

Effects of the adaptive background in the spectral sensitivity of budgerigars (*Melopsittacus undulatus*)

ABSTRACT

The objective of this project was to study if the adaptive background affects the spectral sensitivity of budgerigars (*Melopsittacus undulatus*) tested in bright light. Two budgerigars were trained, by associative learning with food rewards, in dual choice tests to discriminate monochromatic light stimuli of nine different wavelengths from an adaptive background with ultraviolet light (UV) content. The tests were repeated as the UV-light was removed from the background. There were significant differences in the three wavelengths at the UV/blue-range of the spectrum between the two adaptive backgrounds (paired-sample t-test, $n=8$, p-value for 355 nm, 0.0025; 370 nm, 0.0017; 415 nm, 0.0058). The data are compared with predictions from the receptor noise-limited model proposed by Vorobyev and Osorio in 1998.

1. Introduction

1.1 Bird colour vision

Animal colour vision has been studied in a variety of organisms such as birds that have been proven to have a highly evolved colour vision used for several behavioural tasks. Four types of cone pigments mediate bird colour vision: very short (UVS/VS, or violet/ultraviolet) with maximum absorbance peak at very short wavelengths (varies among species), short (SWS, or blue, λ_{\max} 430-463nm), medium, (MWS, or green, λ_{\max} 497-509nm) and long (LWS, or red, λ_{\max} 543-571nm) (Goldsmith and Butler, 2005) wavelength sensitive. A fifth type, the double

cone, mediates brightness vision (Kelber *et al.*, 2003) (Fig.1). The cones contain oil droplets in the inner segments that act as cut-off filters of light of short wavelengths, thanks to their high concentration of carotenoids (Hart, 2001; Bowmaker, 1980). Evidence provided by Vorobyev and colleagues (1998) has shown that oil droplets narrow the spectral tuning of the cones, which benefits colour vision.

The pigeon (*Columba livia*; Bowmaker *et al.* 1997) has been taken as a principal model for the study of tetrachromatic vision, i.e. colour vision mediated by four spectral types of photoreceptor. Other bird species studied for colour vision include Pekin robins (*Leiothrix lutea*; Maier, 1992), chickens (*Gallus gallus*; Osorio *et al.* 1999) and budgerigars (*Melopsittacus undulatus*; Goldsmith & Butler, 2003; Lind & Kelber, 2011). Some behavioural studies in pigeons (Kreithen & Eisner, 1978) and Pekin robin (Burkhardt & Maier, 1989; Maier, 1994) have shown that they are more sensitive in the near-UV than in the visible region of the spectrum.

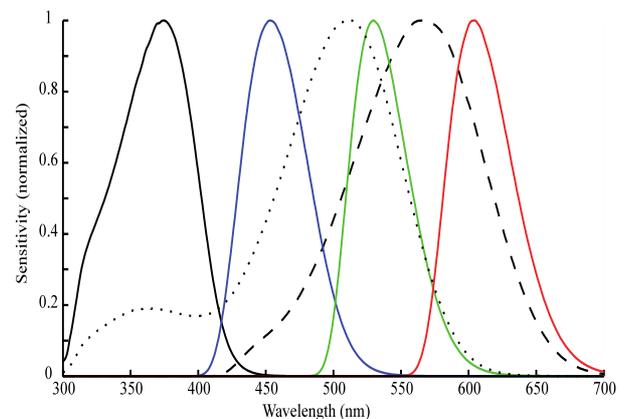


Figure 1 Pigment absorbance for the UV cone (black line), blue cone (blue line), green cone (green

line), red cone (red line), double cone (dashed line) and the rod (pointed line) of budgerigars (*Melopsittacus undulatus*).

Research has been made to assess the great variety of bird colouration and its role in bird ecology and behaviour. Studies have found that many birds possess UV reflection in their plumage and the research on birds' colour vision has evidenced that most of the birds are sensitive in the near UV. Ultraviolet vision has been studied in passerines like the Pekin robin *Leiothrix lutea* (Burkhardt & Maier, 1989), in Hummingbirds (Goldsmith, 1980), in pigeons *Columba livia* (Kreithen & Eisner, 1978) and in budgerigars *Melopsittacus undulatus* (Finger, 1995) among others. Ultraviolet stimuli have been suggested as cues for navigation, foraging and sexual selection (reviewed by Bennett and Cuthill, 1994).

The first hypothesis is supported by the fact that many birds use the sun compass for orientation and that apparently the pigeon has a region in the retina specialized in panoramic vision rather than spatial resolution; thought, this latter cannot be generalized to all birds. The second hypothesis suggests UV reflection as a cue for foraging behaviour. Burkhardt in 1982 found that seeds and fruits have waxy coats that reflect UV-light. Not only fruits but also flowers reflect UV light, which is of remarkable importance for pollinator birds such as the hummingbirds (Goldsmith, 1980). Finally, sexual selection in birds has been extensively investigated since birds' plumage is conspicuous and some species present sexual dimorphism.

UV vision used for sexual selection has been studied in hummingbirds, since these birds present a very varied coloration and are sexually dimorphic (Goldsmith, 1980). Bleiweiss (1994) investigated how UV vision participates in three sunangel hummingbirds' communication and found that some sexual dimorphisms are only visible in the UV, which might be possible also for other species. A recent study by Mullen and Pohland (2008) examines the correlation

between UV peaks in feathers of 1000 birds with violet and ultraviolet sensitive cones. The study found that birds with UV vision more likely possess UV reflective plumage or skin. While, for birds that have less sensitivity for UV light, such as those with nocturnal habits, no UV reflectance has been found. Regarding the psittaciform family, 143 species were surveyed, in which 140 were found to have UV reflectance in at least one part of their body.

1.2 Receptor noise-limited model

Vorobyev and Osorio (1998) proposed a model of animal colour vision - the receptor noise-limited model - that can be used to predict behavioural performance as well as to make inferences about mechanisms of vision, providing insights of vision ecology and eye design. The model assumes that photoreceptor noise is the limiting factor of colour discrimination. There are three assumptions for the model: first, colour is coded by $n-1$ unspecified colour-opponent mechanisms, for receptor channels n . Second, colour opponent mechanisms present no signal for stimuli that differ from the background just in intensity. And third, thresholds are set by receptor noise, and not by opponent mechanisms.

1.3 Measuring colour vision thresholds

There are three ways of exploring colour vision mechanisms and measuring colour vision thresholds: wavelength discrimination, the spectral sensitivity test and colour matching. For the first method, very saturated wavelengths are needed, which are easily obtained using monochromatic light stimuli. Here, the test is used to determine the minimum difference needed between two monochromatic wavelengths to define them as two separate wavelengths. Meanwhile, spectral sensitivity is determined as the inverse of the minimal intensity of monochromatic light needed for detection on

an achromatic or dark background. One advantage of spectral sensitivity is that it provides thresholds about one point in colour space, which means that to model it, assumptions about changes of threshold values across colour space are not needed. A disadvantage of wavelength discrimination is that due to the use of highly saturated wavelengths, the opponency channels may get saturated yielding non-linearities that complicate modelling. Due to the above, spectral sensitivity is found to be more suitable for quantitative analysis (Kelber *et al.*, 2003).

The third method, *colour matching*, provides the number of receptors used for colour vision and does not require known receptor spectral sensitivities. It is based instead on the principle that “if n receptor signals are compared in colour vision, any spectral stimulus can be matched with a specific mixture of n lights” (Kelber *et al.*, 2003). Monochromatic stimuli have been extensively used to demonstrate colour vision; the theory behind states that if changes in relative intensity of two monochromatic lights do not have an effect on the animal’s choice, then it must be using colour vision. Monochromatic light provides precise stimulus intensity and spectra, which are requirements for measuring thresholds (Kelber *et al.*, 2003).

Spectral sensitivity in birds has been studied in bright light but little has been done changing the adaptive background. Maier (1992) studied the spectral sensitivity including UV-light in the adaptive background of the Pekin robin (*Leiothrix lutea*). Two levels of illumination were tested, revealing a high sensitivity in the UV under photopic illumination and a higher overall sensitivity under mesopic illumination. Apart from the higher sensitivity under reduced illumination, a peak at 500 nm was obtained, suggesting the participation of rod pigment.

Goldsmith and Butler (2003) studied spectral sensitivity in Budgerigars under photopic

illumination. The results are consequent with previous findings in other species; the birds have higher spectral sensitivity in the UV (due to the low content of UV-light in the background) and they predict that the sensitivity would be less pronounced under natural sunlight. Goldsmith and Butler (2003) calculated the spectral sensitivity of budgerigars based on the model of receptor noise-limited model proposed by Vorobyev and Osorio (1998) (Fig. 2).

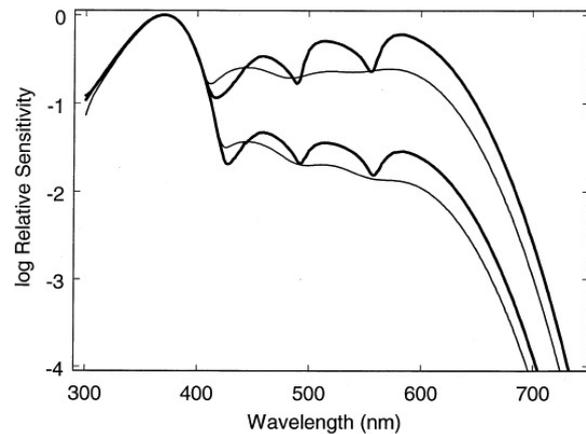


Figure 2 Calculated spectral sensitivities under bright blue skylight (upper curves) and fluorescent light (lower curves). Thick lines represent retinas containing coloured oil droplets; thin lines represent visual pigments unscreened by oil droplets. Figure modified from Goldsmith and Butler (2003).

To my knowledge, no studies have tested how spectral sensitivity changes with different backgrounds, which is what motivates the present study. Experiments were carried out to evaluate the effects of different backgrounds on the spectral sensitivity using budgerigars as a study model.

1.4 *Melopsittacus undulatus*

The budgerigar (*Melopsittacus undulatus*) also known as the shell parakeet is a member of the Psittacidae family. It is native from inland Australia where inhabits mostly arid regions but also shrubby and open woodlands. It has diurnal and nomadic habits and feeds on insects and seeds (Wyndham,

1978). It has been found that parakeets possess fluorescent coloration and UV reflection in their plumage; the latter has been suggested as a cue for mate choice (Pearn *et al.* 2001). The number of UV cones is less than 10% in Budgerigars and in many species of passerines (Goldsmith & Butler, 2003). A vast amount of work on bird vision has been done and the budgerigar has been used as a study model (Lind and Kelber, 2009, Lind and Kelber, 2011). For this reason, this bird species was chosen for the present study, for the purpose of getting a deeper understanding of its colour vision.

This project studies the effect of the adaptive background on the spectral sensitivity of budgerigars (*Melopsittacus undulatus*) under bright light conditions. Two budgerigars were trained to discriminate monochromatic light stimuli from an adaptive background containing white and UV-light and one with just white light. Little is known about the effects of the adaptive background on the spectral sensitivity and the aim of this project is to give some insight in this matter.

2. Materials and methods

2.1 Birds

Two male budgerigars (*Melopsittacus undulatus*) were used for this study. During the experimental days, the birds (Bud and Hampus) were fed only during the behavioural testing with seed mixes enriched with vitamins. Extra food together with fruits and vegetables was provided during the days where no behavioural testing was carried out. The birds were kept in separate cages in a room with three more conspecifics under a 12 h dark/12 h light cycle.

2.2 Experimental cage

The training and the behavioural tests were carried out in a rectangular cage with dimensions 980 mm × 845 mm × 652 mm

(length, width, height). The experimental cage was placed in the same room as the birds' housing cages and was enclosed by a black curtain maintaining complete darkness. Keeping the birds together allowed them to vocally communicate, reducing the birds' stress. The background light was provided by four white light emitting diodes (LEDs; LZC-00NW40, LED Engin Inc., San Jose, USA) and four ultraviolet (UV) LEDs (LZ4-00U600, LED Engin Inc., San Jose, USA) located above the cage. The tests were carried out first with both white LEDs and UV LEDs contributing to the adaptive background (Fig. 3). The tests were then repeated with only white LEDs (Fig. 3). The intensity of the LEDs was maintained with a 175 W dual power supply (CPX200, Thurlby Thandar instruments Ltd., Huntingdon, England) at approximately 26,39 V and 5,70 A for the white light and 18,20 V and 2,08 A for UV light. The luminance of the cage was 1085 Lux measured from the cage floor at the centre of the cage (490 mm from the Perspex board and 422 mm from the side of the cage). Since the UV-light radiance initially changed with time due to warming up of the lighting equipment, the lamp was turned on during an hour prior to the test trials to ensure stable lighting conditions. The stimuli were presented at one end of the cage behind a Perspex board covered at both sides with white diffusion filters (a combination of LF416 3/4, LF251 and LF252 1/8, LEE; LEE Filters Central Way, Walworth Business Park, Andover, Hampshire, SP10 5AN, UK). The stimuli were observed from an initial position (perch) at 775 mm from the stimulus windows. The stimulus windows were separated 280 mm on the horizontal plane and were located at 385 mm height. The diameter of the light stimuli was 110 mm and the visual angle from the starting perch was 8.12°. Two perches and two boxes with hatches filled with the seed mix were placed exactly below the stimuli presentation windows at 220 mm height).

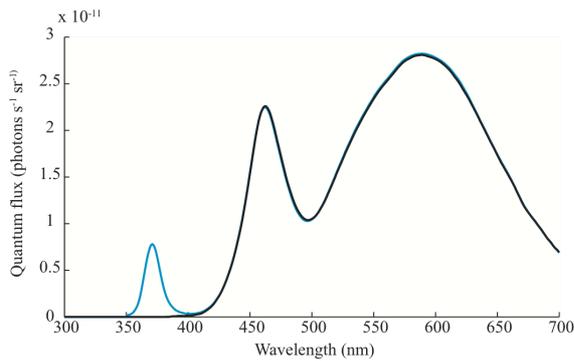


Figure 3 Radiance of the background upon which the monochromatic stimuli were projected. The two curves represent the radiance measured of UV (blue) and white LEDs (black).

2.3 Stimuli

Monochromatic stimuli were provided by a monochromator (TILL Polychrome V software Polycon 3.0 version 3.0.12, Till photonics GmbH, Germany). The intensity of the monochromatic light was measured by a spectroradiometer (RSP900-R; International Light, Peabody, MA, USA). Neutral density filters (ND) were used to increase the intensity range of the monochromator. Nine different wavelengths were used for the first experiment with UV-light in the background (355, 370, 415, 450, 505, 535, 575, 605 and 640 nm) and four for the experiment without UV-light (355, 370, 415 and 575 nm; the last one used as a control). The nine wavelengths tested were chosen based on predictions of the maxima and minima in the receptor noise-limited model proposed by Vorobyev and Osorio (1998). All the wavelengths were presented at 10 nm FWHM (full width at half maximum) except for 415 and 640 nm, which were presented at 15 nm FWHM for Hampus due to the failure of discrimination during the training with 10 nm FWHM. Stimulus intensities at all wavelengths were measured using an International light spectroradiometer PRS900-R (International Light Technologies Inc., Peabody, Massachusetts, USA).

2.4 Training and behavioural test procedure

The birds were trained, to associate stimuli with a food reward, and to discriminate them from the background. Bud and Hampus were fed only when tests were carried out, therefore the reward was the motivation used to obtain results. Initially the birds were familiarized with the experimental cage, the stimulus and reward. Each training session started with the bird at the initial perch hearing a two-tone auditory signal just preceding the presentation of the stimulus. The stimuli were presented one at a time; the birds were trained to choose (right/left) the perch of the feeding box below the stimulus shown by flying towards it to gain the reward. The stimuli were presented only when the birds were facing the presentation board and choice was always made while sitting at the initial perch. The criterion for including the birds in the behavioural tests was a 20-trial test using stimuli of 535 nm wavelength, 10 nm FWHM, at two levels of intensity (100 and 70%, see below). Once the birds reached at least 80% correct choices at both stimulus intensities in two subsequent evaluation tests, the birds were considered to be completely trained and ready for testing.

The behavioural tests commenced using stimuli of 535 nm wavelength. Before each session, the birds were allowed to adapt to the luminance level for 5 min. The threshold of detection was estimated by starting the tests with 100% intensity (e.g. 6.15×10^{12} number of photons at 535 nm wavelength) and decreasing it using the two-down, one-up staircase procedure (Fig. 3). This method targets the 70.7% of performance level and gives an estimate of the threshold by calculating the average of the reversals (turnarounds) in the adaptive track (Leek, 2001). The stimuli were presented randomly to the left and right in all training and test sessions to exclude the risk of bias and ensure that only the detection of the stimulus could be used as a cue to receive the food reward. The stimulus presentation side was randomized using the series of combined *left*

and *right* described by Gellermann (1933). The rewards consisted of access to the food for 7-10 s after which the feeder was closed and the stimulus turned off. Incorrect choices were not punished, but simply followed by turning off the stimulus and the bird had to return to the perch in order to start a new trial. A complete test consisted of 40 trials. The birds were trained and tested individually in two sessions (2 tests each) per day in the morning and afternoon (depending on the birds' willingness to respond).

The same procedure was used to test the other eight wavelengths. A control, consisting on presentation of 10 stimuli at 100% intensity was carried out before each test. The same criterion of minimum 80% correct choices was required to start the test. The whole procedure was repeated to get four data sets at each wavelength with and without UV-light in the adaptive background. The intensity threshold (in number of photons) for detection was determined by calculating the average from all the reversals (turnarounds) during the last 20 trials for each test. For the wavelengths tested with and without UV-light (nine and four wavelengths respectively) in the adaptive background, four data sets were obtained and the intensity threshold calculated. The spectral sensitivity was calculated as the inverse of the intensity threshold. The spectral sensitivities of the four sets were averaged and the mean and the standard error of the mean were plotted to get the spectral sensitivity curve for each bird.

3. Results

3.1 Training and behavioural tests

The choice for the correct stimulus was always made while the birds were standing at the initial perch. When the intensity of the stimulus light was approaching the bird's intensity threshold, the time for making the choice increased since they walked the perch for some seconds probably to better see the stimulus and make the correct choice. In

other cases in the same situation, when an incorrect choice was already made, just before landing on the wrong feeder's perch the choice was corrected with a quick turn towards the correct one. These choices were counted as correct. Examples of the two-down, one-up staircase procedure are shown in Fig. 4.

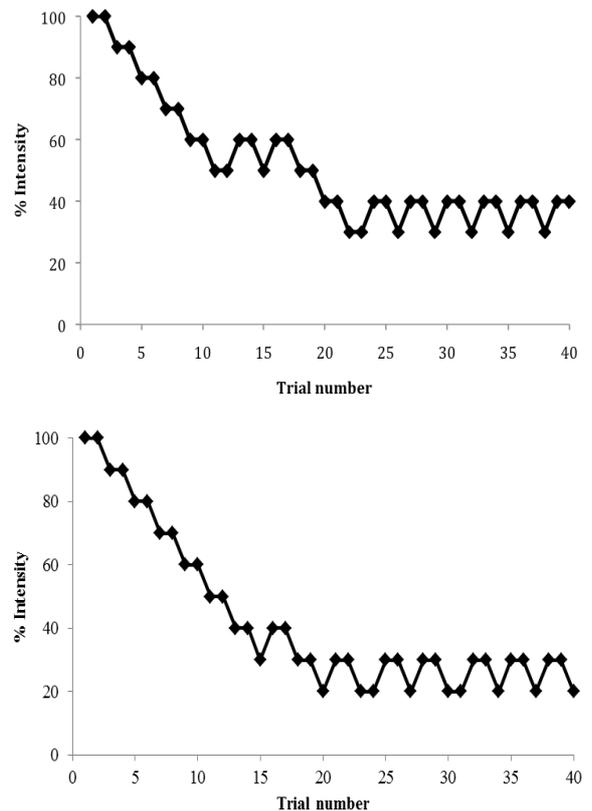


Figure 4 Two-down, one-up staircase procedure. Test using stimuli of 505 nm wavelength, 10 nm FWHM under adaptive background with UV-light for Hampus (Top) and Bud (Bottom). Each point represents the reversals (turnarounds) in the adaptive track over a 40-trial test.

3.2 Spectral sensitivity with UV-light in the adaptive background

The spectral sensitivity curves of both birds for both scenarios are shown in Fig. 5. Bud's spectral sensitivity curve has four peaks of sensitivity with maximum values in the UV at 370 nm, in the blue at 450 nm, in the green at 535 nm and in the red at 605 nm. The spectral sensitivity curve for Hampus shows three distinct peaks: in the blue at 450 nm, in

the green at 535 nm and in the red at 605 nm. Spectral sensitivity for both birds was higher in the UV (355 and 370 nm) and lower in 415 and 640 nm. The normalized sensitivities of photoreceptors are shown in Fig. 1.

To evaluate if there were differences between the spectral sensitivities of both birds t-tests were carried out. None of the spectral sensitivities were significantly different between the birds when tested with UV-light in the adaptive background. There was one exception at 605 nm (paired-sample t-test, $n=4$, p-value 0.0285) and this was due to an outlier in Bud's second set.

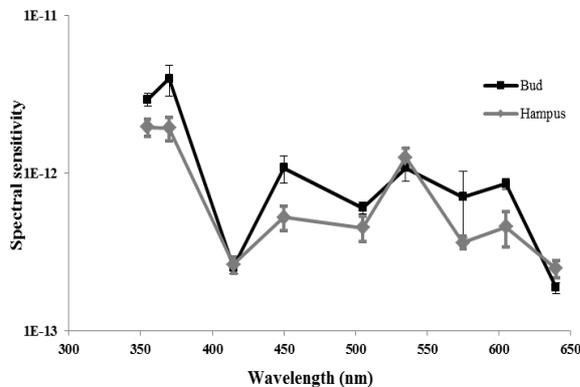


Figure 5 Spectral sensitivity curves (mean \pm standard error of the mean) for Bud (black line) and Hampus (grey line) for adaptive background without UV-light for nine wavelengths.

3.3 Spectral sensitivity without UV-light in the adaptive background

For the tests without UV-light in the adaptive background, there were significant differences at 370 and 415 nm (paired-sample t-test, $n=4$, p-values 0.0260 and 0.0159 respectively) with Bud being more sensitive than Hampus. The spectral sensitivity curve for both birds without UV-light is shown in Fig. 6 and 7. In Fig. 7 there is an evident shift in the spectral sensitivity for both birds when UV-light was removed from the adaptive background. Both show a peak value at 370 nm and a minimum at 415 nm. Bud's results show a higher shift than Hampus at 415 nm that was the lowest value

for both birds under the UV-light experiment. The figure also shows the control wavelength (575 nm) where sensitivity is very similar to the values obtained when tested with UV-light in the adaptive background.

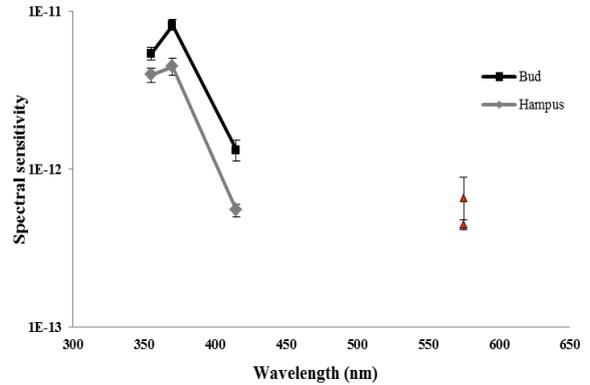


Figure 6 Bottom: Spectral sensitivity curves for Bud (black line) and Hampus (grey line) for adaptive background with UV-light for four wavelengths. The red-marked point represents the control wavelength at 575 nm.

3.4 Differences between scenarios

Paired t-tests were carried out to evaluate if there were significant differences between spectral sensitivities when changing the adaptive background by removing the UV-light (Fig. 7). Considering that both birds were being tested to see if the composition of the light of the adaptive background affected the spectral sensitivities, the data for both birds were combined and t-tests were performed for each wavelength 355, 370 and 415 nm and the control (575 nm). The samples were first tested for normal distribution using Lilliefors test (MATLAB R2011b, The MathWorks Inc., Natick, MA, USA, 2000). All the samples were normally distributed, except for the set of values at 575 nm. All the spectral sensitivities for short wavelengths were significantly different between scenarios (355 nm, paired-sample t-test, $n=8$, p-value 0.0025; 370 nm, p-value 0.0017; 415 nm p-value 0.0058). There was no significant difference for the control wavelength (paired-sample t-test, $n=8$, p-value 0.8843).

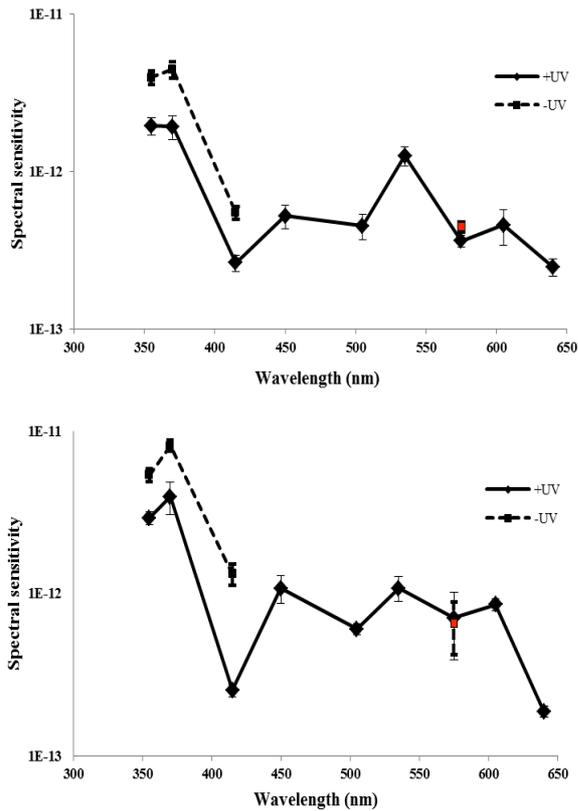


Figure 7 Spectral sensitivity curves with (mean \pm standard error of the mean) of Hampus (top) and Bud (bottom) for adaptive background with UV-light (Continued line) and without UV (dashed line). The red-marked point represents the control wavelength at 575 nm.

4. Discussion

4.1 Spectral sensitivity

The results for the spectral sensitivity tested under the adaptive background containing UV-light, showed a significant difference on the spectral sensitivity between the two study subjects at 605 nm. This was due to an outlier in Bud's second replica. Other than that, there were no significant differences between the spectral sensitivities of Bud and Hampus in the other eight wavelengths tested. For the wavelengths tested under the adaptive background without UV-light, the results showed significant differences between the spectral sensitivities of Bud and Hampus in two of the three wavelengths. These differences, at 370 and 415 nm (p-values 0.0260 and 0.0159 respectively) might

be due to differences in the adaptation of the UV cones of each bird. The data for both birds were pooled to evaluate the effect of UV in the adaptive background on the spectral sensitivity. There is an evident shift in the spectral sensitivity curves between both scenarios for both birds (Fig. 7) and is supported by significant p-values obtained for 355, 370 and 415 nm. An explanation for this is that receptors adapt to the background to ensure colour constancy i.e. a receptor receiving a high amount of light from the background regulates its sensitivity compared to other receptors that receive less light (Goldsmith and Butler, 2003).

The results also show that highest spectral sensitivities were obtained in the UV-range for both birds in both of the scenarios. Behavioural experiments in the homing pigeon (Kreithen & Eisner, 1978) and in the Pekin robin (Burkhardt & Maier, 1989; Maier, 1994) have shown birds to be more sensitive in the near-UV than in the visible region of the spectrum. These findings agree with the results obtained in the present study where the highest spectral sensitivities were found at 370 nm followed by 355 nm in both birds, in both scenarios. This higher spectral sensitivity is hypothesized to be an effect from little UV in the background, as described by Goldsmith and Butler (2003). The theory behind this high sensitivity at the UV-range was studied by Goldsmith (1980), where he described UV sensitivity in three species of hummingbirds. The findings showed that the birds were able to distinguish wavelengths in the near ultraviolet (370 nm) and the structures behind this may be the oil droplets. In pigeons, Kreithen and Eisner hypothesized that fluorescence is the mechanism behind the pigeon's ability to detect UV and that UV light is thought to reach the retina directly due to that the bird's lenses are transparent to UV light. It is known that in budgerigars, the lens transmits UV, fluorescence plays no role (Lind and Kelber, 2009).

Previous studies on *Melopsittacus undulatus* colour vision by Goldsmith and Butler have

assessed the spectral sensitivity under known spectral composition of the adaptive background. On a study in 2003 the receptor noise-limited model proposed by Vorobyev and Osorio (1998), was tested for budgerigars. This model states that the threshold is set by noise originating in the receptors and it was previously tested for the Pekin robin and in honeybees (*Apis mellifera*). The results showed a higher sensitivity in the near-UV as it was seen in other species of birds. They conclude that this higher sensitivity is due to the low UV-light content in the background in the laboratory that in natural conditions the sensitivity should be more even throughout the spectrum.

4.2 Receptor noise-limited model

Fig. 8 shows the spectral sensitivities for the two budgerigars under an achromatic adaptive background with and without UV-light content correlated with the prediction by the receptor noise-limited model (Vorobyev & Osorio, 1998). The values obtained in the present study for the background with UV-light are very similar to those predicted by the model, being closer the values for the maxima values than the values for the minima. It shows also the same patterns, the peaks belong to the same wavelengths and this happens for both birds. While, for the predicted spectral sensitivities in the UV region without UV-light in the background, the values differ more that one logarithmic unit. One prediction of this model is that the receptor output is influenced by the spectral composition of the background light to which the animal is adapted. If this radiation has relatively little energy in the near-UV, the UV cones will be little adapted and therefore will make a prominent contribution to measurements of photopic spectral sensitivity (Goldsmith & Butler, 2003).

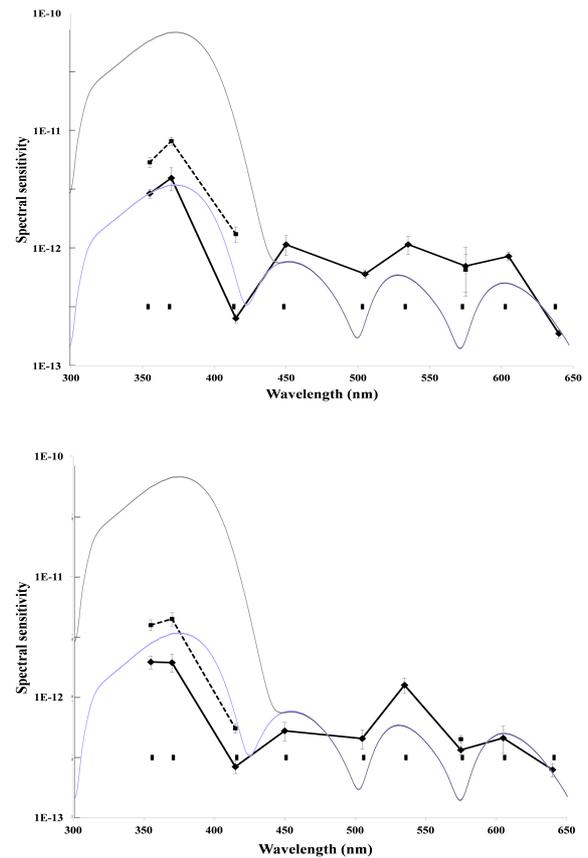


Figure 8 Predicted (curved lines) versus observed (straight lines) spectral sensitivities for Bud (top) and Hampus (bottom) in both scenarios. The predicted curves are based on the receptor noise-limited model proposed by Vorobyev and Osorio (1998) under background light with UV-light content (upper curve) and without UV-light content (lower curve). Observed spectral sensitivities: background with UV content (dashed line) and without UV content (continued line).

This model is a fundament of a vast number of ecological studies (in which colour vision is predicted in birds); the model's validity is from comparisons between the model and spectral sensitivity tests. Thus, the kind of tests made in the present study is of high importance for many future studies.

4.3 Behavioural experiments

The maximum sensitivity peak in the UV for Hampus was not reached for the experiment with UV in the adaptive background as it is shown in Fig. 5. In order to get this peak, a

shorter wavelength than 355 nm needs to be tested. In this scenario, there were no statistical differences between Bud and Hampus, not even in the UV where the peak for maximum intensity for Hampus was not reached. Despite the motivation, the bird's willingness to respond and focus were not always constant and could have introduced variation in the samples.

4.4 Ecology

Budgerigars are sexually dimorphic, monogamous, diurnal and feed on insects and seeds. Their cheek patch and the cere reflect highly UV-light as well as their green, blue and yellow feathers. Like passerines, they have a UV sensitive cone, with maximum peak of sensitivity at 371 ± 5 nm (Bowmaker et al. 1997). Pearn and colleagues (2001) suggested UV reflectance and fluorescence as cofactors for mate choice. The study found UV reflection in the plumage as a cue for mate choice and that fluorescence does not seem to influence. The findings of this study agree with the previous studies showing UV vision in this species. This study provides evidence of how well sexual UV-traits can be detected against green foliage or a blue sky (the latter having much more UV in the background).

5. Conclusions and future studies

The adaptive background affected the spectral sensitivity on both birds. This can be due to the fact that receptors adapt to the background to ensure colour constancy. This means that a receptor that is receiving a high amount of light from the background regulates its sensitivity compared to other receptors that receive less light. The study provides evidence of how the spectral sensitivity is affected by the adaptive background as well as how well sexual UV-traits can be detected since it has been found that they use UV reflection and hence UV vision for sexual selection.

Future studies can be addressed to test different types of adaptive backgrounds with lower intensities than the one already tested in this project affecting the spectral sensitivity. The results can be compared with the present results and observe that while the adaptive background is changed the transition from chromatic vision to achromatic processing is evident. Other approaches could be changing the spectral composition (e.g. more or less red light) in the background and observe how the spectral sensitivity changes.

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