analysis of Biomolecules and Cells* 5699: 9-18.

Biron, K. 2003. Fireflies, dead fish and a glowing bunny: a primer on bioluminescence. *BioTeach Journal* 1: 19-26.

Boles, W. E. 1990. Glowing Parrots - Need for a study of hidden colours. *Birds Int.* 3: 76-79.

Boles, W. E. 1991. Black-light signature for the birds? *Aust. Nat. Hist.* 23: 752.

Burkhardt, D. 1989. UV vision: a bird's eye view of feathers. *J. Comp. Physiol. A:* 164: 787-796.

Chiao, C. C., Cronin, T. W. & Osorio, D. 2000. Color signals in natural scenes: characteristics of reflectance spectra and effects of natural illuminants. *J. Opt. Soc. Am. A* 17: 218-24.

Christy, J. H. 1995. Mimicry, mate choice, and the sensory trap hypothesis. *Am. nat.* 146: 171-181.

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

Church, S. C., Merrison, A. S. & Chamberlain, T. M. 2001. Avian ultraviolet vision and frequency-dependent seed preferences. *J. Exp. Biol.* 204: 2491-8.

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

Driesen, H. H. 1953. Untersuchungen über die Einwanderung diffuser Pigmente in die Federanlage, insbesondere beim Wellensittich (*Melopsittacus undulatus*). *Cell Tissue Res.* 39: 121-151.

Eaton, M. D. & Lanyon, S. M. 2003. The ubiquity of avian ultraviolet plumage reflectance. *Proc. R. Soc. Lond. B* 270: 1721-1726.

Eldred, G. E., Miller, G. V., Stark, W. S. & Feeney-Burns, L. 1982. Lipofuscin: resolution of discrepant fluorescence data. *Science* 216: 757-9.

Endler, J. A. 1978. A Predator's view of animal colour patterns. *Evol. Biol.* 11: 319-364.

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

Endler, J. A. 1993. The color of light in forests and its implications. *Ecol. Monogr.* 63: 1-27.

Endler, J. A. 1995. Ultraviolet light environments in forests and shrubs, and some implications for UV-containing color patterns. *J. Am. Soc. Zool.* 145: 238.

Endler, J. A. & Thery, M. 1996. Interacting effects of lek placement, display behavior, ambient light, and color patterns in three neotropical forest-dwelling birds. *Am. nat.* 148: 421-452.

Endler, J. A. & Mielke, P. W. 2005. Comparing entire colour patterns as birds see them. *Biol. J. Linn. Soc.* 86: 405-431.

Fitze, P. S., Tschirren, B. & Richner, H. 2003. Carotenoid-based colour expression is determined early in nestling life. *Oecologia* 137: 148-152.

Fitzpatrick, S. 1998. Colour schemes for birds: structural coloration and signals of quality in feathers. *Annales Zoologici Fennici* 35: 67-77.

Frost, L., Butler, D. R., O'Dell, B. & Fet, V. 2001. A coumarin as a fluorescent compound in scorpions. In: Pp. 365-368 Fet, V. & Selden, P. A. (eds) Scorpions. In Memoriam Gary A. Polis. Burnham Beeches.

Goldberg, L. 1996. A history of pest control measures in the anthropology collections, national museum of natural history, Smithsonian Institution. *J. m. Inst. Conserv.* 35: 23-43.

Gomez, D. & Théry, M. 2004. Influence of ambient light on the evolution of colour signals: comparative analysis of a neotropical rainforest bird community. *Ecol. Lett.* 7: 279-284.

Hamilton, W. D. & Zuk, M. 1982. Heritable true fitness and bright birds: A role for parasites? *Science* 218: 384-387.

Håstad, O., Victorsson, J. & Odeen, A. 2005. Differences in color vision make passerines less conspicuous in the eyes of their predators. *PNAS* 102: 6391-6394.

Hausmann, F., Arnold, K. E., Marshall, N. J. & Owens, I. P. F. 2003. Ultraviolet signals in birds are special. *Proc. R. Soc. Lond. B* 270: 61-67.

Hawks, C. A. & Williams, S. L. 1986. Arsenic in natural history collections. *Leather Conserv. News* 2: 1-4.

Hawks, C. A. & Von Endt, D. W. 1990. Mercury and mercury compounds in natural history collections: an annotated bibliography. *Nat. Hist. Conserv.* 5: 4-19.

Heindl, M. 2002. Umweltlicht und die Signalfunktion von Vogelgefiederfarben. *J. Ornithol.*143: 510-511.

Heindl, M. & Winkler, H. 2003. Vertical lek placement of forest-dwelling manakin species (Aves, Pipridae) is associated with vertical gradients of ambient light. *Biol. J. Linn. Soc.* 80: 647-658.

Henderson, S. T. & Hodgekiss, D. 1963. The spectral energy distribution of daylight. *Brit. J. Appl. Phys.* 14: 125-131.

Henderson, S. T. 1970. Daylight and its spectrum. London.

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

Huth, H. H. & Burkhardt, D. 1972. Der spektrale Sehbereich eines Violettohr-Kolibris. *Naturwissenschaften* 59: 650.

Kummer, A. 2003. Fluorescence kinetics of the green fluorescent protein (GFP). Ph.-D. Thesis, TU München, pp. 1-53.

Lowe, G., Kutcher, S. R. & Edwards, D. 2003. A powerful new light source for ultraviolet detection of scorpions in the field. *Euscorpius* 8: 1-7.

Maddocks, S. A., Bennett, A. T. D., Hunt, S. & Cuthill, I. C. 2002. Context-dependent visual preferences in starlings and blue tits: mate choice and light environment. *Anim. Behav.* 63: 69-75.

Maddocks, S. A., Bennett, A. T. D. & Cuthill, I. C. 2002. Rapid behavioural adjustments to unfavourable light conditions in European Starlings (*Sturnus vulgaris*). *Animal Welfare* 11: 95-101.

Maier, E. J. 1992. Spectral sensitivities including the ultraviolet of the passeriform bird *Leiothrix lutea*. *J. Comp. Physiol.* 170: 709-714.

Maier, E. J. 1993. To deal with the "Invisible". *Naturwissenschaften* 80: 476-478.

Maier, E. J. 1994. Ultraviolet vision in a passeriform bird: from receptor spectral sensitivity to overall spectral sensitivity in *Leiothrix lutea*. *Vision Res.* 34: 1415-8.

Marchetti, K. 1993. Dark habitats and bright birds illustrate the role of the environment in species divergence. *Nature* 362: 149-152.

Massaro, M., Davis, L. & Darby, J. 2003. Carotenoid-derived ornaments reflect parental quality in male and female Yellow-eyed Penguins (*Megadyptes antipodes*). *Behav. Ecol. Sociobiol.* 55: 169-175.

Mazel, C. H. & Fuchs, E. 2003. Contribution of fluorescence to the spectral signature and perceived color of corals. *Limnol. Oceanogr.* 48: 390–401.

Mazel, C. H., Cronin, T. W., Caldwell, R. L. & Marshall, N. J. 2004. Fluorescent enhancement of signaling in a Mantis Shrimp. *Science* 303: 51.

McGraw, K. J. 2005. The antioxidant function of many animal pigments: are there consistent health benefits of sexually selected colourants? *Anim. Behav.* 69: 757-764.

McGraw, K. J. 2006. Mechanics of Uncommon Colors: Pterins, Porphyrins, and Psittacofulvins. In Hill, G. E. & McGraw, K. J. (Eds) Bird Coloration (pp. 354-399). Cambridge, Massachusetts: Harvard University Press.

McGraw, K. J. & Ardia, D. R. 2003. Carotenoids, immunocompetence, and the information content of sexual colors: an experimental test. *Am. Nat.* 162: 704-12.

McGraw, K. J., Wakamatsu, K., Ito, S., Nolan, P. M., Jouventin, P., Dobson, S., Austic, R. E., Safran, R. J., Siefferman, L. M., Hill, G. H. & Parker, A. R. 2004. You can't judge a pigment by its color: Carotenoid and melanin content of yellow and brown feathers in Swallows, Bluebirds, Penguins, and domestic chickens. *Condor* 106: 390–395.

McNaught, M. K. & Owens, I. P. F. 2002. Interspecific variation in plumage colour among birds: species recognition or light environment? *Evol. Biol.* 15: 505-514.

Merilaita, S. & Lind, J. 2005. Background-matching and disruptive coloration, and the evolution of cryptic coloration. *Proc. R. Soc. Lond. B* 272: 665-670.

Navara, K. J. & Hill, G. E. 2003. Dietary carotenoid pigments and immune function in a songbird with extensive carotenoid-based plumage coloration. *Behav. Ecol.* 14: 909-916.

Nemésio, A. 2001. Colour production and evolution in parrots. *Int. J. Ornithol*. 4: 75-102

Nemésio, A. 2003. Is fluorescence in Budgerigars really functional? *Science* 296: 655b.

Nemésio, A. 2005. Fluorescent colors in orchid bees (Hymenoptera: Apidae). *Neotrop. Entomol.* 34: 933-936.

Newton, I. 2003. Speciation and biogeography of birds. London.

Parker, A. R. 2002. Fluorescence of yellow Budgerigars. *Science* 296: 655.

Parker, A. R. 2005. Seven Deadly colours - the genius of nature's palette and how it eluded Darwin. London.

Pearn, S. M., Bennett, A. T. D. & Cuthill, I. C. 2001. Ultraviolet vision, fluorescence and mate choice in a parrot, the Budgerigar *Melopsittacus undulatus*. *Proc. Biol. Soc.* 268: 2273-2279.

Pearn, S. M., Bennett, A. T. D. & Cuthill, I. C. 2003. The role of ultraviolet-A reflectance and ultraviolet-A induced fluorescence in the appearance of Budgerigar plumage: insights from spectrofluorometry and reflectance spectrophotometry. *Proc. R. Soc. Lond. B* 270: 859-865.

Porta, E. A. 2002. Pigments in Aging: An Overview. *Ann. N.Y. Acad. Sci.* 959: 57-65.

Römpp, H. 1996. Römpp Chemie Lexikon. Stuttgart.

Salih, A., Larkum, A., Cox, G., Kuhl, M. & Hoegh-Guldberg, O. 2000. Fluorescent pigments in corals are photoprotective. *Nature* 408: 850-3.

Schmidt, W. J. 1961. Histologische Untersuchungen an Papageienfedern mit gelbem eigenfluoreszierenden Pigment. *Cell Tissue Res.* 55: 469-485.

Schmidt, W. J. & Ruska, H. 1965. Koproporphyrinführende Brustfedern der Trappe *Eupodotis senegalensis* Im Licht-, Fluorescenz- und Elektronenmikroskop. *Cell Tissue Res.* 66: 427-433.

Schnell, S. A., Staines, W. A. & Wessendorf, M. W. 1999. Reduction of lipofuscin-like autofluorescence in fluorescently labeled tissue. *J. Histochem. Cytochem.* 47: 719-30.

Schönwetter, M. 1932. Vogeleier im filtrierten ultravioletten Licht. *J. Ornithol.* 80: 521-529.

Schulze-Hagen, K., Steinheimer, F., Kinzelbach, R. & Gasser, C. 2003. Avian taxidermy in Europe from the Middle Ages to the Renaissance. *J. Ornithol.*144: 459-478.

Sherwin, C. M. & Devereux, C. L. 1999. Preliminary investigations of ultraviolet-induced markings on domestic turkey chicks and a possible role in injurious pecking. *Br. Poult. Sci.* 40: 429-33.

Sibley, C. G. & Monroe, B. L. 1990. Distribution and taxonomy of birds of the world. New Haven & London.

Sirois, P. J. 2001. The analysis of museum objects for the presence of arsenic and mercury: non-destructive analysis and sample analysis. *Collection Forum* 16: 65-75.

Slagsvold, T. & Lifjeld, J. T. 1985. Variation in plumage colour of the Great Tit *Parus major* in relation to habitat, season and food. *J. Zool. Lond. A* 206: 321-328.

Stachel, S. J., Stockwell, S. A. & Van Vranken, D. L. 1999. The fluorescence of scorpions and cataractogenesis. *Chem. Biol.* 6: 531-9.

Stahnke, H. L. 1972. UV light, a useful field tool. *BioScience* 22: 604-607.

Stein, A. C. & Uy, J. A. C. 2006. Plumage brightness predicts male mating success in the lekking Golden-Collared Manakin, *Manacus vitellinus*. *Behav. Ecol.* 17: 41-47.

Théry, M. 2001. Forest light and its influence on habitat selection. *Plant Ecology* 153: 251-261.

Tsuchida, M., Miura, T., Mizutani, K. & Aibara, K. 1985. Fluorescent substances in mouse and human sera as a parameter of in vivo lipid peroxidation. *Biochim. Biophys. Acta* 834: 196-204.

Uy, J. A. C. & Endler, J. A. 2004. Modification of the visual background increases the conspicuousness of Golden-Collared Manakin displays. *Behav. Ecol.* 15: 1003-1010.

Völker, O. 1936. Über den gelben Federfarbstoff des Wellensittichs (*Melopsittacus undulatus* (Shaw)). *J. Ornithol.* 84: 618-630.

Völker, O. 1937. Über fluoreszierende, gelbe Federpigmente bei Papageien, eine neue Klasse von Federfarbstoffen. *J. Ornithol.* 85: 136-146.

Völker, O. 1947. Über die Struktur der bei Vögeln vorkommenden Porphyrine. *Zeitschrift für Naturforschung* 2b: 316-317.

Völker, O. 1955. Die Pigmentfarben der Vögel. *Naturwissenschaftliche Rundschau* 7: 265-269.

Völker, O. 1964. Federn die am Licht ausbleichen. *Natur und Museum* 94: 10-14.

Völker, O. 1965. Stoffliche Grundlagen der Gefiederfarben der Vögel. *Mitteilungen der Naturforschenden Gesellschaft in Bern* 22: 201-223.

Vukusic, P. & Hooper, I. 2005. Directionally controlled fluorescence emission in butterflies. *Science* 310: 1151.

Wankhede, R. A. 2004. Extraction, isolation, identification and distribution of soluble fluorescent compounds from the cuticle of Scorpion (*Hadrurus arizonensis*). Thesis Marshall University.

Winterbourne, D. J. & Weingast-Johnson, J. 1994. Purines induce lipofuscin formation in a colon carcinoma cell line. *Biochem. J.* 301 ( Pt 2): 373-7.

## Synopsis

The use of reflection spectrophotometry is the most conservative way of obtaining morphometrical data from museum bird skins. Specimens are prevented from damages, as there is no need to extract tissue for DNA-analysis or twist the specimen in order to measure size etc.

Plumage coloration of museum bird skins provides significant morphometrical data, although it is difficult to objectively access the latter. Among the different methods of analyzing coloration, reflection-spectrophotometry is the most effective means to collect such data, coping with the feather's property of often reflecting ultraviolet light. Using coincident illumination and reading fibers of a conventional reflection-spectrophotometer, I advise positioning the latter at a perpendicular angle to the surface as measuring geometry dramatically affects the quality of obtained data. This measuring geometry on average provides both, the brightest reflections and the least variability in the resulting data.

Plumage coloration of museum bird skins has been evaluated with regard to the reliability of the spectral information. Under appropriate storage conditions, the structural iridescent coloration of hummingbirds can be maintained unaltered for more than a hundred years. In contrast, some specimens are subject to variability in their coloration. Whenever dealing with spectral data, a potential a priory variation in plumage coloration has to be taken into account. Variation can be the result of seasonal changes, sexual dichromatism, maturity or intraspecific polymorphism. Furthermore, dietary dependency of coloration as well as possible diseases or mould should be considered when dealing with spectral information.

Museum specimens exposed to light, dust or insect pests are in danger of alteration to their spectral properties and hence, become unsuitable for spectral analysis, either in the first place or due to acquired color changes. Most disadvantageous are the frequently occurring alterations in the ultraviolet as these remain undetectable to the human eye. However, even in the visible spectrum alterations might elude the observer and, in particular, small reflectance peaks could easily be ignored. Furthermore, at low levels of overall brightness and chroma in both, natural dull

feathers or bleached specimens, slight variations in the reflectance spectrum might be entirely annihilated.

It is essential to consider this disadvantageous variability in spectral data when analyzing avian coloration, as this variability does not represent actual differences within a population. If only overall brightness is reduced, a sample might still be suitable for taxonomic research as it might contain valuable information concerning hue. As the entire spectral property of a feather may be involved in avian signaling, only unaltered feathers are suitable for analysis, if behavioral or ecological topics are involved.

In my study, to my knowledge, the most diversified analysis has been conducted involving the distribution of fluorescence in avian plumage. 181 bird species in 14 families with fluorescent plumage parts have been confirmed and hence, avian fluorescence is far more widespread than it was previously assumed. The ecological reasons cannot yet be ascribed to particular context. Evidence for a dependency of both, light environment and biogeographical region was obtained at species level but could not be perpetuated at family level, suggesting an ecological cause of fluorescence rather than plesiomorphy. Despite an increasing number of studies dealing with fluorescent plumage it is still an underestimated phenomenon of avian coloration, thus the interpretation of potential implications is still to be finally settled.

For the first time, the crucial significance of preservation agents for the spectral properties of museum bird skins has been clearly demonstrated. Artificial fluorescence in museum bird skins originated in fluorescent compounds in preservation agents as well as from the remains of body fats due to unsatisfactory preservation techniques. As this affects the results of reflection spectrophotometric measurements, skins must be observed under black light illumination before collecting data.

Key words: Reflection spectrophotometry, museum bird skins, plumage coloration, feather colors, UV-reflections, fluorescence, preservation agents, color changes.

## Complete List of References


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

Amundsen, T., Forsgren, E. & Hansen, L. T. T. 1997. On the function of female ornaments: male bluethroats prefer colourful females. *Proc. R. Soc. Lond. B* 264: 1579-1586.

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

Andersson, S. & Prager, M. 2006. Quantifying Colors. In Hill, G. E. & McGraw, K. J. (Eds) Bird Coloration (pp. 41-89). Cambridge, Massachusetts: Harvard University Press.

Arnold, K. E., Owens, I. P. & Marshall, N. J. 2002. Fluorescent signaling in parrots. *Science* 295: 92.

Auber, L. 1956. The distribution of structural colours and unusual pigments in the class Aves. *Ibis* 99: 463-476.

Badyaev, A. V. & Young, R. L. 2004. Complexity and integration in sexual ornamentation: an example with carotenoid and melanin plumage pigmentation. *Evol. Biol.* 17: 1317-27.

Bailey, S. F. 1978. Latitudinal gradients in colors and patterns of passerine birds. *Condor* 80: 372-381.

Bancroft, W. D., Chamot, E. M., Merritt, E. & Mason, C. W. 1923. Blue feathers. *Auk* 40: 275-300.

Bancroft, W. D. 1924. Preliminary experiments on feather pigments. *J. Phys. Chem.* 1:1

Bennett, A. T. D. & Cuthill, I. C. 1994. Ultraviolet vision in birds: what is its function? *Vision Res.* 34: 1471-8.

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

Bennett, A. T. D., Cuthill, I. C., Partridge, J. C. & Lunau, K. 1997. Ultraviolet plumage colors predict mate preferences in starlings. *PNAS* 94: 8618-21.

Berthold, P. 1965. Über nicht durch Pigment bedingte Rostfärbung bei Vögeln. *Naturwissenschaften* 52: 400-401.

Berthold, P. 1967. Über Haftfarben bei Vögeln: Rostfärbung durch Eisenoxid beim Bartgeier (*Gypaetus barbatus*) und bei anderen Arten. *Zool. Jb. Syst.* 93: 507-595.

Berthold, P. 1968. Haftfarben bei Vögeln. *Umschau in Wissenschaft und Technik* 14: 438-439.

Bhatta, H., Goldys, E. M. & Learmonth, R. 2005. Rapid identification of microorganisms by intrinsic fluorescence. *Imaging, Manipulation, and Analysis of Biomolecules and Cells* 5699: 9-18.

Biron, K. 2003. Fireflies, dead fish and a glowing bunny: a primer on bioluminescence. *BioTeach Journal* 1: 19-26.

Bleiweiss, R. 1994. Behavioural and evolutionary implications of ultraviolet reflectance by gorgets of sunangel hummingbirds. *Anim. Behav.* 48: 978–981.

Bleiweiss, R. 2004. Ultraviolet plumage reflectance distinguishes sibling bird species. *PNAS* 101: 16561-4.

Boles, W. E. 1990. Glowing Parrots - Need for a study of hidden colours. *Birds Int.* 3: 76-79.

Boles, W. E. 1991. Black-light signature for the birds? *Aust. Nat. Hist.* 23: 752.

Bonser, R. H. C. 1995. Melanin and the abrasion resistance of feathers. *Condor* 97: 590-591.

Bowmaker, J. K., Heath, L. A., Wilkie, S. E. & Hunt, D. M. 1997. Visual pigments and oil droplets from six classes of photoreceptor in the retinas of birds. *Vision Res.* 37: 2183-94.

Brush, A. H. 1978. Avian pigmentation. New York.

Brush, A. H. 1990. Metabolism of carotenoid pigments in birds. *Faseb J.* 4: 2969-77.

Brush, A. H. & Power, D. 1976. House finch pigmentation: carotenoid metabolism and the effect of diet. *Auk* 93: 725-739.

Burkhardt, D. 1989. UV vision: a bird's eye view of feathers. *J. Comp. Physiol. A:* 164: 787-796.

Burkhardt, D. 1996. Die Ultraviolett-Tüchtigkeit des Vogelauges und einige Konsequenzen. *Naturwissenschaften* 83: 492-497.

Burkhardt, D. & Finger, E. 1991. Black, White and UV: how birds see birds. *Naturwissenschaften* 78: 279-280.

Burtt, E. H. & Ichida, J. M. 2004. Gloger's rule, feather-degrading bacteria, and color variation among song sparrows. *Condor* 106: 681-686.

Burtt, E. H. J. 1986. An anlysis of physical, physiological, and optical aspects of avian coloration with emphasis on wood-warblers. *Ornithol. Monogr.* 38: 1-126.

Butler, M. & Johnson, A. S. 2004. Are melanized feather barbs stronger? *J. Exp. Biol.* 207: 285-293.

Campenhausen, M. V. & Kirschfeld, K. 1998. Spectral sensivity of the accessory optic system of the pigeon. *J. Comp. Physiol. A* 183: 1-6.

Chen, D. M., Collins, J. S. & Goldsmith, T. H. 1984. The ultraviolet receptor of bird retinas. *Science* 225: 337-40.

Chen, D. M. & Goldsmith, T. H. 1986. Four spectral classes of cone in the retinas of birds. *J. Comp. Physiol. A* 159: 473-479.

Chiao, C. C., Cronin, T. W. & Osorio, D. 2000. Color signals in natural scenes: characteristics of reflectance spectra and effects of natural illuminants. *J. Opt. Soc. Am. A* 17: 218-24.

Christy, J. H. 1995. Mimicry, mate choice, and the sensory trap hypothesis. *Am. Nat.* 146: 171-181.

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

Church, S. C., Merrison, A. S. & Chamberlain, T. M. 2001. Avian ultraviolet vision and frequency-dependent seed preferences. *J. Exp. Biol.* 204: 2491-8.

Cotgreave, P. & Clayton, D. H. 1994. Comparative analysis of the time spent grooming by birds in relation to parasite load. *Behaviour* 131: 171-187.

Cuthill, I. C., Bennett, A. T. D., Partridge, J. & Maier, E. J. 1999. Plumage reflectance and the objective assessment of avian sexual dichromatism. *Am. nat.* 153: 183-200.

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

Doucet, S., Shawkey, M., Rathburn, M., Mays Jr, H. & Montgomerie, R. 2004. Concordant evolution of plumage colour, feather microstructure and a melanocortin receptor gene between mainland and island populations of a fairy-wren. *Proc. R. Soc. Lond. B* 271: 1663-1670.

Driesen, H. H. 1953. Untersuchungen über die Einwanderung diffuser Pigmente in die Federanlage, insbesondere beim Wellensittich (*Melopsittacus undulatus*). *Cell Tissue Res.* 39: 121-151.

Durrer, H. 1965. Bau und Bildung der Augfeder des Pfaus ( *Pavo cristatus* L.). *Rev. Suisse de Zool.* 72: 263-409.

Durrer, H. & Villiger, W. 1962. Schillerfarben der Nektarvögel (Nectariniidae). *Rev. Suisse de Zool.* 69: 801-814.

Durrer, H. & Villiger, W. 1966. Schillerfarben der Trogoniden. *J. Ornithol.* 107: 1-26.

Durrer, H. & Villiger, W. 1975. Schillerstruktur des Kongopfaus (*Afropavo congensis* Chapin, 1936) im Elektronenmikroskop. *J. Ornithol.* 116: 94-102.

Dyck, J. 1966. Determination of plumage colours, feather pigments and - structures by means of reflection spectrophotometry. *Dansk Ornith. Foren. Tidsskr.* 49-76.

Dyck, J. 1976. Structural colours. *Proc.16th Int. Ornithol. Congr.* 426-437.

Dyck, J. 1987. Structure and light reflection of green feathers of fruit doves (*Ptilinopus* spp.) and an Imperial Pigeon (*Ducula concinna*). *Biologiske Skrifter* 30: 1-31.

Dyck, J. 1992. Reflectance spectra of plumage area colored by green feather pigments. *Auk* 109: 293-301.

Eaton, M. D. 2005. Human vision fails to distinguish widespread sexual dichromatism among sexually "monochromatic" birds. *PNAS* 102: 10942-10946.

Eaton, M. D. & Lanyon, S. M. 2003. The ubiquity of avian ultraviolet plumage reflectance. *Proc. R. Soc. Lond. B* 270: 1721-1726.

Eldred, G. E., Miller, G. V., Stark, W. S. & Feeney-Burns, L. 1982. Lipofuscin: resolution of discrepant fluorescence data. *Science* 216: 757-9.

Ellegren, H. 1991. DNA typing of museum birds. *Nature* 354: 113.

Endler, J. A. 1978. A predator's view of animal colour patterns. *Evol. Biol.* 11: 319-364.

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

Endler, J. A. 1993. The color of light in forests and its implications. *Ecol. Monogr.* 63: 1-27.

Endler, J. A. 1995. Ultraviolet light environments in forests and shrubs, and some implications for UV-containing color patterns. *J. Am. Soc. Zool.* 145: 238.

Endler, J. A. & Thery, M. 1996. Interacting effects of lek placement, display behavior, ambient light, and color patterns in three neotropical forest-dwelling birds. *Am. nat.* 148: 421-452.

Endler, J. A. & Mielke, P. W. 2005. Comparing entire colour patterns as birds see them. *Biol. J. Linn. Soc.* 86: 405-431.

Finger, E. & Burkhardt, D. 1994. Biological aspects of bird colouration and avian colour vision including ultraviolet range. *Vision Res.* 34: 1509-14.

Fitze, P. S., Tschirren, B. & Richner, H. 2003. Carotenoid-based colour expression is determined early in nestling life. *Oecologia* 137: 148-152.

Fitzpatrick, S. 1998. Colour schemes for birds: structural coloration and signals of quality in feathers. *Annales Zoologici Fennici* 35: 67-77.

Fox, D. L. 1976. Animal biochromes and structural colours. Berkley, Cal.: Univ. of Cal. Pr.

Frank, F. 1939. Die Färbung der Vogelfeder durch Pigment und Struktur. *J. Ornithol.* 87: 426-523.

Frost, L., Butler, D. R., O'Dell, B. & Fet, V. 2001. A coumarin as a fluorescent compound in scorpions. In Fet, V. & Selden, P. A. (Eds) Scorpions 2001 (pp. 365–368). In Memoriam Gary A. Polis. Burnham Beeches.

Galeotti, P., Rubolini, D., Dunn, P. O. & Fasola, M. 2003. Colour polymorphism in birds: causes and functions. *Evol. Biol.* 16: 635-646.

Giersberg, H. & Stadie, R. 1932. Zur Entstehung der gelben und roten Gefiederfarben der Vögel. *Z. f. Vergl. Physiol.* 18: 696-708.

Goldberg, L. 1996. A history of pest control measures in the anthropology collections, national museum of natural history, Smithsonian Institution. *J. Am. Inst. Conserv.* 35: 23-43.

Goldsmith, T. H. 1980. Hummingbirds see near ultraviolet light. *Science* 207: 786-788.

Goldsmith, T. H., Collins, J. S. & Licht, S. 1984. The cone oil droplets of avian retinas. *Vision Res.* 24: 1661-71.

Goldstein, G., Flory, K. R., Browne, B. A., Majid, S., Ichida, J. M. & Burtt, E. H. 2004. Bacterial degradation of black and white feathers. *Auk* 121: 656-659.

Gomez, D. & Voisin, J. F. 2002. Spectrometry validates subspeciation in the Kerguelen Tern *Sterna virgata*. *Marine Ornithology* 30: 19-24.

Gomez, D. & Théry, M. 2004. Influence of ambient light on the evolution of colour signals: comparative analysis of a Neotropical rainforest bird community. *Ecol. Lett.* 7: 279-284.

Govardovskii, V. I. 1983. On the role of oil drops in colour vision. *Vision Res.* 23: 1739-1740.

Greenewalt, C. H., Brandt, W. & Friel, D. D. 1960. Iridescent colors of hummingbird feathers. *J. Opt. Soc. Am.* 50: 1005-1013.

Grill, C. P. & Rush, V. N. 2000. Analysing spectral data: comparison and application of two techniques. *Biol. J. Linn. Soc.* 69: 121-138.

Hamilton, W. D. & Zuk, M. 1982. Heritable true fitness and bright birds: A role for parasites? *Science* 218: 384-387.

Hart, N. S., Partridge, J. C., Cuthill, I. C. & Bennett, A. T. D. 2000. Visual pigments, oil droplets, ocular media and cone photoreceptor distribution in two species of passerine bird: the Blue Tit (*Parus caeruleus* L.) and the Blackbird (*Turdus merula* L.). *J. Comp. Physiol. A* 186: 375-87.

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

Hart, N. S. 2001b. Variations in cone photoreceptor abundance and the visual ecology of birds. *J. Comp. Physiol. A* 187: 685-97.

Håstad, O., Victorsson, J. & Odeen, A. 2005. Differences in color vision make passerines less conspicuous in the eyes of their predators. *PNAS* 102: 6391-6394.

Hausmann, F., Arnold, K. E., Marshall, N. J. & Owens, I. P. F. 2003. Ultraviolet signals in birds are special. *Proc. R. Soc. Lond. B* 270: 61-67.

Hawks, C. A. & Williams, S. L. 1986. Arsenic in natural history collections. *Leather Conserv.News* 2: 1-4.

Hawks, C. A. & Von Endt, D. W. 1990. Mercury and mercury compounds in natural history collections: an annotated bibliography. *Nat. Hist. Conserv.* 5: 4-19.

Heindl, M. 2002. Umweltlicht und die Signalfunktion von Vogelgefiederfarben. *J. Ornithol.*143: 510-511.

Heindl, M. & Winkler, H. 2003. Vertical lek placement of forest-dwelling manakin species (Aves, Pipridae) is associated with vertical gradients of ambient light. *Biol. J. Linn. Soc.* 80: 647-658.

Henderson, S. T. & Hodgekiss, D. 1963. The spectral energy distribution of daylight. *Brit. J. Appl. Phys.* 14: 125-131.

Henderson, S. T. 1970. Daylight and its spectrum. London: Adam Hilger Ltd.

Hill, G. H. 1998. An easy, inexpensive means to quantify plumage coloration. *J. Field Ornithol.* 69: 353-363.

Hofmann, C. M., Cronin, T. W. & Omland, K. E. 2006. Using spectral data to reconstruct evolutionary changes in coloration: carotenoid color evolution in New World orioles. *Evolution* 60: 1680–1691.

Hudon, J. 2005. Considerations in the conservation of feathers and hair, particularly their pigments. *CAC / ACCR 31st Annual Conference*, pp. 127-148.

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

Huth, H. H. & Burkhardt, D. 1972. Der spektrale Sehbereich eines Violettohr-Kolibris. *Naturwissenschaften* 59: 650.

Inouye, C. Y., Hill, G. E., Stradi, R. D. & Montgomerie, C. R. 2001. Carotenoid pigments in male House Finch plumage in relation to age, subspecies, and ornamental coloration. *Auk* 118: 900–915.

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

Jacobs, G. H. 1993. The distribution and nature of colour vision among the mammals. *Biol. Rev. Camb. Philos. Soc.* 68: 413-71.

Jones, C. D. & Osorio, D. 2004. Discrimination of orientated visual textures by poultry chicks. *Vision Res.* 44: 83-89.

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

Kniprath, E. 1967. Die Bestimmung der Helmholtzkoordinaten von Feder- und Haarfarben im ICI. *Bonn. Zool. Beitr.* 3: 297-307.

Krumbiegel, I. 1925. Versuche über das Abfärben des Turacins. *J. Ornithol.* 73: 440-446.

Kummer, A. Fluorescence kinetics of the green fluorescent protein (GFP). 1-53. 2003. TU München. Dissertation

Land, M. F. 1972. The physics and biology of animal reflectors. *Prog. Biophys. Molec. Biol.* 24: 77-106.

Leeton, P., Christidis, L. & Westerman, M. 1993. Feathers from museum bird skins: a good source of DNA for phylogenetic studies. *Condor* 95: 465-466.

Lowe, G., Kutcher, S. R. & Edwards, D. 2003. A Powerful New Light Source for Ultraviolet Detection of Scorpions in the Field. *Euscorpius* 8: 1-7.

Lubnow, E. 1963. Melanine bei Vögeln und Säugetieren. *J. Ornithol.* 104: 69-81.

Lubnow, E. & Niethammer, G. 1964. Zur Methodik von Farbmessungen für taxonomische Untersuchungen. *Verh. d. Dtsch. Ges. München* 646-663.

Maddocks, S. A., Bennett, A. T. D., Hunt, S. & Cuthill, I. C. 2002. Context-dependent visual preferences in starlings and blue tits: mate choice and light environment. *Anim. Behav.* 63: 69-75.

Maddocks, S. A., Bennett, A. T. D. & Cuthill, I. C. 2002. Rapid behavioural adjustments to unfavourable light conditions in European Starlings (*Sturnus vulgaris*). *Animal Welfare* 11: 95-101.

Mahler, B., Araujo, L. S. & Tubaro, P. L. 2003. Dietary and sexual correlates of carotenoid pigment expression in dove plumage. *Condor* 105: 258-267.

Maier, E. J. 1992. Spectral sensitivities including the ultraviolet of the passeriform bird *Leiothrix lutea*. *J. Comp. Physiol. A* 170: 709-714.

Maier, E. J. & Bowmaker, J. K. 1993. Colour vision in the passerine bird, *Leiothrix lutea*: Correlation of visual pigment absorbency and oil droplet transmission with spectral sensivity. *J. Comp. Physiol. A* 172: 295-301.

Maier, E. J. 1993. To deal with the "Invisible". *Naturwissenschaften* 80: 476-478.

Maier, E. J. 1994. Ultraviolet vision in a passeriform bird: from receptor spectral sensitivity to overall spectral sensitivity in *Leiothrix lutea*. *Vision Res.* 34: 1415-8.

Marchetti, K. 1993. Dark habitats and bright birds illustrate the role of the environment in species divergence. *Nature* 362: 149-152.

Massaro, M., Davis, L. & Darby, J. 2003. Carotenoid-derived ornaments reflect parental quality in male and female Yellow-eyed Penguins (*Megadyptes antipodes*). *Behav. Ecol. Sociobiol.* 55: 169-175.

Mazel, C. H. & Fuchs, E. 2003. Contribution of fluorescence to the spectral signature and perceived color of corals. *Limnol. Oceanogr.* 48: 390–401.

Mazel, C. H., Cronin, T. W., Caldwell, R. L. & Marshall, N. J. 2004. Fluorescent enhancement of signaling in a Mantis Shrimp. *Science* 303: 51.

McGraw, K. J. 2005. The antioxidant function of many animal pigments: are there consistent health benefits of sexually selected colourants? *Anim. Behav.* 69: 757-764.

McGraw, K. J. 2006. Mechanics of carotenoid-based coloration. In Hill, G. E. & McGraw, K. J. (Eds) Bird Coloration (pp. 177-242). Cambridge, Massachusetts: Harvard University Press.

McGraw, K. J. & Ardia, D. R. 2003. Carotenoids, immunocompetence, and the information content of sexual colors: an experimental test. *Am. nat.* 162: 704-12.

McGraw, K. J. & Hill, G. E. 2004. Plumage color as a dynamic trait: carotenoid pigmentation of male house finches (*Carpodacus mexicanus*) fades during the breeding season. *Can. J. Zool.* 82: 734–738.

McGraw, K. J., Mackillop, E. A., Dale, J. & Hauber, M. E. 2002. Different colors reveal different information: how nutritional stress affects the expression of melanin- and structurally based ornamental plumage. *J. Exp. Biol.* 205: 3747-55.

McGraw, K. J. & Nogare, M. C. 2004. Carotenoid pigments and the selectivity of psittacofulvin-based coloration systems in parrots. *Comp. Biochem. Physiol. B* 138: 229-33.

McGraw, K. J. & Nogare, M. C. 2005. Distribution of unique red feather pigments in parrots. *Biol. Lett.* 1: 38-43.

McGraw, K. J., Wakamatsu, K., Ito, S., Nolan, P. M., Jouventin, P., Dobson, S., Austic, R. E., Safran, R. J., Siefferman, L. M., Hill, G. H. & Parker, A. R. 2004. You can't judge a pigment by its color: carotenoid and melanin content of yellow and brown feathers in swallows, bluebirds, penguins, and domestic chickens. *Condor* 106: 390–395.

McNaught, M. K. & Owens, I. P. F. 2002. Interspecific variation in plumage colour among birds: species recognition or light environment? *Evol. Biol.* 15: 505-514.

McNett, G. D. & Marchetti, K. 2005. Ultraviolet degradation in carotenoid patches: live versus museum specimens of wood warblers (Parulidae). *Auk* 122: 793–802.

Merilaita, S. & Lind, J. 2005. Background-matching and disruptive coloration, and the evolution of cryptic coloration. *Proc. R. Soc. Lond. B* 272: 665-670.

Montgomerie, R. 2006. Analyzing colors. In Hill, G. E. & McGraw, K. J. (Eds) Bird Coloration (pp. 90-147). Cambridge, Massachusetts: Harvard University Press.

Navara, K. J. & Hill, G. E. 2003. Dietary carotenoid pigments and immune function in a songbird with extensive carotenoid-based plumage coloration. *Behav. Ecol.* 14: 909-916.

Nemésio, A. 2001. Colour production and evolution in parrots. *Int. J. Ornithol*. 4: 75-102

Nemésio, A. 2003. Is fluorescence in budgerigars really functional? *Science* 296: 655.

Nemésio, A. 2005. Fluorescent colors in orchid bees (Hymenoptera: Apidae). *Neotrop. Entomol.* 34: 933-936.

Newton, I. 2003. Speciation and Biogeography of Birds. London.

Ornborg, J., Andersson, S., Griffith, S. C. & Sheldon, B. C. 2002. Seasonal changes in an ultraviolet structural colour signal in Blue Tits, *Parus caeruleus*. *Biol. J. Linn. Soc.* 76: 237-245.

Osorio, D. & Ham, A. D. 2002. Spectral reflectance and directional properties of structural coloration in bird plumage. *J. Exp. Biol.* 205: 2017-27.

Ödeen, A. & Håstad, O. 2003. Complex distribution of avian color vision systems revealed by sequencing the SWS1 opsin from total DNA. *Mol. Biol. Evol.* 20: 855-61.

Parker, A. R. 1998. Colour in Burgess Shale animals and the effect of light on evolution in the Cambrian. *Proc. R. Soc. Lond. B* 265: 967-972.

Parker, A. R. 2000. 515 million years of structural colour. *J.Opt.A: Pure Appl. Opt.* 2: 1433-1446.

Parker, A. R. 2002. Fluorescence of yellow budgerigars. *Science* 296: 655.

Parker, A. R. 2005. Review. A geological history of reflecting optics. *J. R. Soc. Interface* 2: 1-17.

Parker, A. R. 2005. Seven Deadly colours - the genius of nature's palette and how it eluded Darwin. London.

Pearn, S. M., Bennett, A. T. D. & Cuthill, I. C. 2001. Ultraviolet vision, fluorescence and mate choice in a parrot, the budgerigar *Melopsittacus undulatus*. *Proc. R. Soc. Lond. B* 268: 2273-9.

Pearn, S. M., Bennett, A. T. D. & Cuthill, I. C. 2003. The role of ultraviolet-A reflectance and ultraviolet-A induced fluorescence in the appearance of budgerigar plumage: insights from spectrofluorometry and reflectance spectrophotometry. *Proc. R. Soc. Lond. B* 270: 859-865.

Porta, E. A. 2002. Pigments in Aging: An Overview. *Ann. N.Y. Acad. Sci.* 959: 57-65.

Prum, R. O. 1999. Development and evolutionary origin of feathers. *J. Exp. Biol.* 285: 291-306.

Prum, R. O. 2006. Anatomy, physics, and evolution of structural colors. In Hill, G. E. & McGraw, K. J. (Eds) Bird coloration (pp. 295-353). Cambridge, Massachusetts: Harvard University Press.

Prum, R. O., Torres, R., Kovach, C., Williamson, S. & Goodman, S. 1999. Coherent light scattering by nanostructured collagen arrays in the caruncles of the malagasy asities (Eurylaimidae: aves). *J. Exp. Biol.* 202: 3507-3522.

Prum, R. O., Andersson, M. & Torres, R. 2002. Coherent scattering of ultraviolet light by avian feather barbs. *Auk* 120: 163–170.

Prum, R. O., Torres, R. H., Williamson, S. & Dyck, J. 1998. Coherent light scattering by blue feather barbs. *Nature* 396: 28-29.

Prum, R. O., Torres, R. H., Williamson, S. & Dyck, J. 1999. Two-dimensional Fourier analysis of the spongy medullary keratin of structurally coloured feather barbs. *Proc. R. Soc. Lond. B* 266: 13.

Prum, R. O. & Williamson, S. 2002. Reaction-diffusion models of within-feather pigmentation patterning. *Proc. R. Soc. Lond. B* 269: 781-792.

Raman, C. V. 1935. The origin of colours in the plumage of birds. *Proc. Ind. Nat. Acad. Sci. A* 1: 1-7.

Reneerkens, J. & Korsten, P. 2004. Plumage reflectance is not affected by preen wax composition in Red Knots *Calidris canutus*. *Journal of Avian Biology* 35: 405-409.

Römpp, H. 1996. Römpp Chemie Lexikon. Stuttgart: Thieme.
Rutschke, E. 1964. Grundsätzliches über abweichend gefärbte Vögel. *Der Falke* 6: 195-199.

Salih, A., Larkum, A., Cox, G., Kuhl, M. & Hoegh-Guldberg, O. 2000. Fluorescent pigments in corals are photoprotective. *Nature* 408: 850-3.

Schmidt, W. J. 1961. Histologische Untersuchungen an Papageienfedern mit gelbem eigenfluoreszierenden Pigment. *Cell Tissue Res.* 55: 469-485.

Schmidt, W. J. & Ruska, H. 1965. Koproporphyrinführende Brustfedern der Trappe *Eupodotis senegalensis* Im Licht-, Fluorescenz- und Elektronenmikroskop. *Cell Tissue Res.* 66: 427-433.

Schmitz-Ornés, A. 2006. Using colour spectral data in studies of geographic variation and taxonomy of birds: examples with two hummingbird genera, *Anthracothorax* and *Eulampis*. *J. Ornithol.*

Schnell, S. A., Staines, W. A. & Wessendorf, M. W. 1999. Reduction of lipofuscin-like autofluorescence in fluorescently labeled tissue. *J. Histochem. Cytochem.* 47: 719-30.

Schönwetter, M. 1932. Vogeleier im filtrierten ultravioletten Licht. *J. Ornithol.* 80: 521-529.

Schulze-Hagen, K., Steinheimer, F., Kinzelbach, R. & Gasser, C. 2003. Avian taxidermy in Europe from the Middle Ages to the Renaissance. *J. Ornithol.*144: 459-478.

Selander, R. K., Johnston, R. F. & Hamilton, T. H. 1964. Colorimetric methods in ornithology. *Condor* 66: 491-495.

Shawkey, M. D., Estes, A. M., Siefferman, L. M. & Hill, G. E. 2003. Nanostructure predicts intraspecific variation in ultraviolet-blue plumage colour. *Proc. R. Soc. Lond. B* 270: 1455-1460.

Shawkey, M. & Hill, G. E. 2005. Carotenoids need structural colours to shine. *Biol. Lett.* 1: 121-124.

Sherwin, C. M. & Devereux, C. L. 1999. Preliminary investigations of ultraviolet-induced markings on domestic turkey chicks and a possible role in injurious pecking. *Br. Poult. Sci.* 40: 429-33.

Shi, Y. & Yokoyama, S. 2003. Molecular analysis of the evolutionary significance of ultraviolet vision in vertebrates. *PNAS* 100: 8308-8313.

Sibley, C. G. & Monroe, B. L. 1990. Distribution and taxonomy of birds of the world. New Haven & London: Yale University Press.

Sirois, P. J. 2001. The analysis of museum objects for the presence of arsenic and mercury: non-destructive analysis and sample analysis. *Collection Forum* 16: 65-75.

Slagsvold, T. & Lifjeld, J. T. 1985. Variation in plumage colour of the Great Tit *Parus major* in relation to habitat, season and food. *J. Zool. Lond. A* 206: 321-328.

Smithe, F. B. 1975. Naturalist's color guide. New York.

Stachel, S. J., Stockwell, S. A. & Van Vranken, D. L. 1999. The fluorescence of scorpions and cataractogenesis. *Chem. Biol.* 6: 531-9.

Stahnke, H. L. 1972. UV light, a useful field tool. *BioScience* 22: 604-607.

Stein, A. C. & Uy, J. A. C. 2006. Plumage brightness predicts male mating success in the lekking Golden-Collared Manakin, *Manacus vitellinus*. *Behav. Ecol.* 17: 41-47.

Théry, M. 2001. Forest light and its influence on habitat selection. *Plant Ecology* 153: 251-261.

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

Tsuchida, M., Miura, T., Mizutani, K. & Aibara, K. 1985. Fluorescent substances in mouse and human sera as a parameter of in vivo lipid peroxidation. *Biochim. Biophys. Acta* 834: 196-204.

Uy, J. A. C. & Endler, J. A. 2004. Modification of the visual background increases the conspicuousness of Golden-Collared Manakin displays. *Behav. Ecol.* 15: 1003-1010.

Villafuerte, R. & Negro, J. J. 1998. Digital imaging for colour measurement in ecological research. *Ecol. Lett.* 1: 151-154.

Vorobyev, M. & Osorio, D. 1998. Receptor noise as a determinant of colour thresholds. *Proc. R. Soc. Lond. B* 265: 351-358.

Vorobyev, M. 2003. Coloured oil droplets enhance colour discrimination. *Proc. R. Soc. Lond. B* 270: 1255-1261.

Völker, O. 1936. Über den gelben Federfarbstoff des Wellensittichs (*Melopsittacus undulatus* (Shaw)). *J. Ornithol.* 84: 618-630.

Völker, O. 1937. Über fluoreszierende, gelbe Federpigmente bei Papageien, eine neue Klasse von Federfarbstoffen. *J. Ornithol.* 85: 136-146.

Völker, O. 1947. Über die Struktur der bei Vögeln vorkommenden Porphyrine. *Zeitschrift für Naturforschung* 2b: 316-317.

Völker, O. 1955. Die Pigmentfarben der Vögel. *Naturwissenschaftliche Rundschau* 7: 265-269.

Völker, O. 1961. Die chemische Charakterisierung roter Lipochrome im Gefieder der Vögel. *J. Ornithol.* 102: 430-438.

Völker, O. 1961. Bemerkungen über ein grünes, nicht carotinoides Pigment im Kleingefieder von *Rollulus roulroul* (Galli). *J. Ornithol.* 102: 270-272.

Völker, O. 1962. Experimentelle Untersuchungen zur Frage der Entstehung roter Lipochrome in Vogelfedern. *J. Ornithol.* 103: 276-286.

Völker, O. 1963. Gefiederfarben der Vögel und Carotinoide. *J. Ornithol.* 104: 288-289.

Völker, O. 1964. Federn die am Licht ausbleichen. *Natur und Museum* 94: 10-14.

Völker, O. 1965. Stoffliche Grundlagen der Gefiederfarben der Vögel. *Mitteilungen der Naturforschenden Gesellschaft in Bern* 22: 201-223.

Vukusic, P. & Hooper, I. 2005. Directionally controlled fluorescence emission in butterflies. *Science* 310: 1151.

Wankhede, R. A. 2004. Extraction, isolation, identification and distribution of soluble fluorescent compounds from the cuticle of Scorpion (*Hadrurus arizonensis*). Thesis Marshall University.

Weber, H. 1961. Über die Ursache des Verlustes der roten Federfarbe bei gekäfigten Birkenzeisigen. *J. Ornithol.* 102: 158-163.

Winterbourne, D. J. & Weingast-Johnson, J. 1994. Purines induce lipofuscin formation in a colon carcinoma cell line. *Biochem. J.* 301 ( Pt 2): 373-7.

With, T. K. 1967. Freie Porphyrine in Federn. *J. Ornithol.* 108: 480-483.

Wright, A. A. 1972. The influence of ultraviolet radiation on the pigeon's color discrimination. *J. Exp. Anal. Behav.* 17: 325-337.

Zuk, M., Johnson, K., Thornhill, R. & Ligon, J. D. 1990. Parasites and male ornaments in free-ranging and captive Red Jungle Fowl. *Behaviour* 114: 232-248.

Zuk, M. & Decruyenaere, J. G. 1994. Measuring individual variation in colour: a comparison of two techniques. *Biol. J. Linn. Soc.* 53: 165-173.

## Image bibliography

All photographs were taken by Georg Pohland and Peter Mullen / SUNBIRD IMAGES.

## Appendix

Spectral data acquisition of avian plumage (see enclosed CD)

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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 auszugsweise bei Fachzeitschriften eingereicht und akzeptiert. Ich lehne eine Zulassung von Zuhörern bei der Disputation ab.

# Curriculum vitae

## 1. Personal data

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| Name | Georg Pohland |
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## 2. Educational background

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| 1992 – 1994 | RWE Energie AG (apprenticeship) |
| 1995 – 2001 | Study of biology (Zoology, Botany) at the Heinrich-Heine-University, Düsseldorf |
| 2001 – 2002 | Degree thesis: Untersuchung zur Bedeutung und Wahrnehmung räumlicher Objekte bei Hühnervögeln |
| 2002 | Master of Science degree in biology from the Heinrich-Heine-Universität Düsseldorf, department of neurobiology, Research Group Sensory Ecology, supervisor Prof. Dr. K. Lunau |
| 2003 – 2006 | Rheinische Friedrich-Wilhelms-Universität Bonn, Germany, A. Koenig Zoological Research Museum, Ornithology research group: Biology and Phylogeny of Tropical Birds, supervisor Prof. Dr. K.-L. Schuchmann |

## 3. Language skills

4. Employments

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| 1998 – 2003 | Regular assistantships of courses at the Heinrich-Heine-Universität Düsseldorf, Department of Zoology: Basic experiments in neurobiology and sensory physiology |
| 2001 | Oral presentation at the Aquazoo Düsseldorf. Topic: Poisonous Arthropods of the World |
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| 2005 | Visiting lecturer at the University of UNELLEZ, San Carlos, Venezuela. Course topic: Scientific Photography |
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| | Course at A. Koenig Zoological Research Museum for international exchange students of the “Institut für Interkulturelle Kommunikation” (IIK). Course topic: Application of Scientific Photography |
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| 2006 | Course assistance at the Rheinische Friedrich-Wilhelms-Universität Bonn: Course topic: Wissenschaftliche Fotografie und Bildbearbeitung |
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## 6. Publications

### Journal articles

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2005 Pohland, G. & Mullen, P. 2005. Farben aus der Vogel-perspektive, UV-Sehen und UV-Reflexionen bei Vögeln. *BIUZ* 35: 125-133.

2006 Pohland, G. & Mullen, P. 2006. Preservation agents influence UV-colouration of plumage in museum bird skins, *J. Ornithol*. 147: 464-467.

Mullen, P. & Pohland, G. 2006. UV-vision in Courtship Behavior of the Satin Bowerbird. (submitted)

Mullen, P. & Pohland, G. 2006. Studies on UV reflection in feathers of some 1000 bird species – are UV-peaks in feathers correlated with VS/UVS cones? *Ibis* (in press).

Mullen, P. & Pohland, G. 2006. Liebeslauben im Regenwald: Unterwegs zu den Laubenvögeln Australiens. Newsletter of the Brehm Fund for International Bird Conservation 24: 6-9.

Mullen, P. & Pohland, G. 2006. Die wirklichen Farben der Papageien. Papageien 7: 280-286.

Mullen, P. & Pohland, G. 2006. Botschaft in Ultraviolett. Bild der Wissenschaft 7:45-50.

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