# Behavioural thresholds of blue tit colour vision and the effect of background chromatic complexity

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Blue tit colour vision just-noticeable-differences

ABSTRACT

Vision is a vital attribute to foraging, navigation, mate selection and social signalling in animals, which often have a very different colour perception in comparison to humans. For understanding how animal colour perception works, vision models provide the smallest colour difference that animals of a given species are assumed to detect. To determine the just-noticeable-difference, or JND, vision models use Weber fractions that set discrimination thresholds of a stimulus compared to its background. However, although vision models are widely used, they rely on assumptions of Weber fractions since the exact fractions are unknown for most species. Here, we test; i) which Weber fractions in long-, middle- and shortwave (i.e. L, M, S) colour channels best describe the blue tit (*Cyanistes caeruleus*) colour discrimination, ii) how changes in hue of saturated colours and iii) chromatic background noise impair search behaviour in blue tits. We show that the behaviourally verified Weber fractions on achromatic backgrounds were L: 0.05, M: 0.03 and S: 0.03, indicating a high colour sensitivity. In contrast, on saturated chromatic backgrounds, the correct Weber fractions were considerably higher for L: 0.20, M: 0.17 and S: 0.15, indicating a less detailed colour perception. Chromatic complexity of backgrounds affected the longwave channel, while middle- and shortwave channels were mostly unaffected. We caution that using a vision model whereby colour discrimination is determined in achromatic viewing conditions, as they often are, can lead to misleading interpretations of biological interactions in natural – colourful – environments.

**Key-words:**

Avian vision model, *Cyanistes caeruleus*, discrimination thresholds, pavo, receptor-noise, vision testing, Weber fraction

## 1. INTRODUCTION

Animal colour vision embodies countless forms of spectral discrimination abilities (Chittka & Menzel 1992, Bowmaker 1998, Kelber & Osorio 2010). Animals use colours to guide their behaviour and to acquire information in their environment (Maynard-Smith & Harper 2003, Stevens 2013), which has been demonstrated extensively in behavioural experiments and observations from nature (Endler 1993, Ham et al. 2006, Kelber and Osorio 2010). Colour vision is utilized for example in foraging, mate choice, signalling and navigation (Hunt et al. 1998, Vorobyev 2004, Vincze et al. 2015). To understand how animals with different perceptual capabilities see the world, researchers use vision models that are based on photoreceptor quantum catches and receptor deposition or relative frequencies in the study species' retinas (Gawryszewski 2018). However, in order to verify how well vision models work, it is essential to link the knowledge of well-studied organisms to their behaviour.

Avian colour vision is considered one of the most elaborate and well-adjusted systems for sensing colours (Bowmaker et al. 1997, Bowmaker 2008, Osorio and Vorobyev 2008). Typically, the bird retina has rod cells for sensing changes in luminance and four types of single cone cells for sensing of colour with maximum sensitivities roughly in the ultraviolet, blue, green and red (Bowmaker 2008). In addition, birds have double cones which appear to be sensitive to long wavelength light, but are assumed to serve achromatic tasks, such as luminance and motion sensing, instead of chromatic vision (Osorio and Vorobyev 2005). All cone cells in avian retina have either coloured or clear oil droplets (Bowmaker et al. 1997, Bowmaker 2008, Osorio and Vorobyev 2008), which filter shorter wavelengths, generally displacing the maximum sensitivity of each cone cell type to longer wavelengths. The contributions of both chromatic and achromatic vision are important in visual perception, since objects can be visually discriminated from the background and other objects based on the sensed differences in colour or luminance (Lind et al. 2014, Olsson et al. 2018).

Blue tits (*Cyanistes caeruleus*), of the tit family Paridae, are small passerine birds whose visual system has been studied in detail, with their visual model used widely (Hart et al. 2000, Stoddard & Stevens 2011, Dell'Aglio et al. 2018, Henze et al. 2018, van den Berg & Troscianko et al. 2020). They are a resident species in Europe, parts of the Middle East and western parts of Russia (IUCN 2017). Information on the physical attributes of the blue tit visual system is based on the study by Hart et al. 2000. The following single and double cone cell ratios and sensitivities were measured from one blue tit. UV sensitive SWS1 cones represent 7.6 % of total cone population, blue sensitive SWS2 cones 14.6 %, MWS cones 20.4 % and LWS cones 20.5 %. The remaining 36.9 % of the cone population are double cones. Mean maximum sensitivities for the single cone cells are: SWS1 - 371 nm with transparent oil droplet that cuts off light from < 330 nm, SWS2 - 448 nm with clear oil droplet that cuts off light from 413 nm, MWS - 503 nm with yellow oil droplet that cuts off light from 508 nm and LWS - 563 nm with red droplet that cuts off light from 573 nm. The total spectral sensitivity of blue tits seems to cover wavelengths below 330 nm and above 600 nm; plots of blue tit spectral sensitivity are found in Hart et al. (2000) and Henze et al. (2018).

The receptor noise limited (RNL) vision model by Vorobyev and Osorio (1998) is one of the most commonly utilized vision models (Stoddard & Stevens 2011, Outomuro et al. 2017, Caves et al. 2018, Dell'Aglio et al. 2018, Gawryszewski 2018). The RNL model assumes that colour discrimination thresholds are set by light conditions and photoreceptor noise, which limit colour opponency channels controlling the interpretation of colour (Vorobyev and Osorio 1998, Kemp et al. 2015, Gawryszewski 2018). An important prerequisite for the model is that the stimulus should be large enough (in terms of size) and measured in bright light, and with the condition that the background of the stimulus is achromatic (Vorobyev & Osorio 1998). The RNL model gives an estimate of the smallest colour difference which study subjects are assumed to distinguish, i.e. the just-noticeable-difference (JND) value. The model enables

87 researchers to deduce how other animals perceive different colours in nature and how apparent
88 colours are for the studied species. In the model, the necessary parameters are photoreceptor
89 sensitivities, photoreceptor proportions in the retina, light quality of the test situation and
90 crucially, information on the smallest differences the study species is assumed to discriminate
91 from the background (i.e. the model parameter called Weber fraction).

92 Here, we use the receptor-noise limited RNL model by Vorobyev and Osorio (1998) to validate
93 how well the vision model predicts animal behaviour in different viewing backgrounds. We
94 conduct a behavioural assessment of colour perception of a widely studied model organism,
95 the Eurasian blue tit (*Cyanistes caeruleus*). The study consists of two parts that are meant to
96 provide us with information on blue tit colour discrimination thresholds (i.e. Weber fractions)
97 and suprathreshold (i.e. signal strength above the threshold for discrimination) colour
98 perception (Fig. 1 a). We shed light onto how the model predicts animal behaviour on
99 chromatic backgrounds, although this is not what the model is designed to do by default. That
100 is, however, how many studies have utilized the model in its common use to interpret biological
101 interactions (Siddiqi et al. 2004, Maan and Cummings 2012, Schultz and Fincke 2013, McLean
102 et al. 2014).

103 We ask: i) which Weber fractions in long-, middle- and shortwave (i.e. L, M, S) colour channels
104 best describe blue tit (*Cyanistes caeruleus*) colour discrimination, ii) how do changes in hue of
105 saturated colours influence signal search behaviour of blue tits and iii) how does background
106 noise (in terms of chromatic complexity) impair signal search behaviour of blue tits in different
107 colour channels? This approach excludes testing of UV sensitivity of the tetrachromatic birds
108 but describes how the three colour bands also visible to humans are perceived through the blue
109 tit visual system. In addition to Weber fractions of blue tits, we examine how signal strength
110 affects signal search in complex chromatic backgrounds and how background noise – inspired

by the puzzle video game Tetris (Pajitnov 1984) – affects the search effort of saturated colour signals. We also test how the discrimination thresholds examined in the first experiment describe blue tit behaviour in saturated chromatic environment. As our null hypothesis, we assume that Weber fractions are constant when colour intensity (saturation) is increased and that changes in hue do not change blue tit search behaviour (Fig. 1 a). Also, we hypothesise that background noise impairs blue tit signal search by elongating searching time in all colour channels. This approach, to our knowledge, is the most up-to-date study investigating colour discrimination thresholds in blue tits, whose vision model is broadly used in biological studies without behavioural validation of model assumptions.

## 2. MATERIALS AND METHODS

### 2.1 The RNL model and Weber fraction

In the RNL model, the information of the smallest differences study subjects can discriminate are given in photoreceptor specific Weber fractions, which in vision studies are considered to be equivalent to (and often referred as) the amount of noise in each photoreceptor type (Lind et al. 2014, Olsson et al. 2018). Weber fractions describe the smallest perceivable intensity difference $\Delta I$ – also referred as the just-noticeable-difference (JND) value 1, or as perceptual geometric Euclidean distance ($\Delta S$) value 1 – for a given stimulus of intensity $I$ in a given sensory system. The Weber fraction is a part of a psychophysical rule called the Weber law, in which it is stated that a just-noticeable change in the magnitude of a given stimulus is proportional to the original stimulus (Gescheider 2013). This proportion is called the Weber fraction and is assumed to be constant in all similarly perceived stimuli. When the intensity of a stimulus is higher, the perceivable just-noticeable change is proportionally higher according to the constant Weber fraction.

134 $$\omega = \frac{\Delta I}{I}$$

135 where $\omega$ is the Weber fraction, $I$ is the intensity of stimulus and $\Delta I$ is the smallest perceivable
136 intensity difference in that stimulus. In the RNL model, the Weber fraction represents the noise
137 present in a given receptor channel that combines the output of several photoreceptors of the
138 same spectral type (Vorobyev and Osorio 1998, Lind et al. 2014). The model combines signals
139 from several receptor channels in opponent mechanisms in order to deduct chromatic signals.
140 In the model, intrinsic noise in each single photoreceptor cell is assumed to be equal and the
141 noise of each receptor channel inversely proportional to receptor densities in the retina.

142 $$e_i = \frac{\sigma_i}{\sqrt{\eta_i}}$$

143 where $e$ is photoreceptor noise, σ is the coefficient of variance of noise in a photoreceptor cell,
144 η is the relative density of that receptor type in the retina and $i$ the photoreceptor type. Often
145 the noise of only one photoreceptor type is reported, in which case the noise of other receptors
146 can be calculated with the knowledge of relative abundances of photoreceptor types (see for
147 example Olsson et al. 2018).

148 The RNL models are often utilized with Weber fraction parameters that are not validated, in
149 which case the Weber fractions of 0.05 and 0.10 for long-wave sensitive channel are most
150 commonly used (Siddiqi et al. 2004, Stoddard and Stevens 2011, Maan and Cummings 2012,
151 Bitton et al. 2017, Dell'Aglio et al. 2018). The Weber fraction 0.05 for LWS channel was first
152 introduced by Siddiqi et al. (2004) for their study subject as an intermediate value of human
153 (0.02) and bird (0.10) LWS channels (Wyszecki and Stiles 1982, Vorobyev and Osorio 1998).
154 Studies using assumed Weber fractions are considered reliable but they do not accurately
155 describe how the study species perceive colours in nature, which can be done with Weber

fractions that are determined using controlled behavioural experiments. The Weber fractions of a study species can be inferred by testing behavioural discrimination thresholds of different colours (Olsson et al. 2018). Discriminability of the tested colours are then modelled with the RNL model by adjusting the Weber fraction parameter in such a way that the behaviourally validated smallest perceivable intensity difference – the JND 1 – fits the modelled discrimination threshold. Behavioural limits for just-noticeable-difference varies in studies considering visual perception and is commonly chosen between 50-75 % of the population detecting the difference, depending on the style and overall difficulty level of the test for the studied species (Treutwein 1995, Vorobyev et al. 2001, Lind et al. 2014, Olsson et al. 2015, Lind 2016, Cheney and Green et al. 2019). In this study, a limit of 75 % was chosen.

## 2.2 Experimental conditions, preparations and pretraining

The experiments were conducted in Konnevesi research station. Wild blue tits were used with permission authorized to the research group of Johanna Mappes from the Central Finland Centre for Economic Development, Transport and Environment (VARELY/294/2015) and license from the National Animal Experiment Board (ESAVI/9114/04.10.07/2014).

Blue tits were kept individually in the research station aviary. Food and water were supplied to the birds ad libitum. Birds were sequentially trained to carry out the visual search task prior to the experiments. Training protocol required the birds to 1) retrieve a reward placed on the top of a training stimulus (a printed, highly saturated red, green, blue or black dot on a paper sheet), 2) fetch a reward from a hole pierced through the training sheet, 3) search for a reward underneath the sheet (i.e. placed inside wells) with only a small hole pierced through the paper to aid the search, 4) search for a reward only on a visual basis using the coloured stimulus as a cue to the reward placed underneath the sheet. To get the reward birds had to find the visual stimulus and pierce through the sheet to access it.

Tests were conducted in a specific experimental arena with customized Philips Hue -light set to ensure daylight resembling light conditions (Fig. A1, Appendix A) excluding UV wave lengths. The experimental arena was a plywood box (circa 60x60x70 cm) which had a front wall of plexiglass for observing the study subject and a cup of water in corner for the birds. Blue tits to be tested were moved into the experimental arena about an hour before testing to let the birds get used to the new space. Test sheets were moved in and out from the experimental arena through a thin slit in the bottom of the front wall, with the help of a sight barrier tray – a tray that had a panel ~15 cm high attached perpendicular to the perch to prevent blue tits from viewing the test before landing on the sight barrier (Fig. 1 c).

## 2.3 Experimental designs

### 2.3.1 Design 1: Blue tit Weber fractions on achromatic white background

Fifteen birds were tested in the first part of the behavioural testing of blue tit colour vision during October and November 2018 in Konnevesi research station. In the experiment, blue tit discrimination thresholds were tested for the colours known to humans as red, green, blue and achromatic black from a white background (Fig. 1 b). The stimuli were formatted by selecting seven shades of each colour ranging from very pale to more saturated intensities with the page layout software Swift Publisher 2. Manipulation was done by adjusting the intensity of colour channels (RGB). In RGB increment steps, the maximum value for intensity is 255 (i.e. white corresponds to simultaneous maximum intensity of red, green and blue): varying the RGB levels results in different shades of red, green, blue and black. The RGB values were manipulated channel-specifically by fixing the manipulated colour to its maximum and decreasing the two other colours from their maxima (Table A1). In the most difficult step of colour sets (step 1) the non-manipulated colours were 1 RGB off from white (i.e. RGB 255), thus making the first step RGB value 254, and the following steps 2 RGB further away from

204 the previous step towards more saturated and clearer colour (RGB 252, RGB 250, RGB 248
205 and so forth). A black (or grey) stimulus set was created by decreasing brightness from white
206 (255 RGB) by 1 RGB (of each channel) for the first step and 2 RGBs for every next step
207 resulting in light grey stimuli.

208 The stimuli of each of the four colour sets were printed with a Canon Pixma Pro-10S colour
209 printer on A4 Munken Cream 90g unbleached white printing paper (reflectance curve Fig. A2).
210 One 4 mm diameter stimulus was printed per sheet of paper. With 7 stimuli for all four colour
211 sets and a control (a similar test plate with printed blank paper on it), the whole test totalled 29
212 test sheets (Fig. 1 b). The reflectance of stimuli in each treatment group were measured with a
213 Maya2000 Pro spectrometer and Ocean Optics PX-2 light source, and just-noticeable-
214 difference values (Table A1) calculated with blue tit vision model by Vorobyev and Osorio
215 (1998) in program RStudio 1.2.1335 using package pavo 2.4.0, with illumination measured
216 from the experimental arena (RStudio Team 2019, Maia et al. 2019).

217 Prior to testing, test plates were constructed by taping the printed test sheets on cardboard plates
218 with a 4x3 grid of punctured holes with food rewards in them. The one stimulus dot on each
219 test sheet was always precisely on one of the punctured holes. The 4x3 grid of holes in the
220 cardboard enabled randomizing the location of the stimulus and rule out the possibility that
221 blue tits found the stimuli through means other than visual cues (i.e. smelling or hollow sound
222 of pecking at the location of a puncture).

223 2.3.2 Design 2: Blue tit's ability to discriminate colour from a chromatic background and the
224 effect of chromatic complexity on finding stimuli

225 This experiment was done with 22 blue tits in March and early April 2019. The aim was to test
226 how blue tits discriminate small colour differences from a chromatic background in each colour
227 channel and whether complexity of the background affects the bird's ability to detect stimuli

(Fig. 1 d). This test consisted of three colour channels – red, green and blue – which were each manipulated in three levels resulting in 9 different treatments. The basis for the test was similar to the first part of testing: 7 stimuli were chosen from each colour channel in such a way that the difficulty level of the stimuli ranged from those very similar to the chosen background colour to a more obvious colour difference. Discriminability of the 7 stimuli from each colour channel were tested one by one from an A6-sized area with evenly coloured (ideal) background, low chromatic complexity background and high chromatic complexity background (Fig. 1 d). The printer used in this test was a HP Color LaserJet CP2025 with Staples A4 80 g Copy Paper. Test plates were constructed similar to the first experiment. It is notable that different printers may produce different colours from the same data file. Thus, when choosing a printer for producing this test, stimuli and background colours of the test must be measured with a spectrometer and adjusted again for the printer used.

Colours for the experiments were chosen and modified with the program Gimp 2.10.8 in LCh (i.e. lightness, chroma, hue) colour space. Ideal treatment (even) background colours in each colour channel were individually chosen so that the channel of chosen colour was adjusted to 100 % and two other channels to zero achieving a pure bright shade of red, green and blue. This chosen background colour in each colour channel was always the background for the tested stimuli, even when complexity was added.

Colours for the stimuli of each colour channel were planned in LCh colour space with circularly expressed hue steps that range from 0 (shade of pink before red in colour circle) to 360 (shade of pink after blue in colour circle). Stimuli were adjusted so that the first steps JND value was well under 1 – meaning that most of the birds should not be able to discriminate it from the background colour – the second stimulus close to one, the third around 1 and finally the seventh stimulus well discriminable with a JND value of around 3 or more. Discriminability (Table

252 A2) of stimuli against the chosen ideal background colours, and reflectance of all stimuli and
253 backgrounds (Fig. A3), were measured and modelled by following the method of the first
254 experimental design above.

255 Background complexity was manipulated with a combination of shape and differentiating
256 colours, and was inspired by the tile-matching puzzle video game Tetris (Pajitnov 1984).
257 Shapes in the background were similar to the games shape variation of five equally sized
258 angular objects. An A6 sized area was filled with roughly equal amounts of different Tetris-
259 shapes that were coloured either with three different colours for low complexity background
260 or five different colours for high complexity background – one of the colours always being the
261 ideal background colour for each colour channel. The rest of the colours for complex
262 backgrounds were chosen so that the background colours did not resemble stimulus colours too
263 closely.

264 2.4 Testing protocol

265 In the first experiment, behavioural discrimination thresholds for the colours red, green, blue
266 and achromatic black from a white background were tested with 15 blue tits. In the second
267 experiment, discrimination of colours on saturated red, green and blue backgrounds and a
268 chromatic complexity background was tested behaviourally with 22 blue tits.

269 The testing protocol was similar within these two experiments with a few exceptions. The task
270 for the birds was to detect a stimulus by visual cues, breach through the paper sheet at the
271 location and acquire a food reward. In the beginning of both experiments, the most
272 discriminable stimuli of each treatment were given to the birds one by one to ensure that the
273 birds understood the task. Following that, in the first experiment the rest of the tested colour
274 sets were given to the birds in random order, one colour set at a time, so that the remaining six
275 test plates in one colour set were given to the birds in the order of difficulty from easiest to

hardest. In the second experiment, the six test plates from all nine treatments were given to the bird randomly. Performance of blue tits with each test plate was marked as success or failure (1 or 0). Blue tits were considered to succeed at finding a stimulus if they pecked the stimulus dot so that the paper was damaged. Latency time was measured from when the bird first landed on the sight barrier and saw the task till finding the stimulus or until the 60 seconds time limit was reached. In addition, in the second experiment the number of times blue tit attempted the task (i.e. appoached to look at the test plate) was recorded and the amount of pecks blue tits made while searching the stimulus was counted up to 15 pecks. The number of attempts and pecks were assumed to correlate with the difficulty of the task.

## 2.5 Statistical analysis

### 2.5.1 Determination of Weber fractions

To find out behavioural colour discrimination thresholds (Weber fractions) of blue tits on achromatic backgrounds for colours red, green, blue and achromatic black, probability curves of colour channel specific successes at finding stimuli were fitted against JND values modelled with different Weber fractions. Curves were fitted by using generalized linear mixed models with binomial family, logit link function and fit by maximum likelihood in the program RStudio 1.2.1335 using package lme4: bird identity as random variable, success at finding stimuli as dependent and JND values of stimuli calculated with different Weber fractions as an independent variable (RStudio Team 2019, Bates et al. 2015). A bracketing approach (i.e. a technique of taking several different values of the same subject and approximating the best fitting value) was used to narrow down which Weber fraction produced the JND 1 that coincided the probability of 75 % of blue tits seeing the colour difference.

To see which Weber fractions in each colour channel described blue tit behaviour the best on saturated chromatic backgrounds, colour specific probability curves of finding stimuli from

ideal background treatments were similarly fitted against JND values that were calculated with different Weber fraction settings. The fit was done by using a generalized linear mixed model with binomial family, logit link function and fit by maximum likelihood, again using the lme4 package. Bird identification was included as a random variable, success at finding stimuli as a dependent variable, and independent variables were colour channel, treatment type and the JND values determined with different Weber fractions. The Weber fraction that had produced a JND 1 that approximately coincided with 75 % probability of blue tits seeing the colour difference was bracketed in each colour channel.

### 2.5.2 The effect of chromatic complexity in finding prey

By analysing the blue tits probability of finding stimuli on each treatment background, we were able to compare how different colour channels and complexity treatments affected stimuli search success. In the analysis of the effect of chromatic complexity, the most discriminable stimulus steps in each treatment group were excluded since they were presented to the birds at the start of the experiments to verify that the birds understood the task at hand. Models for analysing the successes at detecting stimuli in the second experiment in red, green and blue colour channels for ideal, low and high complexity background treatments were done using the exact same parameters as when fitting the curve for determination of Weber fractions on saturated chromatic backgrounds. Model selection was performed with the "drop1" command, with which variables were excluded from the full model (including all possible three- and two-way interactions) until the model with lowest Akaike information criterion score was gained. Analyses were done with the program RStudio version 1.2.1335 and package lme4 (RStudio Team 2019, Bates et al. 2015).

Analyses on how chromatic complexity affected the number of pecks, attempts and search latency were done with generalized linear mixed models using package lme4 and model

selections for each analysis performed with the "drop1" command, as earlier. When analysing latency, detection success and latency variables were combined with the "cbind" command to create a binomial dataset (time to event). Binomial family with logit link functions and fit by maximum likelihood were used. Random variable was bird identification, independent variables were colour channel, treatment type and colour specific JND values calculated with the newly determined Weber fractions for saturated chromatic backgrounds. For analysing the number of pecks, Poisson distribution was used with a log link function and fit by maximum likelihood. Random variable was bird identification and independent variables were colour channel, treatment type and JND values determined on chromatic background. Analysis for the number of attempts that the blue tits made to find a stimulus were done with similar parameters as the analysis for the number of pecks.

## 3. RESULTS

### 3.1 Weber fractions against achromatic and chromatic backgrounds

On achromatic backgrounds, the Weber fraction that produced JND value 1 that was perceived by 75 % of blue tits for long wavelengths was 0.05 (Fig. 2). For middle wavelengths the correct Weber fraction was 0.03 and for short wavelengths 0.03 also. The Weber fraction for the achromatic black stimuli was 0.08. The average number of found stimuli and mean latencies of finding stimuli in each colour channel are found in Table 1.

On saturated chromatic ideal (evenly coloured) backgrounds, the Weber fraction of blue tits for long wavelengths was 0.20. For middle wavelengths, the correct Weber fraction was 0.17 and for short wavelengths 0.15. Thus, Weber fractions for saturated chromatic backgrounds were markedly higher from the ones determined for achromatic background, as well as from

347 the Weber fractions 0.05 and 0.10 commonly used for all colour channels in different receptor-
348 noise based models (Fig. 3) (Vorobyev and Osorio 1998, Troscianko and Stevens 2015, van
349 den Berg & Troscianko et al. 2020). The average number of found stimuli and mean latencies
350 of finding stimuli in each treatment background are found in Table 2.

351

352 3.2 The effect of chromatic complexity in finding prey

353 Chromatic complexity of backgrounds in red, green and blue colour channels affected the
354 visual search task in following ways. In comparison to ideal (non-complex) background, low
355 and high complexity treatments lowered the probability of finding stimuli more in the red
356 colour channel than in green and blue (detection success model selection Table 3, model
357 summary Table 4). In the red colour channel, high complexity treatment lessened the
358 probability of finding stimuli more than low complexity treatment (Table 2 and Fig. 3, top
359 row).

360 Latencies of finding stimuli were longer in the red colour channel compared to blue and green
361 colour channels (Tables B1 and B2, Appendix B). In the red colour channel, complexity
362 treatments elongated latency time and high complexity treatment affected latency more than
363 low complexity treatment (Table 2).

364 The red colour channel increased the number of pecks compared to the colour channels green
365 and blue (Tables B3 and B4). In the red colour channel, blue tits pecked on average 7.51 times
366 (s.d. = 6.57) while searching for stimuli, while in the green colour channel the average count
367 of pecks was 5.98 (s.d. = 6.27) and in blue 6.16 (s.d. = 6.09). Complexity treatments increased
368 the number of pecks only in the red colour channel: in the ideal backgrounds, birds pecked on
369 average 5.73 times, in low complexity backgrounds 7.64 times and in high complexity 9.16

370 times. In the green and blue colour channels, the complexity treatments increased pecking
371 approximately by 1 peck or less.

372 The red colour channel also increased the number of attempts that the birds made to find stimuli
373 in the experiments, and the complexity treatments affected the number of attempts more in the
374 red colour channel than in green and blue (Table B5 and B6). In the red ideal treatment, birds
375 made on average 2.89 attempts, in low complexity 4.04 and high complexity 4.21 attempts,
376 while the average number of attempts remained between 2.52 – 2.76 in green and 3.16 – 3.37
377 in blue colour channel throughout the complexity treatments.

378

379 4. DISCUSSION

380 We highlight that using a vision model in which colour discrimination parameters are
381 determined in ideal viewing conditions, as they are by definition, can lead to misleading
382 interpretations in a more colourful context. More specifically, Weber fractions do not stay
383 constant through colour channels when determined against achromatic in comparison to
384 saturated chromatic backgrounds. Weber fractions measured against achromatic background
385 (L: 0.05, M: 0.03, S: 0.03 and achromatic black: 0.08) were considerably smaller than the
386 Weber fractions for saturated chromatic ideal treatment backgrounds (L: 0.20, M: 0.17, S:
387 0.15). Also, chromatic complexity of backgrounds and changes in hue only affected blue tit
388 search behaviour in the red colour channel. These results suggest that the use of too low Weber
389 fractions in the visual model will lead to too high colour discrimination values in more natural
390 contexts. This can challenge the biological interpretation of the vision model results.

391 The behaviourally estimated amount of noise (Weber fraction) in blue tit long-wave channel
392 measured against achromatic background is lower than most estimates of noise in LW channels

393 of other birds (L: 0.10) (Olsson et al. 2018 Table 1). The result is closest to that of chickens
394 *Gallus gallus*, whose estimate of receptor noise (L: 0.06) was measured in a study where
395 chickens had to discriminate between orange and yellow colours on variable grey backgrounds
396 (Olsson et al. 2015). Olsson et al. (2015) paid attention to the lower receptor noise compared
397 to other birds and suggested – on top of the possibility that chickens simply have less noise in
398 their long-wave channel – that exploitation of natural bird behaviour (i.e. pecking at objects to
399 gain food) may promote better performance in discrimination tasks compared to more artificial
400 methods used in behavioural measurements of receptor noise.

401 Larger Weber fractions against chromatic backgrounds imply that for a stimulus to be seen,
402 there needs to be a larger difference compared to background than in achromatic environments.
403 This finding is very important, especially considering how researchers use different Weber
404 fractions in determining the smallest colour differences their study subjects can perceive in
405 their natural environments. An estimate of noise that is too low produces too high colour
406 discrimination predictions. When the exact Weber fractions are unknown, researchers
407 understandably resort in using the commonly used 0.05 or even 0.02 without confirmation of
408 how these assumptions reflect study animals' behaviour in nature (Siddiqi et al. 2004,
409 Outomuro et al. 2017). Thus, there is an obvious risk of researchers assuming considerably
410 smaller colour differentiation thresholds for study subjects than the subjects truly have.

411 Only the red colour channel was affected by changes in the hue of saturated colours and the
412 noise of viewing background. Quantitatively, blue tits found approximately as many stimuli
413 from the red ideal background as from green and blue (64 % of all stimuli on red ideal
414 backgrounds, 70 % on green and 63 % on blue). However, in red low complexity treatments
415 blue tits only found approximately 24 % and in high complexity treatments 16 % of stimuli,
416 while in green and blue complexity treatments birds were able to find 57 – 61 %.

The reason for the lessened detection success of blue tits in the red colour channel could lie in ultimate or proximate mechanisms of colour perception. Less successful performance in the red colour channel could hint of neofobia (fear of new) of the odd combination of saturated colours that were used in this study, or avoidance of colours that are associated with warning signals (Marples and Kelly 1999, Ham et al. 2006, Greggor et al. 2015). Red colour was overall less motivating for the birds, and some of them even expressed reluctancy to engage with the red complexity backgrounds. However, both explanations are unlikely here since the birds were trained to hunt profitable, colourful prey in an artificial environment. Nevertheless, hues of red and yellow are often associated with effective warning colours (i.e. aposematism) that can be avoided by insectivorous birds innately but also based on learned experience (Ham et al. 2006, Stevens and Ruxton 2011). The set of red and yellow hues in the red complexity backgrounds might seem appalling for the birds if they associate most of the hues with warning colours. This finding could also suggest that perhaps the high-noise sensitivity of the red channel – that was highlighted by the increased number of pecks and attempts in the complexity treatments – ultimately facilitates the widespread exploiting of this colour channel in the nature and may also render it available for cheating (Stevens & Ruxton 2012, Mökkönen & Lindstedt 2015).

Proximate mechanisms behind the lessened detection success in red colour channel could be found in the red and yellow oil droplets on bird LWS and MWS photoreceptors responsible for long- and middle-wave sensing. Blue tit MWS photoreceptor has the peak sensitivity at 503 nm and LWS at 563 nm but their oil droplets only pass through light wavelengths longer than the peak sensitivities (cut off for MWS droplet from 508 nm and LWS droplet from 573 nm) (Hart et al. 2000). Generally, the droplets shift the spectral sensitivity peaks to wavelengths approximately 40 nm longer, narrow the spectral bandwidth of the photoreceptors by half and lessen the absolute sensitivity of photoreceptors by around 90 % (Hart and Vorobyev 2005, Wilby and Roberts 2017, Kelber 2019).

442 The result of considerably higher Weber fractions in chromatic environments raises the
443 question of how the noise parameter is used in modelling animal colour vision. As most studies
444 determining the amount of noise in animal visual systems concentrate on achromatic
445 backgrounds, research on validity of the Weber fraction parameter in visual modelling on
446 chromatic environments is scarce. A study by Lind (2016) examined discriminability of colours
447 on contrasting backgrounds. Our results are concordant, as it appears that generally a larger
448 colour difference is needed for discriminating colour changes on chromatic backgrounds
449 compared to achromatic backgrounds. Many studies use the low Weber fractions determined
450 on achromatic backgrounds to infer how animals discriminate colours against chromatic
451 environments (Siddiqi et al 2004, Maan and Cummings 2012, Schultz and Fincke 2013
452 amongst others). Weber fractions which are too low can produce misleading results, for
453 example in studies on crypsis and camouflage where the background of a given signal is mostly
454 chromatic and varying. A low Weber fraction in modelling visual perception of a given
455 predator in camouflage and crypsis studies can lead to a false conclusion that the predator is
456 able to see the camouflaged prey easier than it truly can. Similarly, if the Weber fraction is set
457 too high for a given predator, it might seem like the predator is not able to spot the camouflaged
458 prey through visual cues. What increases the amount of noise in bird visual systems in
459 chromatic environment is still unknown, but Kelber (2019) and Vorobyev and Osorio (1998)
460 suggest that adaptation stage of cone cells can be the reason for less fine colour discrimination
461 in contrasting backgrounds.

462 We conclude that when inferring discrimination abilities of avian vision in natural
463 environments, researchers should carefully select appropriate Weber fraction parameters for
464 modelling. Previously, the Weber fraction of 0.05 has been assumed (van den Berg &
465 Troscianko et al. 2020) safe to use for species whose discrimination thresholds are unknown.
466 However, based on the results of this study with blue tits, we suggest the use of a more

conservative Weber fraction of 0.10, at least for studies considering passerine birds. Thus, the RNL model assumption Weber fraction 0.10 originally proposed by Vorobyev and Osorio (1998) could be a valid choice for modelling blue tit colour vision perception in all colour channels, except if the study especially concentrates on red hues, in which case even higher Weber fraction of 0.13 – 0.15 for LWS colour channel may be in order until more accurate information can be obtained.

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TABLES AND FIGURES

| Colour | Average number of found stimuli | SD of found stimuli | Mean latency | SD latency |
|---|---|---|---|---|
| Red | 4.07 | 3.47 | 28.35 s | 23.51 s |
| Green | 4.93 | 3.21 | 22.57 s | 22.66 s |
| Blue | 5.40 | 2.95 | 17.52 s | 19.03 s |
| Black | 3.53 | 3.52 | 30.11 s | 23.17 s |

Table 1. First experiment, discrimination thresholds on white background: the average number of stimuli found by blue tits (i.e. 7 stimuli were tested per colour channel) and mean latency of finding stimuli in each colour channel.

| Treatment | Average number of found stimuli | SD of found stimuli | Mean latency | SD latency |
|---|---|---|---|---|
| Red | | | | |
| Ideal | 4.45 | 3.37 | 31.57 s | 27.00 s |
| Low complexity | 1.68 | 2.99 | 47.49 s | 20.81 s |
| High complexity | 1.14 | 2.59 | 50.42 s | 18.54 s |
| Green | | | | |
| Ideal | 4.91 | 3.23 | 23.94 s | 30.21 s |
| Low complexity | 4.27 | 3.42 | 26.38 s | 25.57 s |
| High complexity | 4.68 | 3.29 | 25.07 s | 27.13 s |
| Blue | | | | |
| Ideal | 4.41 | 3.39 | 28.80 s | 24.92 s |
| Low complexity | 3.91 | 3.47 | 31.57 s | 23.95 s |
| High complexity | 4.27 | 3.42 | 30.16 s | 24.80 s |

Table 2. Second experiment, discrimination thresholds on chromatic backgrounds and the effect of complexity: the average number of stimuli found by blue tits (i.e. 7 stimuli were tested against each background) and mean latency of finding stimuli in each treatment.

| Model: Detection success | Df | AIC | LRT | Pr(Chi) |
|---|---|---|---|---|
| ~C+T+JND+C*T+C*JND+T*JND+C*T*JND+(1\|BirdID) | | 1014.9 | | |
| ~C+T+JND+C*T+C*JND+T*JND+(1\|Bird ID) | 4 | 1012.3 | 5.441 | 0.245 |
| ~C+T+JND+C*T+C*JND+(1\|Bird ID) | 2 | 1010.3 | 2.002 | 0.368 |

Table 3. Model selection for a GLMM estimating the detection success of blue tits in chromatic complexity backgrounds. C = colour, T = treatment type and JND = colour specific just-noticeable-differences determined on chromatic backgrounds. Asterisk denotes interaction term of the variables and + indicates main effects. The selected model is underlined.

| Random effects: | Groups | | Variance | Std.Dev. |
|---|---|---|---|---|
| | Bird ID | | 0.5831 | 0.7636 |
| Fixed effects: | Estimate | Std. Error | z value | Pr(>\|z\|) |
| Intercept | -2.651 | 0.382 | -6.947 | <0.001 |
| Colour G | -2.036 | 0.595 | -3.419 | <0.001 |
| Colour R | 1.906 | 0.549 | 3.473 | <0.001 |
| Treatment High | -0.164 | 0.330 | -0.498 | 0.618 |
| Treatment Low | -0.426 | 0.332 | -1.283 | 0.200 |
| Chromatic JNDs | 3.717 | 0.357 | 10.416 | <0.001 |
| Colour G : Treatment High | -0.107 | 0.543 | -0.198 | 0.843 |
| Colour R : Treatment High | -2.034 | 0.455 | -4.465 | <0.001 |
| Colour G : Treatment Low | -0.635 | 0.560 | -1.134 | 0.257 |
| Colour R : Treatment Low | -1.288 | 0.441 | -2.921 | 0.003 |
| Colour G : Chromatic JNDs | 1.989 | 0.616 | 3.231 | 0.001 |
| Colour R : Chromatic JNDs | -2.160 | 0.645 | -3.347 | <0.001 |

Table 4. Model summary from the analysis of detection success of blue tits in chromatic complexity backgrounds, where Intercept is the colour blue in ideal treatment background.

Fig. 1. a) Schematic illustration of how the two experiments cover the RGB colour space. Number 1 denotes the first experimental design. Number 2 denotes the second experimental design, where a) is ideal chromatic background, b) low chromatic complexity and c) high chromatic complexity backgrounds.

b) Illustration of the tested colours in the first colour perception experiment. R = red, G = green, B = blue and K = black/grey. Numbers on the left side are the stimulus steps where 1 is the most difficult to detect and 7 the easiest. Dots are circled, larger in size and stimulus colours intensified (squared) in this figure for illustrative reasons.

c) Sight barrier tray, which was used for moving the test sheets in and out of the experimental arena, with a blue high complexity test sheet and blue tit sitting on the sight barrier with a reward.

d) Illustration of the second experimental design inspired by the puzzle video game Tetris (Pajitnov 1984): ideal background in left column, low complexity background in middle and high complexity background in right for red, green and blue colour channel.

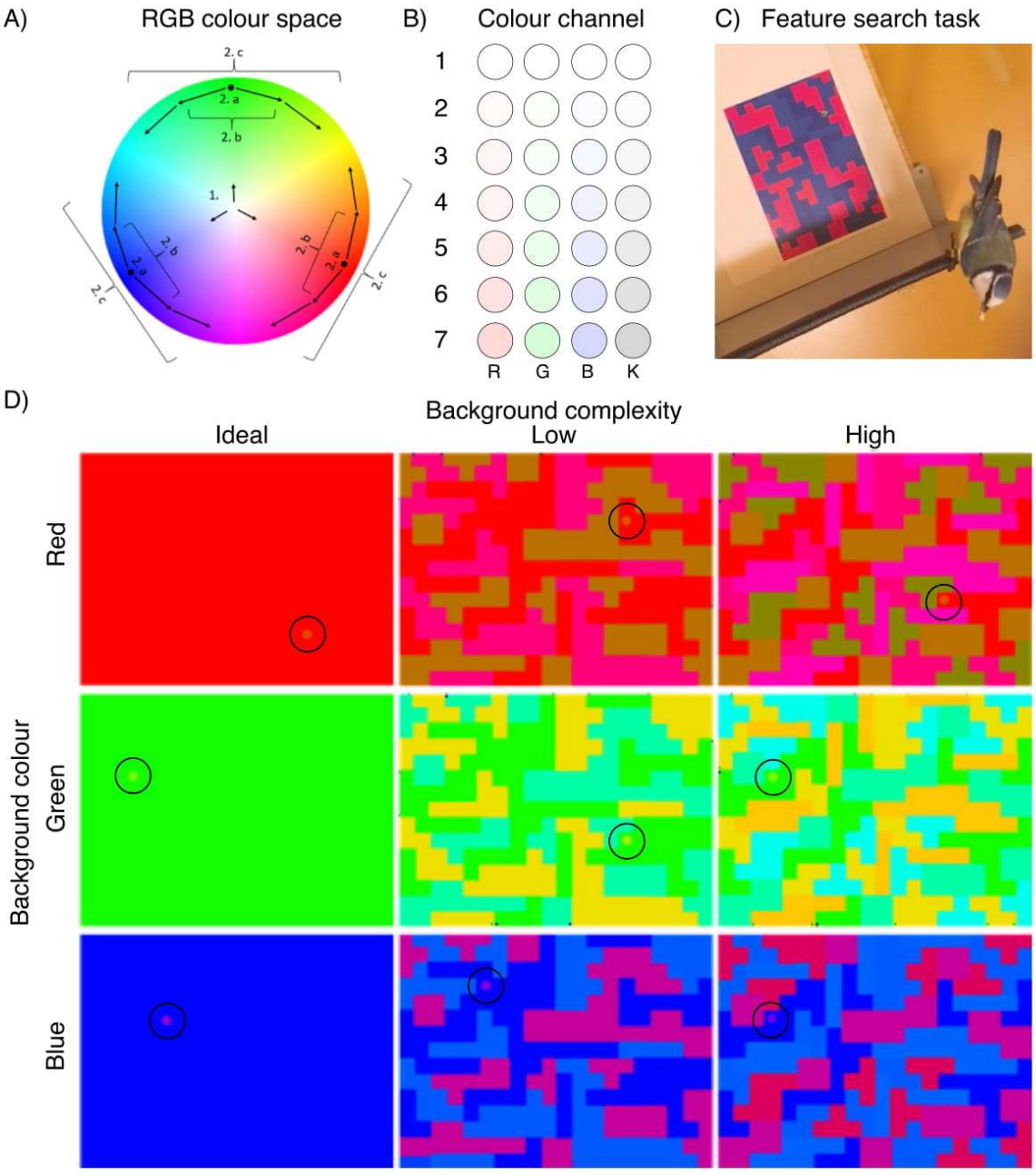

A)
RGB colour space
2. c
2. a
2. b
1.
B)
Colour channel
1
2
3
4
5
6
7
R G B K
C) Feature search task
D)
Background complexity
Ideal
Low
High
Red
Green
Blue
Background colour

Fig. 2. Illustration of bracketing of Weber fractions on achromatic white backgrounds for the red, green and blue colour channels and achromatic (black) channel. For each colour, the behaviourally validated Weber fraction that produced JND value 1 that was perceived by 75 % of blue tits (n = 15) is in the middle. Dashed lines show the positive and negative standard deviations of each probability curve.

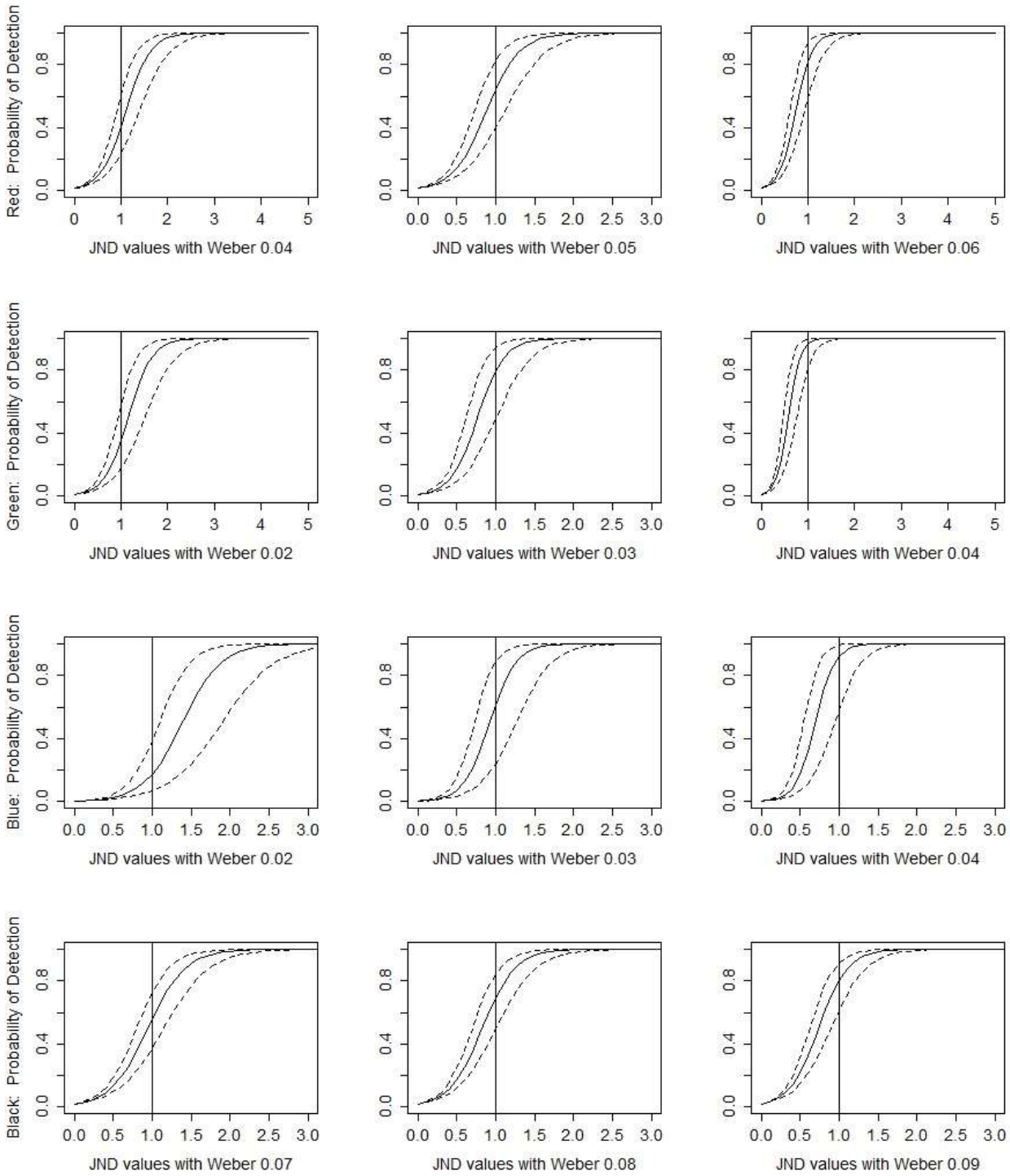
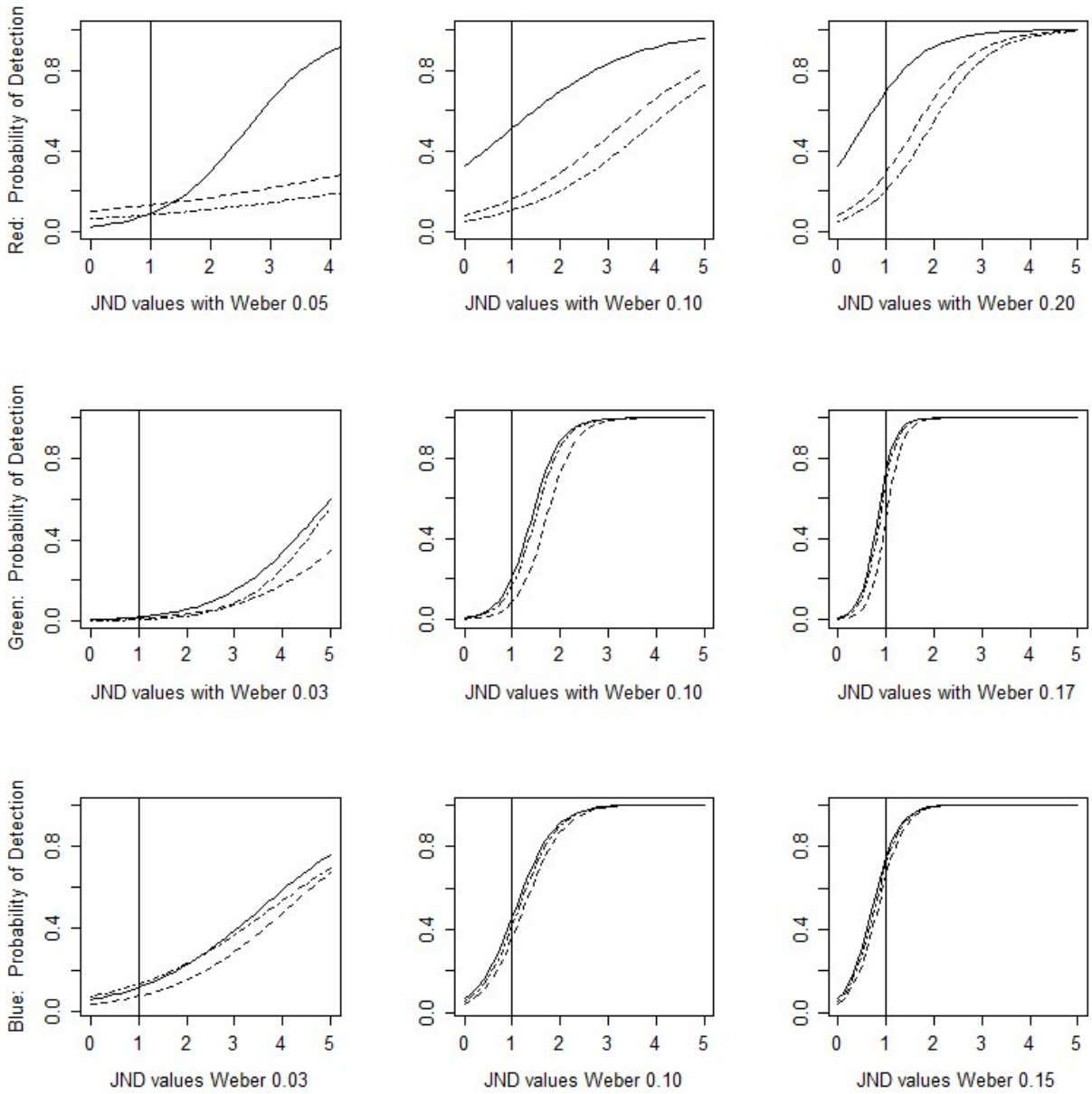


Fig. 3. Comparison of how the just-noticeable-difference (JND) values calculated with different Weber fractions describe blue tit behaviour (n = 22) on saturated chromatic backgrounds in red (top row), green (middle) and blue (bottom row) colour channels. In the left column are the channel specific Weber fractions determined against achromatic backgrounds, in the middle a common model assumption Weber fraction 0.10 and on right the Weber fractions that produced JND 1 that corresponds to behaviourally validated 75 % of birds detecting the colour difference against evenly coloured chromatic backgrounds. Solid lines are the probability curve of ideal (evenly coloured) treatment, long dashes are low complexity and short dashes are high complexity treatment.



APPENDIX A

| | Step 1 | Step 2 | Step 3 | Step 4 | Step 5 | Step 6 | Step 7 |
|---|---|---|---|---|---|---|---|
| RGB value | 254 | 252 | 250 | 248 | 246 | 244 | 242 |
| JNDs of red stimuli | 0.12 | 0.23 | 0.39 | 0.52 | 0.66 | 0.80 | 0.93 |
| JNDs of green stimuli | 0.10 | 0.18 | 0.30 | 0.32 | 0.44 | 0.50 | 0.62 |
| JNDs of blue stimuli | 0.17 | 0.28 | 0.35 | 0.52 | 0.70 | 0.77 | 0.90 |
| JNDs of black stimuli | 0.01 | 0.02 | 0.02 | 0.03 | 0.05 | 0.04 | 0.04 |

Table A1. JND values of stimuli in the red, green, blue and black stimulus sets against white testing backgrounds in experiment 1. RGB value on the top row indicates the value of the two colours in which intensity was decreased to uncover the manipulated colour from white. JNDs were modelled with blue tit vision model in the package pavo 2.4.0 using the default Weber fraction 0.10 and illumination spectra measured from the testing arena (Maia et al. 2019).

| | Step 1 | Step 2 | Step 3 | Step 4 | Step 5 | Step 6 | Step 7 |
|---|---|---|---|---|---|---|---|
| Stimuli JNDs on red | 0.66 | 0.91 | 1.59 | 1.74 | 1.8 | 1.96 | 2.9 |
| Stimuli JNDs on green | 0.67 | 0.97 | 1.48 | 2.57 | 2.77 | 2.95 | 3.1 |
| Stimuli JNDs on blue | 0.28 | 0.77 | 0.81 | 1.49 | 1.91 | 2.6 | 4.7 |

Table A2. JND values of stimuli against the ideal treatment background of each tested colour in the experiment 2. JNDs were modelled with blue tit vision model in the package pavo 2.4.0 using the default Weber fraction 0.10 and illumination spectra measured from the testing arena (Maia et al. 2019).

Fig. A1. Irradiance curve of the light conditions in experimental setups. The large gap represents an open, fully exposed light environment as described by Endler (1993). Figure shows comparison between the experimental large gap light environment used in the behavioral experiment and the large gap conditions measured from the field.

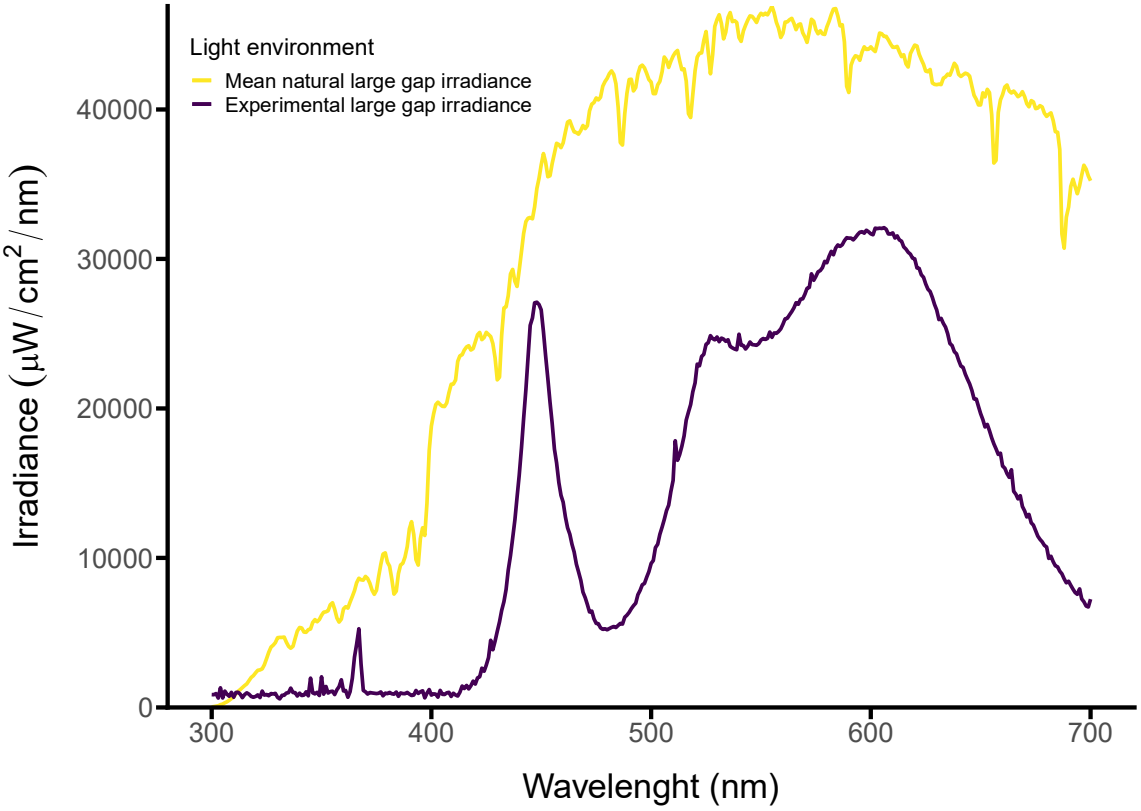


Fig.A2. Reflectance of tested stimuli colours and the background (highest line in each graph) in experiment 1.

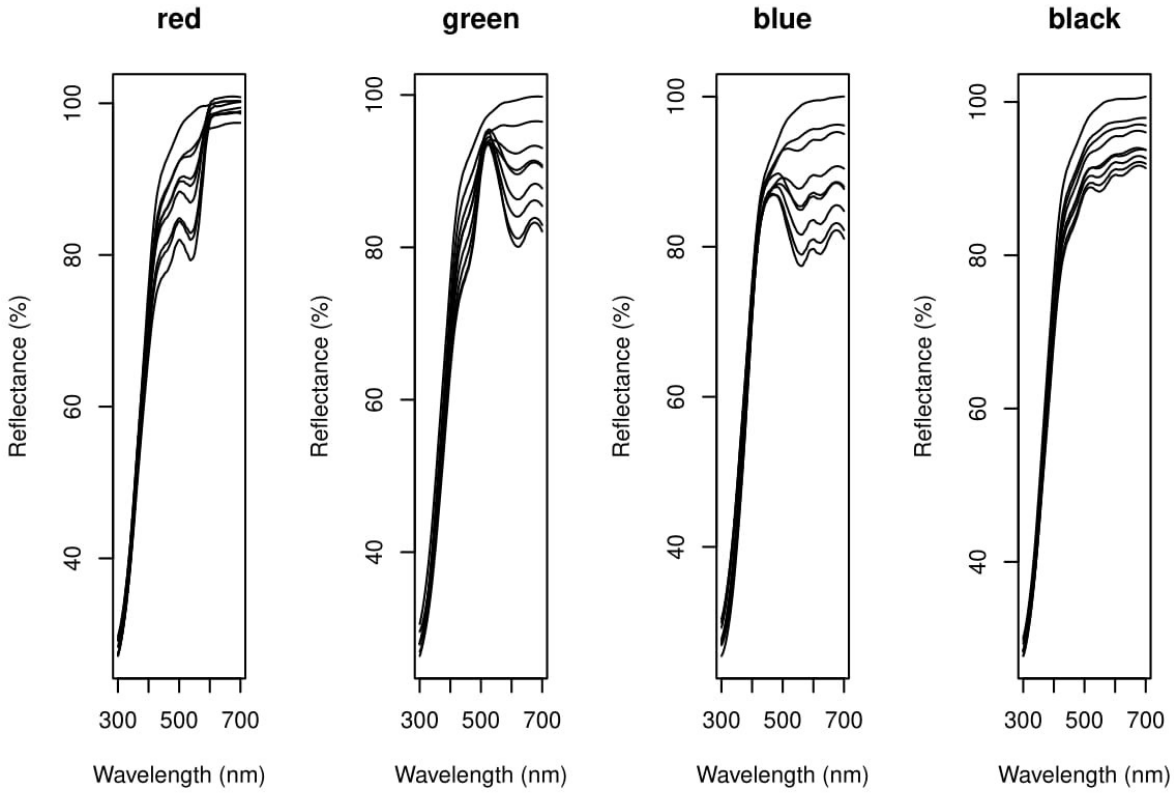
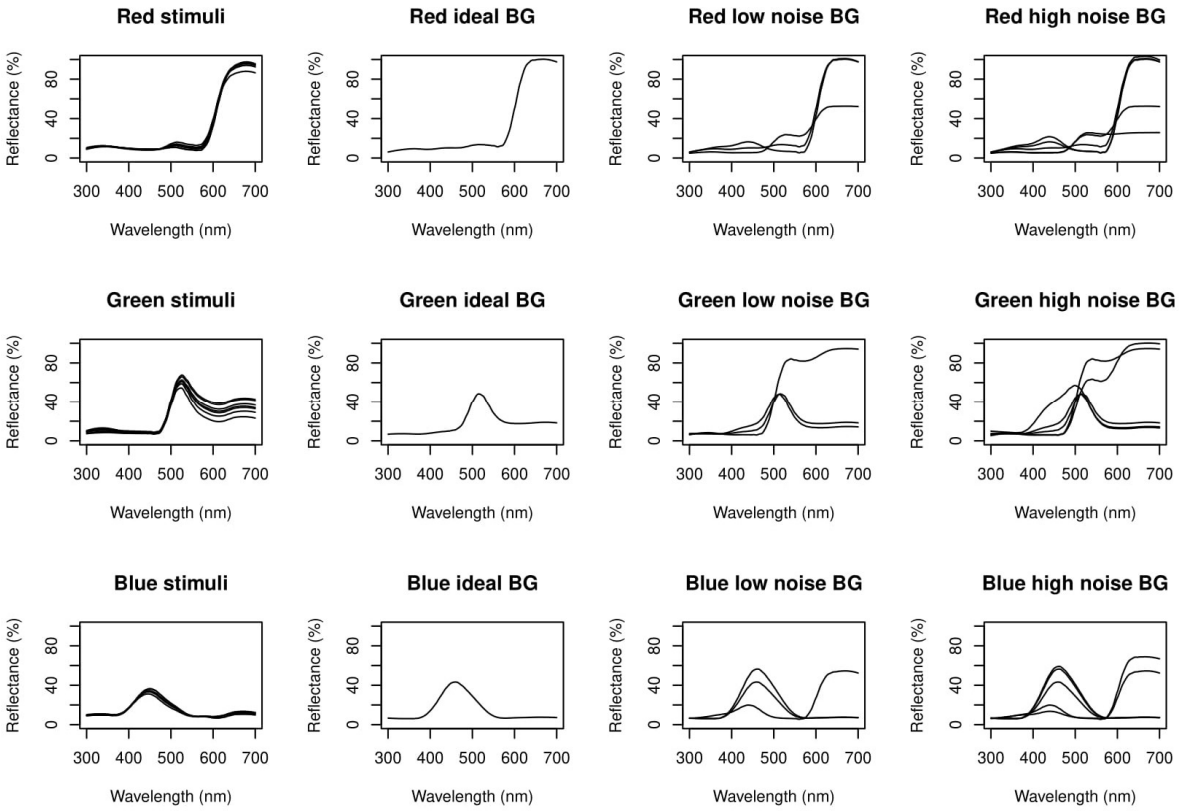


Fig. A3. Reflectance of stimuli and testing background colours in experiment 2.



APPENDIX B

| Model: Latency | Df | AIC | LRT | Pr(Chi) |
|---|---|---|---|---|
| ~C+T+JND+C*T+C*JND+T*JND+C*T*JND+(1\|BirdID) | | 2602.9 | | |
| ~C+T+JND+C*T+C*JND+T*JND+(1\|Bird ID) | 4 | 2598.5 | 3.614 | 0.461 |
| ~C+T+JND+C*T+C*JND+(1\|Bird ID) | 2 | 2596.6 | 2.097 | 0.350 |

Table B1. Model selection for a GLMM estimating the latency to finding stimuli of blue tits in chromatic complexity backgrounds. C = colour, T = treatment type and JND = colour specific just-noticeable-differences determined on chromatic backgrounds. Asterisk denotes interaction term of the variables and + indicates main effects. The selected model is underlined.

| Random effects: | Groups | Name | Variance | Std.Dev. |
|---|---|---|---|---|
| | Bird ID | Intercept | 0.3207 | 0.5663 |
| Fixed effects: | Estimate | Std. Error | z value | Pr(>\|z\|) |
| Intercept | -6.109 | 0.234 | -26.122 | <0.001 |
| Colour G | -1.274 | 0.333 | -3.831 | <0.001 |
| Colour R | 1.162 | 0.373 | 3.119 | 0.002 |
| Treatment High | -0.167 | 0.172 | -0.967 | 0.333 |
| Treatment Low | -0.137 | 0.177 | -0.770 | 0.441 |
| Chromatic JNDs | 2.508 | 0.142 | 17.716 | <0.001 |
| Colour G : Treatment High | -0.167 | 0.244 | -0.682 | 0.496 |
| Colour R : Treatment High | -1.667 | 0.297 | -5.605 | <0.001 |
| Colour G : Treatment Low | -0.507 | 0.248 | -2.044 | 0.041 |
| Colour R : Treatment Low | -1.275 | 0.276 | -4.617 | <0.001 |
| Colour G : Chromatic JNDs | 1.164 | 0.222 | 5.239 | <0.001 |
| Colour R : Chromatic JNDs | -1.203 | 0.420 | -2.864 | 0.004 |

Table B2. Model summary from the analysis of latency of finding a prey, where Intercept is the colour blue in ideal treatment background.

| Model: Pecks | Df | AIC | LRT | Pr(Chi) |
|---|---|---|---|---|
| ~C+T+JND+C*T+C*JND+T*JND+C*T*JND+(1\|BirdID) | | 7975.5 | | |
| ~C+T+JND+C*T+C*JND+T*JND+(1\|Bird ID) | 4 | 7981.5 | 13.96 | 0.245 |

Table B3. Model selection for a GLMM estimating the number of pecks of blue tits while searching stimuli on chromatic complexity backgrounds. C = colour, T = treatment type and JND = colour specific just-noticeable-differences determined on chromatic backgrounds. Asterisk denotes interaction term of the variables and + indicates main effects. The selected model is underlined.

| Random effects: | Groups | Name | Variance | Std.Dev. |
|---|---|---|---|---|
| | Bird ID | Intercept | 0.215 | 0.464 |
| Fixed effects: | Estimate | Std. Error | z value | Pr(>\|z\|) |
| Intercept | 2.721 | 0.117 | 23.362 | <0.001 |
| Colour G | 0.500 | 0.098 | 5.124 | <0.001 |
| Colour R | -0.411 | 0.121 | -3.402 | <0.001 |
| Treatment High | -0.172 | 0.086 | -1.998 | 0.046 |
| Treatment Low | -0.040 | 0.086 | -0.465 | 0.642 |
| Chromatic JNDs | -1.497 | 0.091 | -16.485 | <0.001 |
| Colour G : Treatment High | 0.077 | 0.134 | 0.573 | 0.567 |
| Colour R : Treatment High | -0.062 | 0.164 | -0.376 | 0.707 |
| Colour G : Treatment Low | -0.142 | 0.134 | -1.058 | 0.290 |
| Colour R : Treatment Low | -0.258 | 0.169 | -1.532 | 0.126 |
| Colour G : Chromatic JNDs | -0.347 | 0.131 | -2.643 | 0.008 |
| Colour R : Chromatic JNDs | 0.556 | 0.173 | 3.219 | 0.001 |
| Treatment High : Ch. JNDs | 0.430 | 0.121 | 3.555 | <0.001 |
| Treatment Low : Ch. JNDs | 0.192 | 0.125 | 1.541 | 0.123 |
| Colour G : Treat. H. : Ch. JNDs | -0.056 | 0.173 | -0.325 | 0.746 |
| Colour R : Treat. H. : Ch. JNDs | 0.584 | 0.226 | 2.582 | 0.010 |
| Colour G : Treat. L. : Ch. JNDs | 0.271 | 0.175 | 1.550 | 0.121 |
| Colour R : Treat. L. : Ch. JNDs | 0.666 | 0.234 | 2.844 | 0.005 |

Table B4. Model summary from the analysis of the number of pecks while blue tits were searching stimuli on chromatic complexity backgrounds. Intercept is the colour blue in ideal treatment background.

| Model: Attempts | Df | AIC | LRT | Pr(Chi) |
|---|---|---|---|---|
| ~C+T+JND+C*T+C*JND+T*JND+C*T*JND+(1\|BirdID) | | 4764.5 | | |
| ~C+T+JND+C*T+C*JND+T*JND+(1\|Bird ID) | 4 | 4770.0 | 13.48 | 0.009 |

Table B5. Model selection for a GLMM estimating the number of attempts of blue tits while searching stimuli on chromatic complexity backgrounds. C = colour, T = treatment type and JND = colour specific just-noticeable-differences determined on chromatic backgrounds. Asterisk denotes interaction term of the variables and + indicates main effects. The selected model is underlined.

| Random effects: | Groups | Name | Variance | Std.Dev. |
|---|---|---|---|---|
| | Bird ID | Intercept | 0.274 | 0.524 |
| Fixed effects: | Estimate | Std. Error | z value | Pr(>\|z\|) |
| Intercept | 1.605 | 0.142 | 11.318 | <0.001 |
| Colour G | 0.326 | 0.140 | 2.323 | 0.020 |
| Colour R | -0.199 | 0.174 | -1.146 | 0.252 |
| Treatment High | -0.099 | 0.122 | -0.808 | 0.419 |
| Treatment Low | 0.089 | 0.122 | 0.728 | 0.467 |
| Chromatic JNDs | -0.770 | 0.105 | -7.350 | <0.001 |
| Colour G : Treatment High | 0.066 | 0.197 | 0.334 | 0.738 |
| Colour R : Treatment High | 0.246 | 0.233 | 1.059 | 0.290 |
| Colour G : Treatment Low | -0.285 | 0.196 | -1.454 | 0.146 |
| Colour R : Treatment Low | -0.351 | 0.241 | -1.461 | 0.144 |
| Colour G : Chromatic JNDs | -0.388 | 0.155 | -2.501 | 0.012 |
| Colour R : Chromatic JNDs | 0.077 | 0.233 | 0.329 | 0.742 |
| Treatment High : Ch. JNDs | 0.239 | 0.143 | 1.671 | 0.095 |
| Treatment Low : Ch. JNDs | -0.038 | 0.149 | -0.256 | 0.798 |
| Colour G : Treat. H. : Ch. JNDs | -0.216 | 0.216 | -1.001 | 0.317 |
| Colour R : Treat. H. : Ch. JNDs | 0.095 | 0.308 | 0.307 | 0.759 |
| Colour G : Treat. L. : Ch. JNDs | 0.337 | 0.216 | 1.564 | 0.118 |
| Colour R : Treat. L. : Ch. JNDs | 0.882 | 0.316 | 2.791 | 0.005 |

Table B6. Model summary from the analysis of the number of attempts while blue tits were searching stimuli on chromatic complexity backgrounds. Intercept is the colour blue in ideal treatment background.