Determination of Plumage Colours, Feather Pigments and -Structures by Means of Reflection Spectrophotometry

By

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(Med et dansk resumé: Objektiv farvebestemmelse og undersøgelser af fjerpigmenter og -strukturer ved hjælp af refleksionsspektroskopi.)

CONTENTS

INTRODUCTION

The present paper deals with an objective method for measuring the colours of birds.

The theoretical background for the method is shortly described, a review of earlier papers dealing with the subject is given and the experimental work is described. The measured reflection curves and colours are discussed in relation to the pigments and structures of the feathers.

At the Danish Defence Research Board a great number of objective colour-measurements on biological, mainly botanical, objects (e.g. leaves, grass), but also including many animal species, has been carried out since 1952. In 1963 measurements on birds were included in this programme and some of the results of these measurements are those which are discussed in the present paper.

THE THEORY FOR OBJECTIVE MEASUREMENT OF COLOUR

The differences in colours of objects are due to the fact that the objects in different degrees reflect the radiation (light) of various wave-lengths in the visible spectrum (380–770 nm = mμ).

A green object reflects much radiation at wave-lengths corresponding to green light (500–530 nm) but less radiation at wave-lengths corresponding to blue (440–480 nm) or red light (630–770 nm). Conversely a red object reflects only a little radiation with wave-lengths corresponding to blue or green light, but of course much radiation at wave-lengths corresponding to red light. An ideal white object would reflect 100% radiation of all wave-lengths in the visible spectrum.

The best approximation of an ideal white object is generally recognized to be a plate with a coating of magnesiumoxide. When freshly prepared it reflects some 98–99% of the incident light in the visible region. In the near-infrared region (to about 2000 nm) it reflects more than 95% (KORTÜM ET AL. 1963).

With a photo-electrical detector the amount of radiation reflected from the object is compared with the radiation reflected from the white standard at various wave-lengths. The reflection (generally expressed as a percentage) as a function of wave-length is represented by the reflection curve, which serves as a measure of the colour.

Fig. 1 shows the reflection curves of blue, green and red feathers.

It is of course not very convenient to use a curve as a measure of colour. CIE (COMMISSION INTERNATIONALE DE L'ECLAIRAGE) has given methods whereby the curves can be transformed into tristimulus coordinates, which numerically design the colour as viewed by a standard observer.

It is a well known fact that every colour can be matched by an additive mixing of three spectral colours, for instance a red, a blue and a green. This means, that a colour can be characterized as containing for instance 0,2 parts red, 0,4 parts green and 0,4 parts blue. However, standardiza-

tion of the light source is also necessary, as the colour of an object depends on the light-source illuminating it (e.g. artificial light or daylight).

In the CIE-system 3 primary spectrum colours, a green, a red and a blue have been laid down and hence a colour can be characterized by the amount X of the red primary, the amount Y of the green primary and the amount Z of the blue primary, which by beeing blended match the given colour under the same illumination conditions.

The green primary has been chosen so as to correspond to the relative luminosity function for daylight vision and hence carries all the luminosity, while the two other primaries are unassociated with luminosity.

It is convenient to substitute for the tristimulus values X, Y, Z the two ratios $x = \frac{X}{X+Y+Z}$ and $y = \frac{Y}{X+Y+Z}$ combined with the luminous reflectance Y. The two ratios x and y are known as chromaticity coordinates. The third chromaticity coordinate $z \left(= \frac{Z}{X+Y+Z} \right)$ is unnecessary as arithmetically the sum of x, y and z is unity.

To calculate X, Y and Z it is necessary to multiply the measured reflectances (R_λ) by constants corresponding to the wavelengths, add up etc. The constants given by the primaries have been laid down by CIE. Even if these calculations are simple, as they include only multiplication and addition, they are rather time-absorbing to carry out and a calculating machine is necessary.

The necessary constants and illustrative calculations can be found in "Handbook of Colorimetry" (HARDY 1937). A more exhaustive description than the one given here, has been given by a variety of authors, e.g. JUDD (1950), LUBNOW & NIETHAMMER (1964) and WRIGHT (1964).

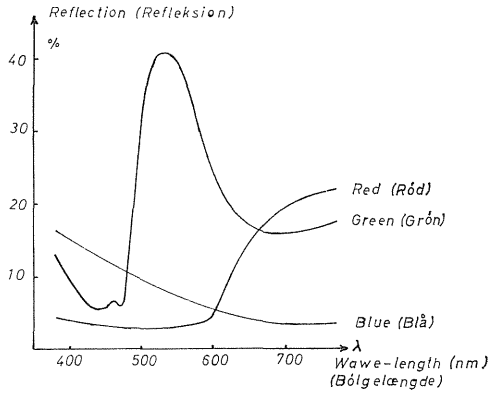

Fig. 1. Reflection curves of differently coloured plumage areas. Blue: *Garrulus glandarius* (Wing-coverts). Green: *Melopsittacus undulatus* (Belly) Red (ruby): *Ptilinopus viridis* (Throat).

Refleksionskurver af forskelligt farvede fjerpartier. Blå: Garrulus glandarius *(Vingedækfjer). Grøn:* Melopsittacus undulatus *(Bug). Rød (blårød):* Ptilinopus viridis *(Hals).*

If one is not very accustomed to work with the CIE-system, the calculated values x, y and Y for a given colour will not give one much idea as to what the colour looks like. It is therefore customary to transform x, y and Y to the more illustrative terms: Dominant wave-length (hue, λ_d), purity (saturation, σ) and luminous reflection (lightness, luminosity, Y).

If a colour can be matched by adding some part of the spectrum to white light, the wave-length of the added light corresponds to the dominant wave-length of the colour. Thus for instance yellow colours are those with dominant wavelengths (λ_d) somewhere between 580 and 620 nm. The lightness (Y) which may vary between 0 and 100%, and as the name indicates, is lower the darker the colour, is given directly by the amount of the green primary (as mentioned above).

The saturation (σ) may vary between 0 and 100% (spectral lights showing purities of 100%) and determines the degree of its difference from the grey colour of the same lightness.

As an illustration of the terms, hue, saturation and lightness of the feather colours, the reflection curves of which are shown in fig. 1, have been calculated and are given in table 1.

Plumage area *(Fjerparti)*	Hue λ_d (nm)	Saturation σ (%)	Lightness Y (%)
Melopsittacus:			
Belly	561,2	60,40	31,71
Garrulus: Wing-coverts	479,0	32,5	7,38
Ptilinopus:			
Throat	$\div$ 492,6	26,6	3,39

Table 1. Hue, saturation and lightness calculated from the reflection curves shown in fig. 1.

Farve, mætning og lyshed beregnet ud fra refleksionskurverne vist på fig. 1.

It will be seen that the red throat of *Ptilinopus* instead of showing a dominant wave-length somewhere in the red region (630–700 nm), is assigned to a negative dominant wave-length. This is due to the colour not appearing as a pure red, but rather as a ruby colour. Since ruby, violet and purple colours do not exist in the sun spectrum the dominant wave-length of such colours are given as the negative wave-length of the light with which the colour mix to give a neutral grey colour. For the ruby throat of *Ptilinopus* with a dominant wave-length $\lambda_d = \div 492,6$, this means, that the ruby colour must be mixed with a certain amount of blue of $\lambda_d = 492,6$ to give a neutral grey colour.

REVIEW

This method for objective measurements of colours was first used on birds by BOWERS (1956) in his study on the colour-variation in the Wren-tit *(Chamaea fasciata)* (1960). He preferred, however, a visual comparison, which he found more accurate.

GREENEWALT ET AL. (1960) measured the reflection of iridescent hummingbird feathers in their study on the structure of the feathers.

JUHN (1964) has compared the pigments in feathers from the pectoral region of the two sexes of the Brown Leghorn Fowl by measurements of the reflection, but she as well as GREENEWALT ET AL. have measured the reflection of microscopical small feather parts, so their reflection curves do not permit a characterization of the plumage colour as viewed by the unaided human eye.

The reflection curves for the feathers of the Blue-throat *(Luscinia svecia (L.))*, the Robin *(Erithacus rubecula (L.))* and the Yellow Wagtail *(Motacilla fl. flava)* were determined by PEIPONEN (1963) in his experimental investigations on the colour vision and reactions to differently coloured objects in these species.

JOHNSTON & SELANDER (1964) have used the method in analyzing the geographic variation in colour in the House Sparrow *(Passer domesticus)* in North America.

LUBNOW & NIETHAMMER (1964) have given a detailed account on the method and some of its applications, especially with regard to systematics.

Recently BARTH (1964) has given a preliminary account of the mantle colours of Herring Gulls *(Larus argentatus)* and Lesser Blackbacked Gulls *(Larus fuscus)* in British and Scandinavian waters. His colour designations are not given in the CIE-terms (dominant wave-length, purity and lightness) but instead in equivalent Munsell terms (hue, chroma and value).

EXPERIMENTAL

Methods of measuring.

The radiance from a perfectly diffusing surface is the same in all directions. Consequently the measured reflection of such a surface is independent of the position of the photo-electrical detector. Since no actual surfaces are diffusing perfectly, a specular component often being more or less pronounced, the position of light source, object and photo-electrical detector relative to each other plays a major role.

It is customary to place the photo-electrical detector in a direction normal to the surface, the reflection of which is to be measured and the light source so that the angle of incidence becomes 45°. The method is mainly used for smooth, more or less glossy, surfaces, as the specular component is hereby eliminated. The reflection measured under these conditions is designated as $R_{45/0}$.

For surfaces with a more or less rough structure it is generally recommended to use diffuse illumination, the surface being placed over an opening to the inner white-coated surface of a sphere (Ulbricht-sphere). The sphere has further openings for the light source and photo-electrical detector. The incoming radiation is reflected and re-reflected from the inner surface of the sphere so as to reach the object from all directions.

The reflection measured under these conditions is designed $R_{d/0}$.

With the Ulbricht-sphere used in the present investigation (ZEISS-RA 3) the specular component only partially leaves the sphere through the opening for the incoming light and thus is partially included in the reflection measured.

The two conditions can be compared in fig. 2 and 3. Both methods have been used in the present investigation.

Apparatus.

The apparatus for measuring $R_{45/0}$ consisted of a 6 W incandescent lamp, the light from which was focussed by a convex lens on the actual part of a bird, the angle of incidence being approximately 45°. The radiation reflected at right angles to the feather surface was spectrally filtered by an interference filter (SCHOTT & GEN.) and the radiation reaching the photo-electrical detector was measured by means of a D.C. amplifier. There were two

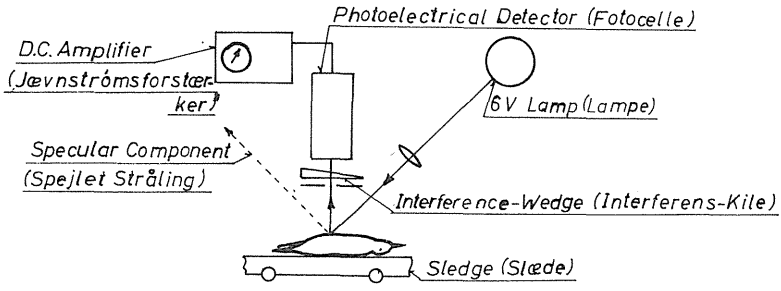

Fig 2. See text.
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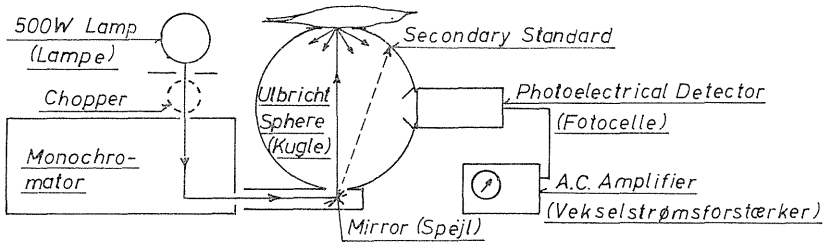

Fig. 3. See text.
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mountings for measuring, one for the visible region with a photomultiplier tube as detector and one for the near-infrared region with a PbS-cell as detector. With this apparatus the reflection could be measured at 25 fixed wave-lengths in the region 421–1124 nm.

When measuring, the bird and a standard (both mounted on a sledge), were alternately placed in the light-beam and the corresponding readings were noted (fig. 2).

In order to achieve a better spectral resolution and examine how much the reflection depended on the measuring conditions, the reflection spectra of a number of birds were measured with a prism monochromator as dispersing element under 0/d-conditions (which are equivalent to measuring under d/0-conditions).

Radiation from a 500 W incandescent lamp after having passed a chopper (400 Hz) was spectrally filtered in a quartz-doublemonochromator (HILGER & WATTS, D 300). The monochromatic radiation was passed into an Ulbricht-sphere (ZEISS, RA 3) and by means of a mirror focussed on the actual part of a bird, placed in a sample holder. The angle of incidence was 0°. The mirror could be held in two positions, corresponding to the light-beam either reaching the bird or a part of the inner surface of the sphere, which acted as a secondary standard. In the visible region a photomultiplier tube (PHILIPS, 51 UVP) and in the near-infrared region a PbS-cell (PHILIPS) was used, their out-puts being fed to an A.C. amplifier (fig. 3).

With this apparatus, measurements were carried out in the spectral region 380–2000 nm, with intervals of 10 nm between 380 and 770 nm and intervals of 100 nm between 800 and 2000 nm. In regions of special interest measurements with smaller wave-length intervals were carried out.

Calculations.

For each wave-length the reflection is calculated as: $R_\lambda = \frac{R_{Bird}}{R_{MgO}}$. When a secondary standard was used instead of MgO, this was measured against MgO, whereafter the reflection relative to the sec. standard could be converted to the reflection relative to MgO.

When measuring the reflection under diffuse conditions a little correction is necessary:

If a perfectly black body (in this case, a tall cylinder made from black cardboard) is placed above the sphere-opening, it will show an apparent reflection of about 0,3–0,5%. This is caused by light-scattering from lenses and mirror. A part of the scattered light does not reach the opening, but falls instead upon the inner surface of the sphere, thus giving an apparent reflection. This has to be subtracted from the measured reflection. This correction is of course most important, when measuring dark objects with low reflection.

The reflection curves were drawn from the calculated R_λ-values and the tristimulus values calculated by summing up for each 10 nm. The constants used in the calculation were those corresponding to illumination by a light source with the same spectral characteristics as diffuse daylight (CIE Standard Illuminant C).

Calculations were made partly by means of a calculating machine, partly by means of a digital computer, which directly gave the values of λ_d, σ and Y.

Material.

Measuring was mainly carried out on stuffed specimens borrowed from the Ornithological Department, Zoological Museum, University of Copenhagen.

A few fresh-killed birds were also included. To prevent putrefaction, a formaldehyde-glycerine mixture was injected.

Reproducibility and Sources of Error.

To give an idea of the reproducibility the standard errors of the mean for successive measurements are given in table 2.

For the two types of apparatus are given: (1) The standard error of the mean for the reflection of a secondary standard measured at a given wave-length on different days. (2) The standard error of the mean for the reflection of a given part of a bird measured at a given wave-length but with different orientations of the bird.

The values refer to the visible part of the spectrum. In the near-infrared part the variations were somewhat greater.

Standard error of the mean % (relative)	$R_{45/0}$	$R_{0/d}$
Secondary standard, different days	0,6	1,8
Feather part, different orientations	3,4–7,1	1,6 (–11,3)

Table 2. Explanation is given in the text.
Forklaring i teksten.

One fact derived from table 2 is that the reproducibility is poorer when measuring the reflection of birds than when measuring the reflection of the secondary standards.

This is partly caused by the fact that the feather surfaces are far from being plane, small variations in the placing thus giving rather great variation in reflection.

This error can partly be eliminated by reducing the illuminated part of the bird, but the desire for measuring on a fair part of the body to eliminate small variations in the feather surface counteracts this possibility. A compromise is necessary.

With the $R_{45/0}$ apparatus, where the bird was laid upon a sledge and rather loosely tied with rubber bands, the illuminated part varied from about 10 cm^2 to about 1 cm^2 for the smallest birds, where the measuring errors were greatest.

In the $R_{0/d}$-apparatus the bird was placed in a special holder and the reproducibility equalled the one achieved for the secondary standard when measuring birds that were not too small. The illuminated part is 25 mm in diameter, which causes the variations to be great when measuring birds of robinsize (up to 10% or even more, table 2).

The variation in the feather surface made it necessary to specify exactly the part of the bird, which was measured (in mm behind the tip of the bill).

Another fact derived from table 2 is that the variations in the reflection of birds are smaller, when measured with the $R_{0/d}$-apparatus than when measured with the $R_{45/0}$-apparatus. This is due to the fact that the reflection, when measured with the $R_{45/0}$-apparatus varies to a rather high degree with the orientation of the bird relative to the incident light.

The reflection at a given wave-length used to vary as much as 10% (relative) according to whether the body-axis of the bird lay parallel to or perpendicular to the plane, which was defined by the incident light beam and the direction to the photo-electrical detector, and according to whether the bill was pointing towards the light source or away from it. The orientations that gave the greatest reflection were different for different birds and might even vary with the wave-length for a given feather tract. An example is given in table 3.

λ (nm)	Rλ at different orientations of the bird. → W	↓ W	← W	↑ W
445	2,95	3,13	2,80	2,81
645	6,08	6,62	6,03	6,28

Table 3. $R_{45/0}$ (relative to a secondary standard) of part of the back of *Ptilinopus viridis*. The figures show the different orientations as viewed from the photo-electrical detector. Symbols: → Bird, W Light-source.
$R_{45/0}$ *(i forhold til en sekundær standard) af et rygparti hos* Ptilinopus viridis. *Figurerne viser de forskellige orienteringer af fuglen, som set fra fotocellen. Symboler:* → *Fugl,* W *Lampe.*

No doubt the variations are due to the structure of the feathers. The pattern of barbs and barbulss shades differently in different directions, and the glossy component varies too. The coherence between orientation and reflection, however, is complex and needs special investigation.

For the present purpose it is sufficient to state, that the variations impede the colour definition and hence the $R_{0/d}$-apparatus, where these variations are almost eliminated, is preferable.

Comparison of the two types of apparatus.

A comparison of reflections measured with the two types of apparatus is given in table 4.

Table 4 shows that the results agree within 5–7%.

In two cases the $R_{0/d}$-apparatus gave the highest reflection, in the other two cases the situation was reversed.

Plumage area *(fjerparti)*	λ nm	Rλ (%) $R_{45/0}$	$R_{0/d}$
Picus viridis (Back)...	421	4,06	3,69
	547	16,0	17,0
Ptilinopus viridis (Back)	445	2,92	2,79
	645	6,25	6,67

Table 4. Comparison of the reflection measured with the two types of apparatus.

Sammenligning af refleksionen målt med de to apparaturer.

Comparison of the reflections from a smooth surface measured in the two types of apparatus, invariably showed that $R_{0/d}$ was greater than $R_{45/0}$, caused by the partial inclusion of the specular component when measuring with the $R_{0/d}$-apparatus. This indicates that the specular component from a feather-surface is of minor importance when measuring reflection. This is confirmed by the fact that with a glossmeter (Photovolt-Glossmeter 660) gloss from birds was found to be $\leqq 1\,^0/_{00}$.

A fundamental difference between the two types of apparatus is that when measuring with the 45/0-apparatus the bird is illuminated with all wavelengths emitted by the lamp, whereas when measuring with the 0/d-apparatus the bird is illuminated with monochromatic radiation. This gives a difference when measuring the reflection of fluorescent objects, i.e. the object emits radiation in the visible region, when exposed to for instance ultraviolet radiation. This emitted radiation will be included in the 45/0-apparatus, but not in the 0/d-apparatus, where no ultraviolet radiation reaches the object. A few feather pigments are known to fluoresce: some yellow pigments of unknown constitution in parrots *(Psittaciformes)* (Völker 1937(b)), and some varieties of melanin (Lubnow 1963).

It must therefore be borne in mind that when measuring the reflection of feathers containing such pigments with the 0/d-apparatus, the fluorescent component is not included.

To illustrate the extent to which the reflection curves might differ, 4 reflection curves of the belly of the same specimen of *Melopsittacus undulatus* are shown, two measured with the 45/0-apparatus, two with the 0/d-apparatus (fig. 4). The discrepancies are due to the various factors mentioned above (different orientations of the bird in the 45/0-apparatus, the difficulty of measuring exactly the same area of the bird each time, and so on).

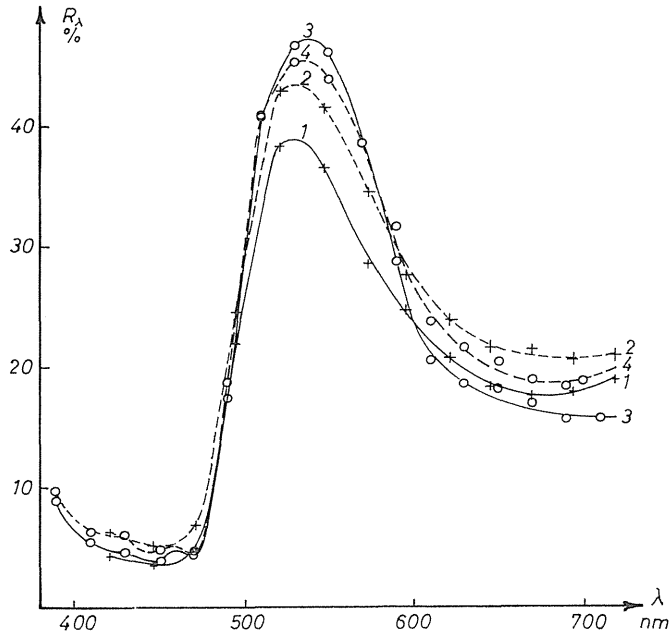

Fig. 4. Four reflection curves for part of the belly of the same wild-coloured specimen of *Melopsittacus undulatus*. 1,2: Measured with the 45/0-apparatus. 3,4: Measured with the 0/d-apparatus.

Fire refleksionskurver af et parti af bugen af samme eksemplar af en vild-type farvet undulat (Melopsittacus undulatus). *1,2: Målt med 45/0-apparatur. 3,4: Målt med 0/d-apparatur.*

In table 5 are given hue, saturation and lightness calculated from the curves shown in fig. 4.

It can be seen from table 5, that the $R_{0/d}$-measurements agree better mutually than the $R_{45/0}$-measurements. Further it can be seen from table 5, that the purity is greater when measured with the 0/d-apparatus, than with the 45/0-apparatus. This is probably related to the better spectral resolution given by the 0/d-apparatus.

Curve	Apparatus	Hue (nm)	Saturation (%)	Lightness (%)
1	$R_{45/0}$	563,5	63,7	29,18
2	$R_{45/0}$	563,1	59,6	33,36
3	$R_{0/d}$	560,3	68,27	35,32
4	$R_{0/d}$	562,7	66,29	35,88

Table 5. Hue, saturation and purity from 4 reflection measurements of part of the belly of the same specimen of *Melopsittacus undulatus*.
Farve, mætning og renhed fra 4 refleksionsmålinger af et bugparti af det samme eksemplar af Melopsittacus undulatus.

THE RELATIONSHIP BETWEEN ABSORPTION AND REFLECTION

Radiation incident on an opaque object is partly absorbed by the object (transformed to heat), partly transmitted through the object and partly reflected at the surface as well as from scattering particles in the object. Thus

$$A + T_{diff.} + R_{diff.} = 100,$$

where A, $T_{diff.}$ and $R_{diff.}$ respectively are percentage absorbed, transmitted and reflected radiation.

Generally no radiation is transmitted through a layer of feathers ($T_{diff.} = 0.$) Thus it holds good that $A + R_{diff.} = 100$, which means that there is a close connection between the absorption of the pigments deposited in the feathers and the reflection of the feathers. High absorption giving low reflection and vice versa, assuming structural colours do not interfere.

Many feather pigments e.g. carotenoids show strong absorption at definite wavelengths (absorption bands) in the visible spectrum, the positions of which can be used for identification purposes. With the pigment dissolved its absorption has a well-defined intensity, which for a given wavelength only depends on the nature and concentration of the pigment.

With the same pigment deposited as granules in a matrix, e.g. keratin making up feather barbs, the incident radiation is partly absorbed by the pigment granules and keratin, partly scattered as a consequence of the non-homogenous structure.

The reflection is therefore determined by the ratio between absorbed radiation a, and scattered radiation s. With greater $\frac{a}{s}$ the reflection becomes smaller.

The scattering, s, is dependent on the number, shape and size of the particles as well as on the refractive indices of particles and matrix. These different factors work together in a very complicated way, which makes calculations on a theoretical basis very difficult.

If the absorbing pigment occurs in low concentrations there will, however, generally be a similarity between the absorption spectrum of a solution of the pigment and the reflection spectrum of the same pigment, even bands related to molecular vibrations may be suppressed in the reflection spectrum (KORTÜM ET AL. 1963).

Three factors are responsible for discrepancies between absorption and reflection spectra:

1. The scattering is dependent on the wave-length.
2. The adsorption of pigment molecules onto the matrix surface often has the effect that the absorption spectrum of the pigment is shifted to longer wave-lengths.
3. When the pigment occurs in high concentrations, the molecules are often found in "stacks", which interact to cause a flattening of absorption maxima. See ALLEN (1964), KORTÜM ET AL. (1963), BELLIN (1965).

To summarize, reflection spectra of pigments generally differ from their absorption spectra in showing reflection minima (analogous to absorption maxima) which are flattened and shifted to longer wave-lengths.

Reflection spectra can also be quantitatively evaluated by means of the KUBELKA-MUNK function $\frac{(1 \div R)^2}{2R}$. This is proportional to $\frac{a \cdot c}{s}$, where a is the absorptivity, c the concentration of the absorbing pigment and s the scattering. Assuming a and s are constant, $\frac{(1 \div R)^2}{2R}$ is proportional to the concentration of the pigment and hence can be used for quantitative purposes.

However, several assumptions have to be fulfilled if the method is to be used. The principal matter is, that R designates the diffuse reflection when the reflection from the outer surfaces has been eliminated. This can be accomplished in two ways (compare KORTÜM ET AL. 1963).

RESULTS

In the appendix all the measurements are collected. For each measurement is given the species (sex, age), place and time of collection, condition of the bird (freshly collected or museum specimen), part of plumage measured, wave-length region, the type of apparatus and the calculated values for hue, purity and lightness.

Examples of reflection curves are given below, where also the values for hue, purity and lightness are commented on.

PLUMAGE COLOURS AND REFLECTION CURVES

White and slightly pigmented plumage areas.

When feathers appear white this is due to reflection of light from the innumerable small keratin surfaces of the feathers (BANCROFT ET AL. 1923, FRANK 1939). In many species there is also reflection from air spaces in the rachis and barbs (BANCROFT ET AL. 1923, FRANK 1939) and finally reflection caused by variations in the refractive index of keratine (quills of white goose and hen) (BANCROFT ET AL. 1923).

Part of the incident radiation is absorbed by the keratin and perhaps part of it is also transmitted to the underlying down feathers (if no absorption or transmission occurred, the reflection would be 100%). As keratin may vary in its chemical composition (SCHENK 1932), its absorption – and consequently the resulting reflection – may also vary, but very likely the reflection mainly depends on the structure of the feathers.

Examples of reflection curves of white

plumage areas and plumage areas with very slight pigmentation are given in fig. 5.

Fig. 5 shows that most whitish plumage areas reflect 20–35% of the incident light. The reflection rises slightly with increasing wave-length, so as to give an s-shaped curve, particularly characteristic in curve 2. Of the curves in fig. 5 only curve 2 (rump of *Garrulus*) refers to a plumage area completely devoid of pigment (judged by the unaided eye) in a fresh-killed specimen. Curve 1 *(Acrocephalus)* differs partly by showing great reflection (up to 52%) in the visible region, partly by a steep rise. The last fact is caused by a slight content of melanin, which gives a faint brown coloration. Curve 5 *(Passer)* differs in having a rather low reflection, caused by a faint melanin pigmentation of the feathers, and perhaps also by dirt, which is known often to alter the coloration of House Sparrows to a rather high degree (HARRISON 1963 (b)). Curve 2 and 5 refer to freshly collected specimens, while the others refer to museum specimens, which may show reflections, that are too low.

The reflection of a purely white surface is represented by a horizontal line. The stated discrepancy must be due to absorption by the keratin. This has been measured on keratin from white hairs of the rabbit by LUBNOW (1963), who found a spectral dependance, which the present s-shaped reflection curves match. This corresponds to the view that the white plumage areas are due to a combination of diffuse reflection and the absorption of keratin. The transmission has not been measured.

Dominant wave-length (λ_d), purity (σ) and lightness (γ) corresponding to the curves shown in Fig. 5 are given in table 6.

It is seen from table 6, that while the slightly melanin pigmented plumage areas *(Acrocephalus, Passer)* show purities of 14 and 18% respectively, the purity is otherwise so low ($\leqq$ 10%), that the lightness alone suffices to characterize the colour. It varies between 23 and 46%.

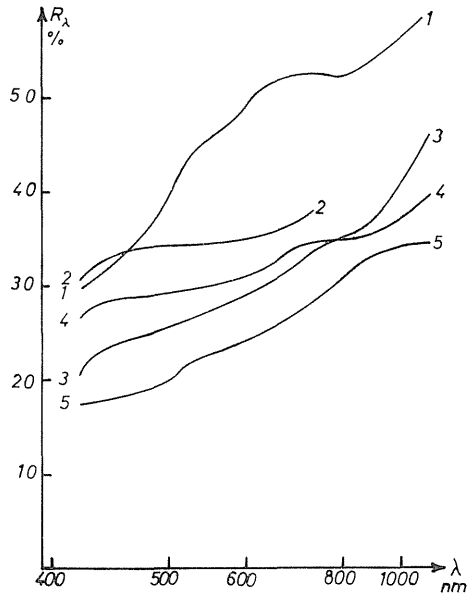

Fig. 5. $R_{45/0}$ of whitish plumage areas. 1. *Acrocephalus scirpaceus:* Belly. 2. *Garrulus glandarius:* Rump. 3. *Vanellus vanellus* (pull.): Belly. 4. *Certhia familiaris:* Belly. 5. *Passer domesticus* (♀): Belly. The wavelength are presented on a wavenumber (reciprocal) scale.

$R_{45/0}$ af hvidlige fjerpartier. 1. A. s.: *Bug. 2.* G. g.: *Overgump. 3.* V. v.: *Bug. 4.* C. f.: *Bug. 5.* P. d.: *Bug. Bølgelængderne er afsat efter en bølgetal (reciprok) skala.*

Plumage area *(fjerparti)*	λ_d (nm)	σ (%)	γ (%)
Acrocephalus:			
Belly *(Bug)*	573,1	18,5	45,65
Garrulus: Rump			
(Ov.gump)	585,4	3,10	34,90
Vanellus: Belly *(Bug)*..	581	9,4	27,50
Certhia: Belly *(Bug)*...	576	6,0	30,57
Passer: Belly *(Bug)*...	581,5	14,3	23,03

Table 6. Hue, purity and lightness of white plumage areas.

Farvetone, renhed og lyshed af hvide fjerpartier.

Blue feathers.

As is the case of white feathers no pigment is responsible for blue colours in feathers, as these are purely structural.

Blue colours may be due to structures causing interference of light, by which iridescent blue colours are produced (see for instance Fox & Vevers 1960). More often, however, they are due to Tyndall scattering (see for instance Bancroft et al. 1923, Frank 1939, Fox & Vevers 1960), produced by minute air-filled cavities in the barbs.

The reflection curve of the blue wing coverts of *Garrulus glandarius* is shown in Fig. 1, which shows clearly how the reflection decreases with increasing wavelength in qualitative accordance with the theory (scattered radiation inversely proportional with λ^4). The reflection, however, does not follow the Raleigh equation quantitatively, which is due to the fact that the wing coverts are not pure blue, but have black and white bars as well. Haecker & Meyer (1902) found good agreement with the Raleigh equation when measuring the reflection from a blue *Malurus* feather. Peiponen (1963) obtained a similar reflection curve from blue breast feathers from *Luscinia svecia*, but the reflection in the blue part of the spectrum, was about twice that measured for *Garrulus* corresponding to a more vivid blue colour.

Calculation from the reflection curve gave $\lambda_d = 479{,}0$ nm, $\sigma = 32{,}5\%$ and $Y = 7{,}3\%$.

Iridescent colours.

Iridescent colours, caused by the interference of light, are widespread among birds and found in many families, see Auber (1957). The colour-producing structures have been investigated by many scientists, for references see Fox & Vevers (1960). The newest and perhaps the most satisfactory investigation is that by Greenewalt et al. (1960) on hummingbird feathers. They have found that iridescent colours in this family are produced by stacks of small elliptical platelets in the barbules. The platelets consist of melanin each containing an air gap. The thickness of the platelets averages 150 nm. The surfaces separating air and melanin in these stacks are responsible for the iridescent colours.

Fruit pigeons, belonging to the genera *Ptilinopus* and *Megalopreia* show green colours, also caused by interference (Bancroft et al. 1923). It is characteristic of these colours, that they are not iridescent (metallic), which means that the colour does not vary with the viewing angle. The colour appears dull, not lustrous. According to the investigations of Schmidt (1952), this is due to the fact that the melanin platelets causing interference do not lie in

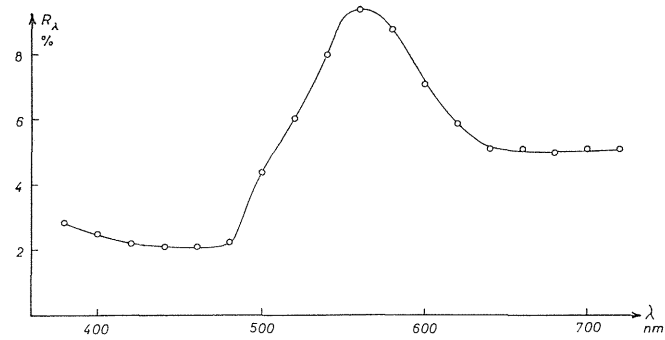

Fig. 6. $R_{0/d}$ of *Ptilinopus viridis*: Back.
$R_{0/d}$ *af* Ptilinopus viridis: *Ryg.*

a plane parallel to the surface of the barbule (as in hummingbirds) but instead are placed in spheres in the upper surfaces of the barbules.

This causes the green light, produced by interference, to be reflected in all directions, whereby the feather surface appear to reflect diffusely.

The reflection curve of the green back of *Ptilinopus viridis* is shown in Fig. 6.

This reflection curve shows a maximum about 570 nm, corresponding to the light, produced by interference. GREENEWALT ET AL. found similar reflection curves for iridescent hummingbird feathers with a single maximum in the visible part (apart from a small satellite peak in the blue region in some cases).

Carotenoid in the distal parts of the barbules (FRANK 1939) causes the reflection to be lower in the blue part (where carotenoids have great absorption) than in the red part of the spectrum. The reflection curves of *Ptilinopus* are dealt with in detail more p. 66.

Melanin.

Melanin is the most widespread feather pigment, and probably occurs in nearly all species. It gives rise to a variety of colours ranging from black, grey, brown and light brown to yellow and orange colours, and also plays a role in many structural colours as mentioned above.

It is customary to distinguish between different varieties of melanin that differ in colour, solubility in alkalis and ability to fluoresce (FOX & VEVERS 1960). It is known that the black (eu-) melanins are produced by oxidation and polymerization of the amino acid tyrosine, while the method of formation for the brown (phaeomelanin) and orange varieties is unknown. It has often been suggested that there is only a quantitative but not a qualitative difference between black and for instance yellow melanin pigmented feathers, a low concentration of melanin granules giving a yellow colour and a high concentration giving a black colour.

This has recently been shown by LUBNOW (1963) not to be the case, as solutions of black and yellow melanin from rabbit hair show characteristically different absorptions and consequently reflection spectra, in the visible region. Furthermore he has shown that the difference is due to a greater amount of protein in black melanin than in yellow melanin, melanin being composed of a colour component (melanoid) attached to a protein (SERRA 1946).

So the genetically defined colour races of rabbits (and probably all mammals) differ according to LUBNOW not in the colour component but in the protein part.

Melanin is found as granules in feathers as well as in the horny layers of bills and legs. Often melanin granules of more than one variety are found in the same feather part (HARRISON 1963a).

A detailed account of melanin is given by for instance FOX & VEVERS (1960).

Fig. 7 shows the reflection curves of some plumage areas, exclusively pigmented by melanin.

Fig. 7 shows that the reflection in all cases rises more or less steadily with the wave-length, showing no characteristic maxima or minima in accordance with the well-known fact that solutions of melanin show no characteristic absorption maxima in the visible spectrum. The inclination is least for the black (1) and grey (7) plumage areas, greater for the brown (2,3,5) and very pronounced for the orange breast of Erithacus (4).

Further it can be seen from the figure, that a common feature for the orange to brown plumage areas is an inflexion ($\frac{dR}{d\lambda}$ being maximum) in the region 470–550 nm (with the chosen logarithmic ordinate), most pronounced and at the shortest wave-lengths in curve 3 and 4,

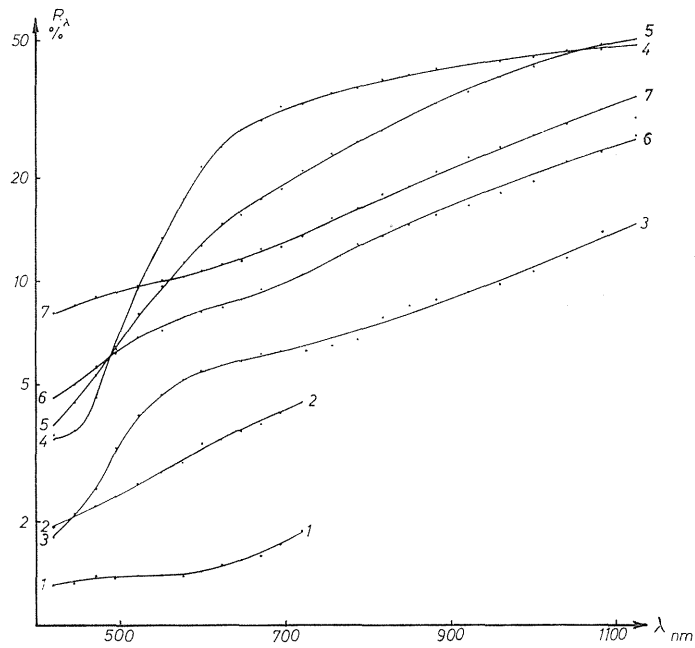

Fig. 7. $R_{45/0}$ of melanin pigmented plumage areas. 1. *Garrulus g. glandarius:* Tail. 2. *Turdus merula* (♀, juv.): Back. 3. *Erithacus rubecula:* Back. 4. *Erithacus rubecula:* Breast. 5. *Acrocephalus scirpaceus:* Back. 6. *Passer domesticus:* Rump. 7. *Prunella modularis:* Throat.

$R_{45/0}$ af melanin-pigmenterede fjerpartier. 1. Garrulus g. glandarius: *Hale. 2.* Turdus merula (♀, *juv.) Ryg. 3.* Erithacus rubecula: *Ryg. 4.* Erithacus rubecula: *Bryst. 5.* Acrocephalus scirpaceus: *Ryg. 6.* Passer domesticus: *Overgump. 7.* Prunella modularis: *Hals.*

less pronounced and shifted to longer wave-lengths in curve 5 and 2. The grey (curve 7) and black (curve 1) plumage areas show conversely an inflexion $\left(\frac{dR}{d\lambda}\right.$ being minimum) about 550 nm. Curve 6 (rump of *Passer domesticus*) is intermediate in showing slight inflexions of both kinds.

On the basis of LUBNOW's statement that yellow and black melanin differ in the amount of protein attached to the colour component, it is tempting to assume, that the first group with $\frac{dR}{d\lambda}$ showing a maximum in the short-wave region corresponds to melanin granules with proportionately low contents of protein, and the second group with $\frac{dR}{d\lambda}$ showing a minimum about 550 nm correspond to melanin granules with proportionately high contents of protein.

The corresponding values of hue, purity and lightness are given in table 7.

Plumage area *(fjerparti)*	λ_d (nm)	σ (%)	Y (%)
Garrulus: Tail *(Hale)* .	585,4	3,32	1,40
Turdus: Back *(Ryg)* ..	585,7	18,7	2,85
Erithacus: Back *(Ryg)* .	577,4	40,0	4,68
Erithacus: Breast *(Bryst)*	584,0	63,8	15,25
Acrocephalus: Back *(Ryg)*	582,0	43,6	10,30
Passer: Rump *(Ov.gump)* ..	578,6	20,70	7,46
Prunella: Throat *(Hals)*	580,5	10,11	10,21

Table 7. Hue, purity and lightness of melanin pigmented plumage areas.

Farvetone, mætning og lyshed af melaninpigmenterede fjerpartier.

As seen from table 7 it is characteristic for melanin pigmented plumage areas that the hue always is nearly the same, varying only between approximately 577 to 586 nm, as also stated by LUBNOW & NIETHAMMER (1964). This means that the colour variations perceived by man are only variations in lightness and purity. To take the extremes, the difference in colour between the black tail of *Garrulus*

and the orange breast of *Erithacus* is merely due to a much greater purity and a somewhat greater lightness of the latter.

A high lightness can also be produced by a low concentration of melanin granules in the feathers, the reflection being dependent on the absorption of the melanin granules as well as on "white-reflection". This is how, for example, grey colours may be produced (FRANK 1939). The effect can be seen if comparing curve 1 and 7, where the former corresponds to a black plumage area, the latter to a grey. The two curves show nearly identical shapes in the visible region and differ mainly with respect to lightness, which is about 7 times greater for the grey than for the black plumage area.

It is possible to correct for this dilution effect but this needs special analysis which has not been carried out in the present investigation. JUHN (1964) corrects by subtracting a constant value throughout the visible spectrum. This approximation, however, is not quite valid, as the reflection of an unpigmented feather is not constant through the visible spectrum as shown above (p. 59).

Apart from dilution the appearances of melanin pigmented plumage areas are also dependent on the form of and the mode in which the melanin granules are deposited in the various feather parts, cf. FRANK (1939).

Carotenoids.

Next to the melanins the carotenoids form the most widely distributed feather pigments among the birds. Carotenoids are best known as the colouring substances in many yellow and red feathers (*Oriolus*, *Serinus* etc.). Green pigments (*Somateria*, *Netta)* are also supposed to be carotenoids (STRESEMANN 1927) but this does not seem to have been closely investigated.

In contrast to those occurring in plants and mammals feather carotenoids mostly contain oxygen which is attached as hydroxyl or ketonegroups (VÖLKER 1960).

A number of different carotenoids are known from feathers, some of them being chemically identified (lutein, zeaxanthin, astaxanthin and rhodoxanthin) while others are still unidentified (canaryxanthophyll, picofulvin and many red carotenoids).

Often one carotenoid dominates in the feathers, for example lutein in the yellow feathers of *Motacilla flava* and *Oriolus oriolus* and canaryxanthophyll in the feathers of *Cloris cloris* and *Serinus canaria* (VÖLKER 1960). However, closer investigation shows that a number of different carotenoids may occur in the same feather parts. Thus, in the feathers of the Andean Flamingo *(Phoenicoparrus andinus)* FOX & HOPKINS (1965) found canthaxanthin, astaxanthin and two unidentified carotenoids present.

In contrast to the melanins, which are deposited in the feathers in the form of granules, the carotenoids are homogeneously dispersed in the keratin making up the feather parts. They are most frequently met with in the barbs, and occasionally a synchronous reduction of the barbules occurs, e.g. in the red breast feathers of *Lybius torquatus* (SALOMONSEN 1938) and in the red crown feathers of *Picus viridis* (FRANK 1939).

Carotenoids often work together with other pigments or colour-producing structures so as to produce other colours than red and yellow. For instance yellow carotenoids in combination with structural blue, caused by Tyndall scattering, give rise to intensive green colours. Together with melanins, carotenoids may give an olive-green effect; some parts of the feathers being pigmented with carotenoid, others with melanin (FRANK 1939).

An important tool when identifying carotenoids is their absorption spectrum, which usually show several distinct maxima in the short-wave region of the visible spectrum.

In the following are described the reflection curves of some species, in which carotenoid pigmentation plays a major role in the visual appearance of the bird.

A. Aegithina tiphia.

A measurement has been carried out on a specimen of *Aegithina tiphia (Irenidae)* in winter plumage with olive-green back and yellow belly. Observation with low magnification showed that in the olive-green back feathers, the barbs and innermost parts of barbules (approximately 1/5 of the total length of the barbules) are yellow pigmented, whereas the outer parts of the barbules are black pigmented. This distribution of yellow and black pigments seems according to FRANK (1939) to be typical for olive-green feathers (e. g. *Parus major*). In the yellow feathers of the belly of *Aegithina* a greater part of the barbules are yellow pigmented, and in some barbules (especially in the distal parts of the feather) the black pigmentation vanishes completely. The reflection curves of back and belly are shown in fig. 8.

It is seen from fig. 8 that the two curves are very much alike, with distinct absorption bands in the short wave-length region showing the presence of one or more carotenoids, and a distinct rise about 500 nm to an almost constant reflection between 500 and 770 nm.

The absorption bands (seen in the figure as reflection minima) occur at the following wave-lengths (table 8):

Plumage area *(Fjerparti)*	Reflection minima nm *(Refleksionsminima)*				
Back *(Ryg)*	481	450	430	404,5	384
Belly *(Bug)* ...	481	449	430	404	385

Table 8. Reflection minima of *Aegithina tiphia. Refleksions minima* Aegithina tiphia.

The reflection minima of the two curves occur at nearly the same wave-length, as can be seen from table 8, and show ap-

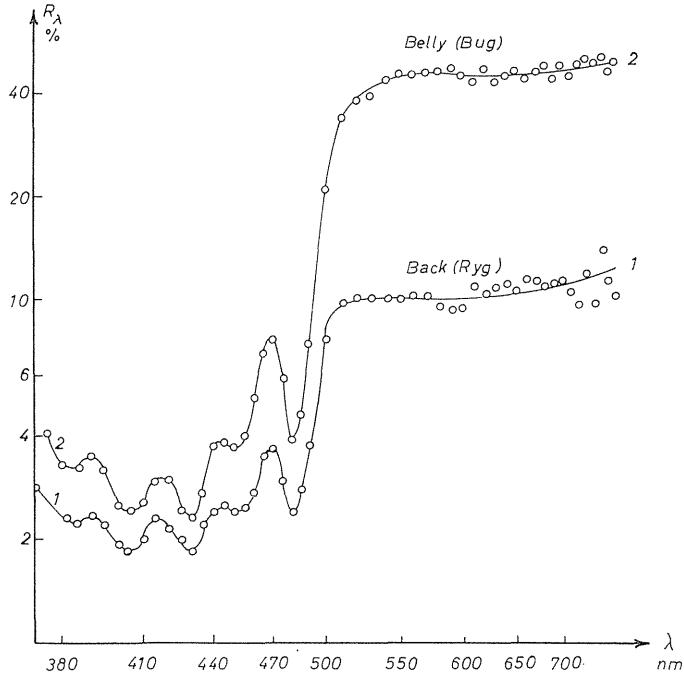

Fig. 8. $R_{o/d}$ of back (1) and belly (2) of *Aegithina tiphia.* $R_{o/d}$ *af ryg (1) og bug (2) af* Aegithina tiphia.

proximately the same relative intensities, which shows that the same carotenoid occurs in both back and belly which was of course to be expected. This, however, is not always the case. VÖLKER (1960) mentions that in *Chloronerpes yucatensis* the belly feathers mainly contain picofulvin whereas the back feathers mainly contain lutein.

The identity of the carotenoid is difficult to establish. The presence of five well-defined absorption bands in the visible spectrum perhaps can not be assigned to a single carotenoid, as carotenoids according to KARRER & JUCKER (1948) show three (seldom four) absorption bands in the visible region. It is therefore possible, that the reflection minima are due to two or more carotenoids occurring in comparable concentrations.

VÖLKER (1934) found that a carotenoid absorbs at 9–11 nm lower wave-lengths when dissolved in petroleum ether, compared to when it is embedded in feather keratin (in the region 450–500 nm). Thus a petroleum ether solution of the carotenoid of *Aegithina* must be expected to absorb at approximately 471–441–421–397–379 nm. No further investigation of the carotenoid has been undertaken, except that an epiphasic carotenoid was found, which absorbed at 472–443–420 in petroleum ether. The epiphasic carotenoid, which probably is the one giving rise to the reflection minima at 481–450–430 nm, may be identical with canaryxanthophyll, which according to VÖLKER (1934) absorbs at 472–443–418 nm, and is widespread among birds. Other possibilities, based on their spectra, are the xanthophylls taraxanthin and violaxanthin, which, however, not yet have been found in birds.

It is impossible to say anything certain about the origin of the reflection minima at 384–404 nm. They may be due to another carotenoid than the one causing the three reflection minima at higher wave-lengths. However, KARRER & JUCKER (1948) mention no natural carotenoids absorbing at these low wave-lengths, so this possibility does not seem very probable. It is also possible, that the great number of absorption bands may be related to the carotenoid being present in the feather in some way other than in solution (e.g. bound to keratin, esterified?).

The difference in the amount of carotenoid in the belly and back feathers is clearly indicated by the reflection curves, the more pronounced reflection minima in the belly curve being due to the greater quantity of carotenoid present here. On certain assumptions the quantities of carotenoid present can be calculated from the reflection curves, but these calculations are postponed until it is established whether these assumptions are fulfilled or not.

The black pigment which is probably melanin, reduces the reflection of the back feathers and thereby gives rise to the yellow colour appearing as olive-green. It is well-known that yellow colours with reduced lightness give rise to olive-green colours, and this is bound up with the fact that the relative spectral sensitivity of the human eye changes with decreasing light intensity. The values of hue, purity and lightness also show that the colour shift is mainly a matter of lightness (table 9).

Plumage area *(Fjerparti)*	λ_d (nm)	σ (%)	Y (%)
Belly *(Bug)*	573,5	78,77	40,61
Back *(Ryg)*	572,2	57,28	9,57

Table 9. Hue, purity and lightness of *Aegithina tiphia.*

Farvetone, renhed og lyshed af Aegithina tiphia.

Table 9 shows that, apart from a much reduced lightness, the olive-green back shows a somewhat reduced purity, related to the smaller quantity of carotenoid present here, whereas the dominant wave-length is practically the same in the two cases.

B. Picus viridis.

Examination of the olive-green back feathers of *Picus viridis* with low magnification showed a structure almost identical with that found in the back feathers of *Aegithina tiphia.*

The reflection curve, which is shown in fig. 9, is very much like that found for the back feathers of *Aegithina tiphia.*

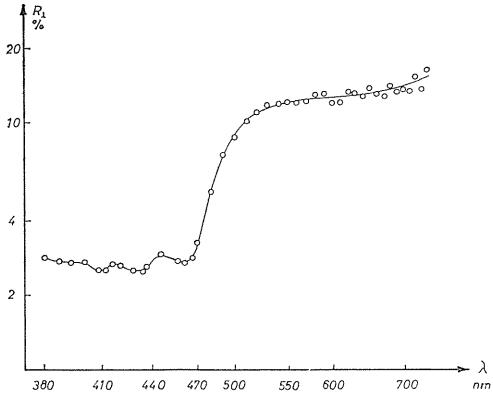

Fig. 9. $R_{0/d}$ of *Picus viridis:* Back. The scattering of the reflection values in the red part of the spectrum is due to noise from the photomultiplier. Ideally the values should have lain along the smooth curve drawn.

$R_{0/d}$ *af* Picus viridis: *Ryg.*

Here again the olive-green coloration is due to combined pigmentation by melanin and carotenoid. The only difference from *Aegithina* is the position of the absorption bands which here occur at 460–432–407 nm, thus showing the possible occurrence of another carotenoid. The absorption band at 460 nm corresponds to that found visually by VÖLKER (1934). The carotenoid, which generally is called "picofulvin", has not yet been chemically identified. Another difference from the reflection curve of the back of *Aegithina* (curve 1, fig. 8) is, that the reflection minima are less pronounced in the reflection curve of the back of *Picus*. This must be due to the fact, that *Picus* has other carotenoids besides picofulvin. These tend to mask the absorption bands of picofulvin, which otherwise are stated (VÖLKER 1960) to be very distinct.

Calculations gave $\lambda_d = 573{,}0$ nm, $\sigma = 57{,}84\%$ and $Y = 11{,}65\%$, which closely correspond to those calculated for the back of *Aegithina.* The difference in chemical composition of the carotenoid apparently has little effect on the visual appearence.

C. Ptilinopus viridis.

The green colour of *Ptilinopus viridis* is due to a combination of the interference-producing structure (as mentioned above) and carotenoid pigmentation in the distal parts of the barbules (FRANK 1939). Fig. 10 shows the reflection curves of the green belly, the green back and the ruby throat.

Curve 1 (belly) shows clearly the absorption bands of the carotenoid, which occur at: 476–445–419–396 nm.

The identity of this carotenoid is uncertain. An epiphasic carotenoid with absorption bands at 471–442–420 nm (petroleum ether) was found. These positions are nearly the same as those found in *Aegithina,* so here again canaryxanthophyll is a possibility. VÖLKER also states (1953) that the yellow carotenoids in the *Ptilinopodinae* are lutein or canaryxanthophyll. But as with *Aegithina,* here there are also additional reflection minima in the short-wave region, with a minimum at approximately 396 nm (although only slightly indicated), which was not found in the spectrum of the dissolved carotenoid. It is again not possible to say anything definite about the origin of this reflection minimum.

Supposing that the reflection minima at 476–445–419 nm are due to the carotenoid, dissolved in petroleum ether, absorbing at 471–442–420 nm, the usual wave-leng thshift of 9–11 nm, is seen here to be only 4–6 nm (in the region 450–500 nm).

It is striking, that the reflection minima are much less pronounced in curve 2 (back) than in curve 1 (belly). Micro-

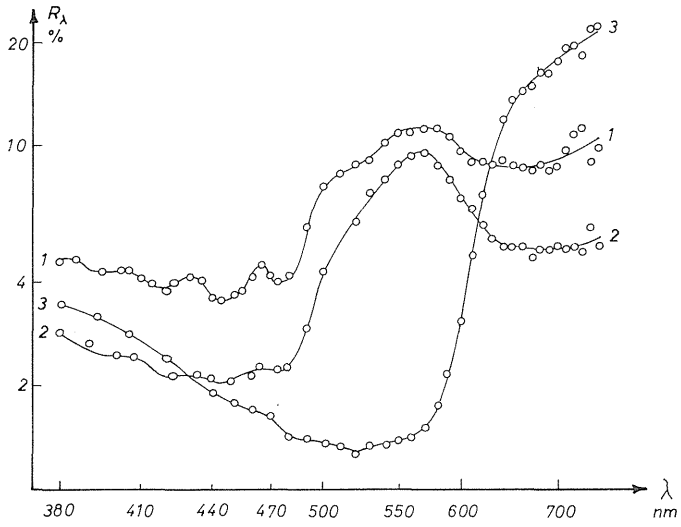

Fig. 10. $R_{0/d}$ of belly (1), back (2) and throat (3) of *Ptilinopus viridis*.

$R_{0/d}$ *af bug (1), ryg (2) og hals (3) af* Ptilinopus viridis.

scopical investigation shows that a somewhat greater part of the barbules of the belly feathers is pigmented by carotenoid compared to the barbules from the back feathers, (in belly barbules the carotenoid pigmented part constitutes 0,5–0,6 of the total length, in back barbules the corresponding figures are 0,25–0,4). This difference, however, is probably not solely responsible for the difference in the spectra. Perhaps the carotenoid concentration is lower in the back barbules than in the belly barbules. The greater carotenoid content in the belly feathers can also be seen in the more pronounced shoulder (about 500 nm) in curve 1.

Another difference between the reflection spectra is that the reflection of the back in the visible region outside the interference peak all over is somewhat lower than that of the belly. This must be due to a pigment with a nearly constant absorption throughout the visible spectrum, probably melanin, and related to a more developed interference structure in the back.

The colour difference expressed in figures can be seen from table 10.

Plumage area *(Fjerparti)*	λ_d (nm)	σ (%)	Y (%)
1. Belly *(Bug)*	570,9	42,62	9,71
2. Back *(Ryg)*	569,5	54,59	7,32
3. Throat *(Hals)* ..	÷493,1	37,95	2,46

Table 10. Hue, purity and lightness of different plumage areas of *Ptilinopus viridis*.

Farvetone, renhed og lyshed af forskellige fjerpartier hos Ptilinopus viridis.

It is seen from table 10 that the back shows nearly the same hue as the belly but greater purity and lower lightness.

VÖLKER (1953) has shown that in many species of *Ptilinopodinae*, purplish red, violet and blue colours are all due to the same red carotenoid, rhodoxanthin, which he isolated. Rhodoxanthin has the rather unique property that it adsorbs differently on different substrata (e.g. different silicates) and so the different feather colours must be attributed to differences in the composition of the feather keratin.

The ruby throat of *Ptilinopus viridis* may also be due to rhodoxanthin, but this species was not investigated by VÖLKER.

Rhodoxanthin absorbs at longer wavelengths than yellow carotenoids and shows

absorption bands at 520 and 485 nm when dissolved in petroleum ether. The displacement of the absorption to longer wave-lengths can be seen from the reflection curve (curve 3, fig. 10) which shows very low reflection (about 530 nm) whereas the absorption bands cannot be localized with certainty as also stated by VÖLKER (1953). Hue, purity and lightness are given in table 10.

The meaning of the negative dominant wave-length was explained above (section 2).

The yellow pigment of Melopsittacus.

In the parrots *(Psittaciformes)* diffusely distributed yellow and red feather pigments occur. VÖLKER (1937a) has shown that these pigments are not carotenoids as would be expected from their appearance. They differ from the carotenoids in a number of ways (solubility, histogenesis, dependance on carotenoid in the food). Like the carotenoids they show strong absorption in the short-wave region of the visible spectrum, with several distinct absorption bands.

Measurements have been carried out on a wild-coloured specimen of the Budgerigar *(Melopsittacus undulatus)*, in which a yellow pigment of this type occurs. The green colour of the belly, which is due to a combination of Tyndall blue and yellow pigmentation, is restricted to the barbs, while the reduced barbules are unpigmented (or only very slightly). The barred back is due to the barbs and adjacent barbules being alternately black and yellow pigmented.

The reflection curves of the back and the belly are shown in fig. 11.

Curve 1 shows three reflection minima in the blue part of the spectrum. In curve 2 (back) the minima are only slightly indicated. The minima occur at:

469, 443 and 419 nm.

This corresponds rather closely to that found visually by VÖLKER (1937):

468 and 445 nm.

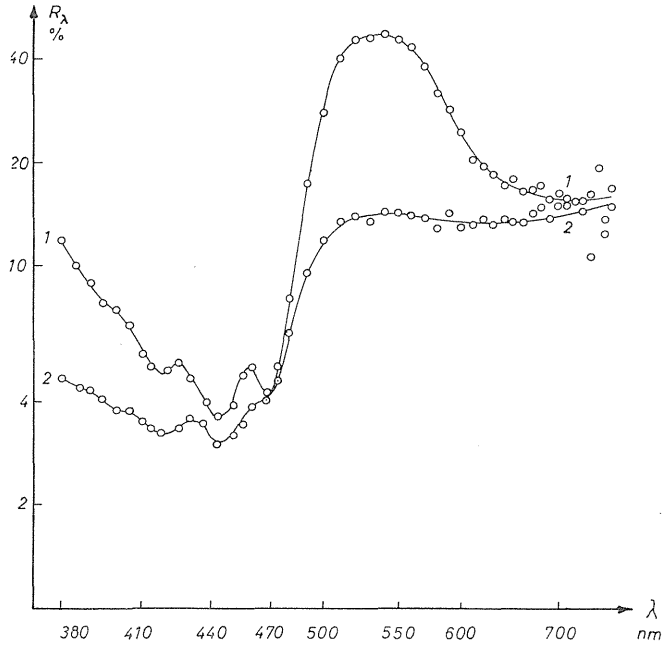

Fig. 11. $R_{0/d}$ of belly (1) and back (2) of *Melopsittacus undulatus.*

$R_{0/d}$ *af bug (1) og ryg (2) af* Melopsittacus undulatus.

Although this yellow pigment is not a carotenoid, its effect on the coloration is very much like that of a carotenoid. The reflection curve from the back (2), which is due to alternating black and yellow pigmentation is very much like those of the olive-green backs of *Aegithina* and *Picus* (fig. 8 and 9), which are also due to alternating black and yellow pigmentation. Apart from the difference in the chemical composition of the yellow pigment, the only difference is that in *Picus* and *Aegithina*, in contrast to *Melopsittacus*, the blending of the yellow and black parts occur at the microscopical level. When examined closely the feather areas obviously differ in coloration, but viewed at some distance they are similar. Compare also the values for hue, purity and lightness.

The combination of the yellow pigment with the structure producing Tyndall blue gives rise to an intensive green colour which manifests itself as a very pronounced peak at 535 nm (curve 1). The peak differs from those characteristic for interference colours (compare fig. 6 & 10) in not being symmetrical. The gradual rise with decreasing wave-length from about 660 nm due to the "blue-structure" is "suddenly" interrupted by the absorption of the yellow pigment and the result is that the inclination is greater in the short-wave part of the peak than in the long-wave.

λ_d, σ and Y are given in table 11.

Plumage area *(Fjerparti)*	λ_d (nm)	σ (%)	Y (%)
1. Belly *(Bug)*	560,3	68,27	35,32
2. Back *(Ryg)*	570,0	52,76	13,35

Table 11. Hue, purity and lightness of different plumage areas of *Melopsittacus undulatus*.

Farvetone, renhed og lyshed af forskellige fjerpartier hos Melopsittacus undulatus.

Table 11 shows that the green colour of the belly is of very high purity.

Reflection spectra in the near-infrared region.

The preceding sections have dealt with the reflection spectra in the visible region. In order to compare the reflection spectra in the near-infrared region (800–2000 nm), four examples are shown in fig. 12.

Fig. 12 shows that the curves are very similar in this spectral region, all showing a more or less pronounced rise to a region (1400–1800 nm) with high reflection (50–70%). Most curves show a minimum at 1500 nm, in some cases, however, it is only slightly indicated (curve 1: *Ptilinopus:* Back). Other curves which are not shown here, all showed the same characteristic shape.

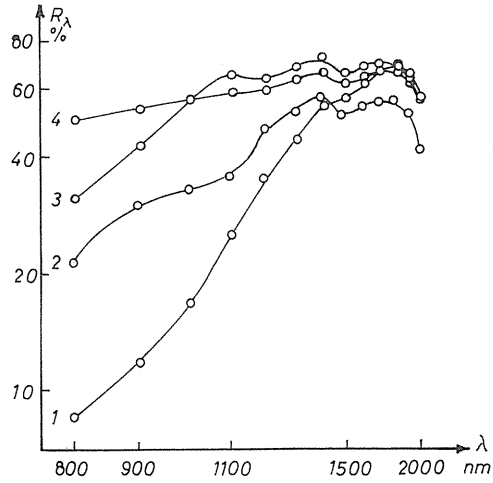

Fig. 12. $R_{0/d}$ in the near-infrared region, 800–2000 nm.
1. *Ptilinopus viridis:* Back *(Ryg)*
2. *Ptilinopus viridis:* Throat *(Hals)*
3. *Jacana spinosa:* Back *(Ryg)*
4. *Aegithina tiphia:* Belly *(Bug)*

$R_{0/d}$ *i det nær-infrarøde område, 800–2000 nm.*

Thus the pigments involved (various types of melanin (including a reddish brown type in the back of *Jacana*), various carotenoids (kanarienxanthophyll, rhodoxanthin)), thus apparently all absorb very little in this region. Stair & Coblentz (1933) similarly found that a film of

xanthophyll ($C_{40}H_{56}O_2$) showed high transmission and no distinctive absorption bands in the region 1000–2000 nm.

The common features of the curves (especially the reflection minimum at 1500 nm) must thus be attributed to the only common component, namely keratin.

Apparently the region is of little analytical value when investigating feather pigments.

CONCLUSIONS

It is clearly that it is possible to measure the diffuse reflection of birds and from this to calculate the values of hue, purity and lightness and to use these as a measure of the colour.

It is, however, equally clear that an accurate colour specification is more difficult to obtain with a bird than with for instance a piece of paper or a ceramic tile. As described earlier, this is mainly due to the fact that the plumage area of a bird does not represent a plane, homogenously coloured surface. The other difficulty mentioned above is related to the structure of the feathers, which causes the reflection to vary with the direction. This second point makes it advisable, when measuring the reflection of birds for colour specification purposes, to use diffuse illumination, preferably with the aid of an Ulbricht-sphere.

In ornithology the numerical colour specification is of special importance in systematics, where colour specification has always been a difficult problem. The usefulness of this method in systematics has been discussed in detail by LUBNOW & NIETHAMMER (1964).

The reflection curves show a clear coherence with the absorption spectra of the feather pigments and with the structures producing colour. The reflection curves thus make it possible to evaluate objectively the influences of the different elements on the resulting colour, as it is expressed in terms of hue, purity and lightness. This evaluation has hitherto always been made by eye. It must be emphasized however that the colour of a plumage area is not in all cases completely defined in the terms of hue, purity and lightness. This holds good only for matt surfaces. As mentioned above the gloss of plumage areas was found to be insignificant, but this is not true for all birds. Many birds show very vivid gloss, often related to interference structure. FRANK (1939) has discussed the optical effects, produced by different elaboration of barbs and barbules, and AUBER (1957) has given an account of the distribution of such colours in the class Aves. If such colours are also to be evaluated numerically, specification of gloss will be necessary.

From the reflection curves it is often possible to deduce which pigments and structures occur in the plumage areas. The reflection curves are thus analytical tools in the investigation of bird colours.

A few points can be emphasized:

1. The reflection curves of whitish plumage areas are typically S-shaped in the visible region, this is very probably related to the absorption by keratin. The reflection values do not generally exceed 50% in the visible region. Whether the remainder of the incoming radiation is all absorbed by keratin, or transmitted to underlying parts, has not been investigated.

2. Tyndall blue feathers show decreasing reflection with increasing wave-length in accordance with theory.
3. Iridescent colours show a single peak corresponding to the fact that they are produced by interference.
4. Melanin pigmented plumage areas show, with increasing wave-length, a steadily rising reflection without characteristic absorption bands in the visible and near-infrared region. The hue is nearly constant (579–585 nm), while the purity varies from about 3% for black areas to 60–70% for orange areas, corresponding to greater rise and possibly to decreasing amounts of protein attached to the melanoid. Lightness mainly depends on the degree of dilution.
5. Carotenoid pigmented plumage areas show reflection minima corresponding to the absorption bands of the carotenoids. This gives possibilities for identifying the carotenoids involved, assuming that only one carotenoid occurs in a given plumage area, or at least that one carotenoid is dominant. According to the investigations of VÖLKER (1960) the last is often the case, so it seems likely to me that it will often be advantageous to use reflection spectra for obtaining preliminary information as to the identity of feather carotenoids.

   As mentioned above, VÖLKER (1934) found a rather constant wave-length shift when comparing absorption maxima of carotenoids dissolved in petroleum ether and embedded in keratin. He made, however, only few such comparisons and more are needed to state, if a given carotenoid always absorbs at approximately the same wave-lengths when occurring in feathers of different species.

   Furthermore, it seems that the reflection spectra may also differ from the absorption spectra in showing more absorption bands (the example of *Aegithina* being notable in this respect), but whether this difference is caused by mixtures of carotenoids or is perhaps related to the carotenoids being bound to keratin, or to their occurring as esters must be left for future investigation. Obviously further work in this field is needed.
6. Olive-green plumage areas produced by melanin and carotenoid pigmentation show the same hue as yellow plumage areas pigmented only by a carotenoid. The colour difference is mainly a difference in lightness.
7. The pigment of *Melopsittacus* shows three absorption bands in the blue region. VÖLKER (1960) found only one or two absorption bands in the yellow and red pigments of parrots, probably because he was unable to detect the bands in the violet end of the spectrum visually.

   Reflection spectra may show of special importance in investigating these parrot pigments, which are difficult to dissolve without alteration (VÖLKER 1937 a).

The reflection curves will no doubt also be of great value in the investigation of the biological functions of colours (concealing coloration, signal colours and so on). It is intended later on to discuss some of these aspects.

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DANSK RESUMÉ

Objektiv farvebestemmelse og undersøgelser af fjerpigmenter og -strukturer ved hjælp af refleksionsspektroskopi.

Artiklen beskriver en objektiv metode til måling af fugles farver. Teorien for metoden gennemgås kort, resultaterne af nogle målinger gives og diskuteres i relation til fjerenes pigmenter og struktur. Målingerne er udført ved Forsvarets Forskningsråd, København.

Grundlaget for metoden er optegnelsen af det pågældende fjerpartis refleksionskurve i det synlige spektrum, d. v. s. 380–770 nm. Refleksionen bestemmes som den del af det indfaldende lys, der reflekteres af fjerpartiet ved den pågældende bølgelængde. I praksis gøres det på den måde, at fjerpartiets refleksion sammenlignes med refleksionen fra en plade med et lag magniumoxyd, idet dette stof med god tilnærmelse i det synlige område reflekterer lyset 100%. På fig. 1 er vist refleksionskurverne for et blåt, rødt og grønt fjerparti, og man ser, hvordan fx. det blå fjerparti reflekterer mest lys ved bølgelængder omkring 4–500 nm, hvilket netop svarer til at lys med bølgelængder i dette interval af mennesker opfattes som blå. Den internationale Belysningskommission (CIE) har fastlagt metoder, hvorved sådanne refleksionskurver kan omsættes til tal, der udtrykker, hvordan farven fremtræder for en såkaldt »standard-observatør«. Farven kan enten udtrykkes ved de såkaldte tristimulus-værdier, der angiver de mængder af tre valgte grundfarver, der skal blandes for at ækvivalere den oprindelige farve. Tristimulusværdierne kan ved hjælp af diagrammer omsættes til tre andre tal: dominerende bølgelængde, renhed (eller mætning) og lyshed. Den dominerende bølgelængde (eller farvetonen) er den tilsvarende spektralfarves bølgelængde (f. eks. 600 nm for en gul farve). Ikke-spektrale farvers farvetone angives ved den negative bølgelængde af den komplementære spektralfarve (f. eks. kan en purpurfarve have dominerende bølgelængde, $\lambda_d = \div 530$ nm). Renheden (σ) kan variere mellem 0 og 100%, og angiver, hvor forskellig farven er fra en rent grå farve af samme lyshed (der har renheden 0). 100% renhed svarer til stråling af samme dominerende bølgelængde (spektralren farve). Lysheden (Y) kan ligeledes variere mellem 0 (rent sort) og 100% (rent hvid farve) og svarer i øvrigt til mængden af den fastlagte grønne grundfarve, der er valgt således at den korresponderer med det menneskelige øjes følsomhedskurve i dagslys. Tabel 1 angiver farvetone, renhed og lyshed af de på fig. 1 viste refleksionskurver.

Der gives en kort oversigt over tidligere arbejder, hvori refleksionsmålinger på fugle er udført.

Den målte refleksion afhænger i nogen grad af målebetingelserne, specielt hvordan belysningskilde og fotocelle er anbragt i forhold til den flade, hvis refleksion skal måles. To metoder anvendes hyppigst. Ved den ene anbringes lampen således, at lyset rammer fladen under en indfaldsvinkel på 45°, og fotocellen anbringes lodret over det belyste sted. På denne måde måles den del af lyset, der spejles i overfladen ikke med (fig. 2), og refleksionen målt under disse betingelser betegnes $R_{45/0}$. Ved den anden metode belyses fladen med diffust lys, d. v. s. lys, der rammer fladen under alle tænkelige vinkler, og fotocellen anbringes som før lodret over den belyste flade. I laboratoriet kan diffus belysning opnås ved at anbringe fladen over et hul til en

indvendig hvidmalet kugle (Ulbricht-kugle) (fig. 3). Refleksionen målt ved denne metode betegnes som $R_{d/0}$.

Begge de ovenfor nævnte målemetoder er benyttet i foreliggende undersøgelse. Karakteristisk for apparaturet til måling af $R_{45/0}$ (fig. 2) var, at fuglen belystes af lys fra en 6 V glødelampe, hvorpå en del af det reflekterede lys passerede en interferens-kile, og intensiteten af passeret lys i det snævre bølgelængdeområde, som bestemtes af interferens-kilens stilling, måltes ved hjælp af fotocelle og jævnstrømsforstærker. Med $R_{0/d}$-apparaturet (fig. 3) (som, idet $R_{0/d} = R_{d/0}$, benyttedes i stedet for $R_{d/0}$-apparatur) kunne en væsentlig bedre spektral opløsning opnås ved hjælp af en prismemonokromator end med $R_{45/0}$-apparaturets interferens-kile. Med $R_{45/0}$-apparaturet måltes refleksionen ved 25 fastsatte bølgelængder i intervallet 421–1124 nm, med $R_{0/d}$-apparaturet med 10 nm's intervaller i området 380–770 nm og 100 nm's intervaller i området 800–2000 nm, idet der dog måltes med mindre bølgelængdeintervaller i områder af særlig interesse.

Udfra de målte refleksionsværdier er refleksionskurver optegnet og tristimulus-værdier beregnet svarende til CIE's Standard C-belysning (der har samme spektrale sammensætning som diffust dagslys). Disse beregninger er matematisk set simple, men temmelig tidsrøvende og kræver i hvert fald en regnemaskine. Fordelagtigt er det at lade beregningerne udføre af en elektronregnemaskine, som det her er gjort i en del tilfælde.

Der måltes overvejende på skindlagte fugle, men også på enkelte frisk indsamlede fugle.

Reproducérbarheden ved måling af fugles refleksion (tabel 2) er ikke så god, som den der kan fås ved målinger af f. eks. tekstil- og maleprøver. Dette skyldes bl. a., at en fjeroverflade ikke er helt plan og ikke helt ensartet, idet der altid er små variationer i fjerdragten. Det er derfor nødvendigt nøje at specificere, hvor på fuglen der måles for at kunne opnå nogenlunde reproducérbare resultater. $R_{45/0}$ afhænger yderligere af, hvordan fuglen er orienteret i forhold til det indfaldende lys (tabel 3). Det er lettest at opnå reproducérbare resultater med $R_{0/d}$-apparatur, der derfor må være at foretrække til måling af fugles farver, også fordi den bedst ækvivalerer de betingelser, hvorunder fuglene ses i naturen.

Sammenligning af refleksioner målt med de to typer apparatur er givet i tabel 4 & 5 og fig. 4. Overensstemmelserne var i det store og hele gode, svarende til at ingen af de undersøgte fjerpartier var nævneværdigt spejlende (under $1^0/_{00}$ målt med et Photovolt-Glossmeter 660).

En pigmentopløsning viser ofte i gennemfaldende lys specifikke absorptionsbånd, der kan benyttes til identifikation af pigmentet. Sådanne absorptionsbånd vil ofte kunne erkendes som tilsvarende refleksions-minima på refleksionskurven af det samme pigment indlejret i keratin. Ofte er sådanne refleksions-minima dog fladere og ikke så tydelige som de tilsvarende absorptionsbånd og kan evt. være forskubbet mod den røde del af spektret.

Refleksionskurver af hvide og ganske svagt pigmenterede fjerpartier er vist på fig. 5 og de tilsvarende værdier for farvetone, mætning og lyshed er samlet i tabel 6. Refleksionerne er i det synlige område af størrelsen 20–50%; disse værdier kan dog evt. være for lave, da 4 af de 5 kurver refererer til skindlagte, gamle, evt. ældede eksemplarer. Kurve 2, 3 og 4 viser et forløb, der svarer til keratins absorption i det synlige område.

Refleksionskurven af de blå vingedækfjer hos en Skovskade *(Garrulus glandarius)* er vist på fig. 1. Den blå farve skyldes Tyndall-spredning forårsaget af bittesmå luftblærer i keratinet, i forbindelse med absorption i et underliggende melaninlag af den langbølgede del af strålingen. Farvetone = 479,0 nm, σ = 32,5% og Y = 7,3%.

Farver, der skyldes lysets interferens, fremtræder som regel metalliske. Frugtduer af slægten *Ptilinopus* har imidlertid grønne ikke-metalliske fjerpartier, som skyldes interferens af en særlig struktur. Et eksempel er vist på fig. 6, og man ser, at refleksionskurven viser et enkelt refleksionsmaximum svarende til det ved interferens fremkaldte grønne lys.

Nogle refleksionskurver af fjerpartier, der kun er pigmenteret af melanin er vist på fig. 7 og de tilhørende værdier for farvetone, mætning og lyshed er givet i tabel 7. Af fig. 7 ses, at melaninpigmenterede fjerpartier viser en med bølgelængden ret jævnt stigende refleksion. Grå og sorte fjerpartiers refleksionskurver er dog på karakteristisk vis noget forskellige fra brune til rustrøde fjerpartiers, og denne forskel hænger muligvis sammen med et større proteinindhold i førstnævnte fjers melaninkorn. Farvetonen viser kun ringe variation for forskellige fjerpartier: fra 577,4 til 585,7 nm.

Refleksionskurver af ryg og bug af et eksemplar af *Aegithina tiphia* er vist på fig. 8, som eksempel på carotenoid-holdige fjerpartiers refleksion. Man ser tydelige refleksionsminima svarende til carotenoidets absorptionsbånd i området 380–500 nm, de nøjagtige positioner er angivet i tabel 8. Farveforskellen imellem den gule bug og den oliven-grønne ryg er udtrykt i tal i tabel 9, og viser sig væsentligst at skyldes den ændrede lyshed.

Den oliven-grønne ryg af Grønspætten *(Picus viridis)* viser en refleksionskurve svarende til den fundet hos *Aegithina tiphia*, blot findes refleksionsminima ved andre bølgelængder svarende til tilstedeværelsen af et andet carotenoid (fig. 9).

Den grønne farve hos *Ptilinopus viridis* skyldes en kombination af den tidligere omtalte inter-

ferensstruktur med carotenoidaflejring i bistrålernes yderste dele, hvilket også kan ses af refleksionsminima på kurverne, fig. 10. Den røde hals, der også skyldes et carotenoid, har refleksionsminima forskudt til ca. 520 nm.

Fig. 11 viser refleksionskurver, der skyldes et gult pigment af en type med ukendt kemisk sammensætning karakteristisk for papegøjer, i kombination med henh. Tyndall-blåt (bug) og melanin (ryg). Kombinationen med Tyndall-blåt giver en intensiv grøn farve, smlgn. tabel 11.

Nogle fjerpartiers refleksion i det nær-infrarøde område er vist på fig. 12. Man ser, at kurverne ikke er iøjnefaldende forskellige.

I konklusionen omtales foruden den værdi refleksionskurver kan have ved analysen af fjerenes pigmenter og strukturer, og som forhåbentlig er demonstreret ovenfor, også den talmæssige farvebeskrivelses værdi for systematikken og endelig peges der på, at kurverne sikkert i fremtiden vil få værdi ved undersøgelserne af farvernes biologiske betydning (kamouflage, pardannelse etc.).

I appendix er angivet de beregnede værdier for farvetone, mætning og lyshed udfra alle udførte refleksionsmålinger.

APPENDIX

The appendix contains the results of all the measurements on birds. For each measurement the species (sex, age, if known), time and place of collection, measured plumage area, apparatus used, wave-length region and the calculated values of hue, purity and lightness are given.

Species *(Art)*	Collected*) *(Indsamlet)*	Plumage area**) *(Fjerparti)*	Apparatus *(Apparatur)*	Measuring region (nm) *(Måleområde)*	Hue (nm) *(Farvetone)*	Purity (%) *(Renhed)*	Lightness (%) *(Lyshed)*
Jacana spinosa		Back *(Ryg)*, (140)	0/d	380–2000	590,7	67,0	3,98
Vanellus vanellus	May 1892,	Back *(Ryg)*	45/0	421–1124	583,2	29,7	5,55
(pull.)	Denmark (M)	Belly *(Bug)*	45/0	421–1124	581	9,4	27,50
Pluvialis apricarius	Aug. 1907,	Back *(Ryg)*, (115)	45/0	421–1124	579,7	30,1	6,69
(♀, ad.)	Holland (M)	Belly *(Bug)*	45/0	421–1124	583,6	23,0	4,42
Ptilinopus	1908, Molucca	Back *(Ryg)*, (95)	45/0	421–1124	568,6	46,4	6,85
viridis (♂)	Is. (M)	Back *(Ryg)*, (104)	0/d	380–2000	569,5	54,59	7,32
		Belly *(Bug)*, (93)	0/d	380–2000	570,9	42,62	9,71
		Throat *(Hals)*	0/d	380–2000	÷493,1	37,95	2,46
		Throat *(Hals)*	45/0	421–1124	÷492,6	26,6	3,39
Melopsittacus	Feb. 1939,	Back *(Ryg)*, (38	0/d	380–2000	570,0	52,76	13,35
undulatus (♂)	Denmark (M)	from crown)					
		Belly *(Bug)*, (59					
		from crown)	0/d	380–2000	560,3	68,27	35,32
		» »	0/d	380–700	561,2	60,40	31,71
		» »	45/0	421–1124	563,5	63,7	29,2
		» » (50					
		from crown)	45/0	421–1124	563,1	59,6	33,4
Caprimulgus	August 1925,						
europæus (♀)	Siberia (M)	Back *(Ryg)*, (110)	45/0	421–1124	584,4	22,8	11,1
Picus viridis (♂)	Nov. 1917,	Back *(Ryg)*, (160)	45/0	421–719	572,9	62,3	10,64
	Sweden (M)	Belly *(Bug)*, (160)	45/0	421–719	575,2	37,12	23,3
		Crown *(Isse)*	45/0	421–719	605,6	17,00	6,44
Picus viridis	Sept. 1921,						
(♂, ad.)	Estonia (M)	Back *(Ryg)*, (144)	0/d	380–2000	573,0	57,84	11,65
Alauda arvensis	Mar. 1904,						
(♂)	Denmark (M)	Back *(Ryg)*, (80)	45/0	421–1124	580,2	36,8	4,91
Anthus pratensis	Oct. 1915,						
	Denmark (M)	Back *(Ryg)*, (80)	45/0	421–1124	579,3	43,0	5,35

Species *(Art)*	Collected*) *(Indsamlet)*	Plumage area**) *(Fjerparti)*	Apparatus *(Apparatur)*	Measuring region (nm) *(Måleområde)*	Hue (nm) *(Farvetone)*	Purity (%) *(Renhed)*	Lightness (%) *(Lyshed)*
Aegithina tiphia	Oct. 1921, Siam (M)	Back *(Ryg)*, (55)	45/0	421–1124	572,4	58,3	9,07
		Back *(Ryg)*, (53)	0/d	380–2000	572,2	57,28	9,57
		Belly *(Bug)*, (62)	0/d	380–2000	573,5	78,77	40,61
		Belly *(Bug)*, (62)	45/0	421–1124	574,4	73,4	33,9
Prunella modularis	Sept. 1963, Denmark (RC)	Belly *(Bug)*	45/0	421–1124	572,6	10,35	37,71
		Back *(Ryg)*	45/0	421–1124	584,7	29,5	4,66
Prunella modularis (♂)	April 1922, Denmark (M)	Back *(Ryg)*	45/0	421–1124	582,0	36,6	5,99
		Throat *(Hals)*	45/0	421–1124	580,5	10,11	10,21
Erithacus rubecula (♀, *juv.*)	Dec. 1912, Denmark (M)	Throat *(Hals)*	45/0	421–1124	584,0	63,8	15,25
		Back *(Ryg)*	45/0	421–1124	580,6	31,2	6,32
Erithacus rubecula	Sept. 1963, Denmark (RC)	Back *(Ryg)*	45/0	421–1124	577,4	40,0	4,68
		Belly *(Bug)*	45/0	421–1124	570,5	10,6	33,4
		Throat *(Hals)*	45/0	421–1124	583,2	69,6	10,99
Turdus merula (♀, *juv.*)	Jan. 1964, Denmark (RC)	Back *(Ryg)*, (75)	45/0	421–719	585,7	18,7	2,85
		Back *(Ryg)*, (75)	45/0	421–719	580,6	20,2	3,19
Acrocephalus scirpaceus (♂, *sec.*)	Aug. 1912, Denmark (M)	Back *(Ryg)*, (62)	45/0	421–1124	582,2	43,6	10,30
		Belly *(Bug)*, (57)	45/0	421–1124	573,1	18,5	45,7
Phylloscopus trochilus (juv.)	Aug. 1963, Denmark (RC)	Belly *(Bug)*	45/0	421–1124	572,9	41,1	37,4
		Belly *(Bug)*	45/0	421–1124	574,0	44,0	35,3
		Back *(Ryg)*	45/0	421–1124	578,6	44,7	7,64
		Back *(Ryg)*	45/0	421–1124	577,3	35,68	8,07
Phylloscopus trochilus (juv.)	Sept. 1963, Denmark (RC)	Back *(Ryg)*	45/0	421–1124	578,4	38,54	6,65
		Belly *(Bug)*	45/0	421–1124	571,0	29,6	35,2
Phylloscopus trochilus (♀, *ad.*)	May 1891, Denmark (M)	Belly *(Bug)* (Yellowish part)	45/0	421–1124	577,3	29,02	29,90
		Belly *(Bug)* (Whitish part)	45/0	421–1124	573,3	17,94	35,30
Certhia familiaris	Nov. 1914, Denmark (M)	Belly *(Bug)*	45/0	421–1124	576	6,0	30,6
		Back *(Ryg)*	45/0	421–1124	582,7	31,2	8,00
Passer domesticus (♀)	Nov. 1963, Denmark (RC)	Back *(Ryg)*	45/0	421–1124	582,5	27,4	5,89
		Rump *(Overgump)*	45/0	421–1124	578,6	20,7	7,46
		Belly *(Bug)*	45/0	421–1124	581,5	14,3	23,03
Passer domesticus (♀)	Nov. 1887, Denmark (M)	Belly *(Bug)*, (55)	45/0	421–1124	580,5	17,5	27,0
		Back *(Ryg)*, (50)	45/0	421–1124	581,9	33,2	4,94
Garrulus glandarius (ad.)	Mar. 1964, Denmark (RC)	Back *(Ryg)*	45/0	421–1124	583,4	13,34	9,51
		Upper tail *(Haleoverside)*	45/0	421–719	585,4	3,32	1,40
		Rump *(Overgump)*	45/0	421–719	585,4	3,10	34,90
		Wing coverts *(Vingedækfjer)*	45/0	421–719	479,0	32,5	7,38

*) M: Stuffed Museum specimen *(Skindlagt museumseksemplar)*.
RC: Recently Collected *(Nylig indsamlet)*.

**) Number indicates length (mm) from tip of bill to measured plumage area.
(Tallet angiver afstanden (mm) fra næbspids til målt fjerparti).

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