Plumage colour of male Common Crossbills *Loxia curvirostra*: visual assessment validated by colorimetry

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We describe here an affordable method for assessing patterns and colour variations in male Crossbills *Loxia spp*. Our aim was to validate qualitative colour categories obtained in the field through visual inspection with quantitative data obtained from a colorimeter. Patterns and colour variations of 219 male Common Crossbills *Loxia curvirostra* were measured using both techniques. We found that there was a close correspondence between the tristimulus scores generated by the colorimeter and our visual scoring system. These results support the accuracy of our visual colour assessment procedure and provide amateurs, field ornithologists and researchers interested in Crossbills with an easy, inexpensive, repeatable and objective alternative to the use of modern electronic devices. In a more general sense, our results suggest that visual colour inspection may in fact be more objective and useful than currently thought.

Key words: Common Crossbill, *Loxia curvirostra*, colour measurement, colorimeter, plumage coloration, visual colour assessment.

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In recent years, the evolution of bird coloration has become an important issue in behavioural and evolutionary ecology (reviewed in Hill & McGraw 2006a, b) and the rapid development of this topic has led to the proposal of a variety of different methods for assessing colour (see Andersson & Prager 2006).

Most researchers today show a clear preference for using advanced techniques independent of the human visual system when quantifying plumage coloration. Modern digital colorimeters have been shown to be very efficient for measuring the uneven surface of a bird's plumage and for capturing the colour perceived by the observer (Hill 1998, Figuerola *et al*. 1999, Domènech *et al*. 2000). These electronic devices characterize colours on a three-dimensional scale under standardized conditions, providing accurate values beyond the human visible spectrum (Figuerola *et al*. 1999). They are easy to use, battery-operated, compact and portable, features that make them especially useful when working in the field (Hill 1998). However, such technology is still rather expensive for most amateur ornithologists and ringing stations.

Ranking and matching procedures are the most traditional methods for colour quantification. The objectivity of these procedures has been strongly criticized, since they have been shown to depend critically on the perceptual biases of the user, the environmental variation of the background and lighting conditions (Endler 1990, Zuk & Decruyenaere 1994, Repentigni *et al*. 1997). Despite this criticism, these traditional methods of colour assessment are still popular within the scientific community and are considered very useful if carefully applied and interpreted (see e.g. Bortolotti *et al*. 1996, Repentigni *et al*. 1997, Senar *et al*. 1998).

For sixteen years, an easy procedure for evaluating plumage coloration in Common Crossbills *Loxia curvirostra* was used, based on the assignment of colours and patterns by visual inspection. The Common Crossbill is a cardueline finch which occurs in coniferous forests throughout the Palearctic (Cramp & Perrins 1994). Male coloration exhibits great variability, ranging from dull yellow to bright red, although the majority of birds are red-orange (Stradi 1998). This coloration is mainly attributed to carotenoid derivatives (Stradi *et al*. 1996), which reflect primarily in the visible spectrum (Goodwin 1973, Gross 1987, Moss & Weeden 1999). The aim of this study was to test for a correspondence between our visual colour scoring system and colour measures obtained from a digital colourimeter (Figuerola *et al*. 1999). In most passerine birds with ornamental plumage, variation in colour is very subtle and cannot be accurately measured with a simple visual scoring system (Hill 1998). Nevertheless, we predicted that there would be a good correspondence between visual and colorimetric measurements because the plumage of Common Crossbills shows an important gradation in colour between individuals (see also Hill 1998, Senar *et al*. 1998, Grill & Rush 2000).

Material and Methods

A total of 219 Crossbill males were captured between 2003 and 2005 with mist nets placed at drinking sites and salt sources in various subalpine areas of the Catalan Pyrenees and Pre-Pyrenees (1200-2400 m a.s.l.). Birds were marked with numbered aluminium rings to facilitate individual recognition. Sex and age were determined according to Svensson (1992) and Jenni & Winkler (1994). We scored the general plumage colour of individual birds along a visual scale ranging from yellow through orange to red, as per the work published by Hill (1992) on House Finches *Carpodacus mexicanus*. We also determined whether the main colour pattern was patchy or uniform. Colours and patterns were always assigned by the same observer.

Additionally, we used a CR200 Minolta chromometer to measure the crown, breast and throat colours of each bird, which were defined by three variables: lightness, saturation and hue

Table 1. Principal Component Analysis (PCA) of colorimetric measurements of male Common Crossbill plumage (n = 219). PCA1: three first principal components (PC1-PC3) of a PCA of the combined values of lightness, chroma and hue from three body areas (crown, throat and breast). PC Hue, PC Lightness, PC Chroma are the result of three independent PCAs on the values of lightness, chroma and hue of the three body parts (crown, throat and breast), respectively.
Anàlisi de Components Principals (PCA) de les mesures colorimètriques del plomatge de mascles de trencapinyes (n = 219). PCA1: representa els tres components principals (PC1-PC3) d'un PCA dels valors combinats de lluminositat, contrast, i to de tres àrees del cos (pili, gola, i pit). PC Hue, PC Lightness, PC Chroma és el resultat de tres PCA independents, cadascuna representa el valor de lluminositat, contrast, i to de tres àrees del cos (pili, gola, i pit) respectivament.

	PC1 Hue	PC2 Lightness	PC3 Chroma	PC Hue	PC Lightness	PC Chroma
H crown	0,87	0,18	0,31	-0,94	—	—
L crown	0,14	-0,78	-0,26	—	-0,82	—
C crown	-0,22	-0,43	0,65	—	—	0,81
H throat	0,87	0,21	0,25	-0,92	—	—
L throat	0,36	-0,68	-0,15	—	-0,79	—
C throat	-0,20	-0,56	0,50	—	—	0,77
H breast	0,89	0,03	0,16	-0,90	—	—
L breast	0,37	-0,67	-0,33	—	-0,83	—
C breast	-0,27	-0,12	0,66	—	—	0,66
Eigenvalue	2,8	2,1	1,5	2,55	2,0	1,7
% variance exp.	31	23	17	85	66	56

(Minolta Corporation 1994). 'Lightness', also called brightness, corresponds to the physical light intensity on a scale from zero (black) to 100 (white). 'Chroma' or saturation or intensity refers to the colour purity on a scale from zero (white) to 100 (pure colour). 'Hue' corresponds to the wavelength of the colour and is expressed in degrees of a circle starting with red, continuing through yellow, green and blue before returning to red (Figuerola *et al.* 1999, Fairchild 2005).

Principal Component Analyses (PCA) were conducted in order to reduce the number of colour variables and control for confusing or correlated variables (Montgomerie 2006). Only males were analysed. The first PCA included as variables lightness, chroma and hue values obtained from the crown, throat and breast of each bird (i.e. three colour parameters × three areas = nine variables). We obtained three main Principal Components (PCs). The first Principal Component (PC1) had strong positive loads for colour hues (H); PC2 showed higher negative loads for lightness (L), and PC3 had positive loads for colour chromas (C). Hence, each axis represented one of the colour descriptors provided by the colourimeter (H, L, C, respectively) and together explained 71% of the variance in plumage coloration displayed by the male Crossbills (Table 1). We refer to these components as PC1 Hue, PC2 Lightness and PC3 Chroma.

Since values of hue, chroma and lightness are measured on different scales and might potentially affect the efficiency of the PCA, we additionally performed three independent PCAs, one for each of the colour descriptors provided by the colourimeter (L, C and H), taking as variables the respective colour values obtained from the three different body areas. The first PCA for the hue values for crown, throat and breast resulted in a first component, which summarized 85% of the variance. All the variables loaded positively, indicating that the hue values from the three body areas were highly correlated and that the PC1 could be taken as a weighted average value of overall hue (PC Hue). A second PCA for the lightness of the same body regions resulted in a first component in which, again, all the variables loaded positively; this component explained 66% of the variance and was taken as a weighted average value of overall lightness (PC Lightness). The last PCA for the values of chroma of the crown, throat and breast, again resulted in a first component for which all variables loaded positively; this component summarized 56% of the variance and was taken as a weighted average value of the overall chroma (PC Chroma) (Table 1).

We then correlated the weighted averaged values of hue, lightness and chroma as obtained from the PCAs with the arithmetic means of

Table 2. Correlation (R) between different colour measurements in male Common Crossbills. Mean values refer to the average of crown, throat and breast measurements. "Hue PC1 LCH" refers to the first component (PC1), related to hue, from a PCA based on the lightness, chroma and hue values from the three Crossbill body areas used in the study (crown, throat and breast) (see Table 1). "Lightness PC2 LCH" refers to the second component (PC2) from this PCA analyses, related to lightness. "Chroma PC3 LCH" refers to the third component (PC3) from this PCA analysis, related to chroma (see Table 1). Principal Components (PC1 H, PC1 C, PC1 L) refer to the first components (PC1) obtained from three independent PCAs on the three Crossbill body areas used in the study (crown, throat and breast) for every colour component (LCH) (see Table 1).

Valor de correlació (R) entre diferents mesures de coloració de mascles de trencapinyes. Els valors mitjans es refereixen al valor mitjà del pili, de la gola, i del pit. "Hue PC1 LCH" es refereix al primer component (PC1), relacionat amb el to, d'un PCA (Anàlisi de Components Principals) basat en valors de lluminositat, contrast i to de tres àrees usades en aquest estudi (pili, gola i pit) (veure taula 1). "Lightness PC2 LCH" es refereix al segon component (PC2) del PCA, relacionat amb la lluminositat. "Chroma PC3 LCH" es refereix al tercer component (PC3) del PCA, relacionat amb el contrast. Els components principals (PC1 H, PC1 C, PC1 L) es refereixen als components principals (PC1) obtinguts de tres PCA independents de les tres àrees del cos (pili, gola, i pit) dels trencapinyes utilitzades en aquest estudi per a cada component de color (LCH).

	Mean Hue	Mean Lightness	Mean Chroma
Mean Hue	—	0,14 *	-0,16 *
Mean Chroma	—	0,09 ns	—
Hue PC1 LCH	0,95 ***	—	—
Lightness PC2 LCH	—	0,86 ***	—
Chroma PC3 LCH	—	—	0,79 ***
Hue PC1 H	0,95 ***	—	—
Lightness PC1 L	—	0,86 ***	—
Chroma PC1 C	—	—	0,79 ***

*p < 0.05; ** p < 0.01; *** p < 0.001

hue, lightness and chroma directly obtained by averaging the original values (not PCA transformed) of the three body areas. Analyses showed that the PCA scores correlated strongly to the untransformed mean values (Table 2). This indicated that the simple averages of hue, lightness and chroma from the three body areas summarised in an unbiased way the overall colour variability of the bird. Therefore, in subsequent analyses, we only used mean colorimeter measurements of LCH averaged from the three body areas. Factorial ANOVAs testing for correspondences between these colorimetric data and our visual categories were then performed to validate our qualitative method for colour assessment. Independent variables included mean hue, chroma and lightness as measured with the colourimeter. The factors used were visually assessed colours (with three levels: yellow, orange and red) and patterns (with two levels: uniform and patched).

Results

Colour categories assigned by general visual inspection (yellow, orange and red) differed significantly in hue (Table 3). Yellow birds showed higher scores than orange or red individuals, the latter having the lowest values of the three categories (Table 4). Colour pattern (uniform vs. patched) was not related to colourimetric hue, although we found a significant interaction between this variable and our visual colour categories (Table 3). Differences in hue in relation to colour patterns were found in orange males ($F_{1,142} = 19.32$; $p < 0.001$), showing that hue values were greater in birds with patched pattern (mean ± SE = 60.88 ± 0.81; n = 82) than in uniformly coloured birds (mean ± SE = 55.20 ± 1.04; n = 62). No differences in hue in relation to coloration pattern were found in either yellow ($F_{1,20} = 1.74$; $p = 0.20$) or red birds ($F_{1,51} = 2.87$; $p = 0.10$).

Yellow, orange and red individuals did not differ in colour chroma. However, coloration pattern did seem to significantly affect this variable (Table 3). Patched individuals had lower values of chroma than uniform ones, irrespective of the colour category analyzed (Table 4).

Finally, visual colour categories differed significantly in lightness (Table 3). Yellow birds were brighter than orange and red ones, the latter having lower values than the other two categories (Table 4). No differences in lightness were found in relation to coloration pattern (Table 4).

Discussion

The results, as expected, showed a good correspondence between the tristimulus scores generated by the colorimeter and our visual scoring system, a finding that supports the accuracy of this qualitative method for colour assessment in male Crossbills. The three visible colour classes used (yellow, orange and red) were mainly related to hue, and to a lesser extent to lightness parameters. The distribution pattern of the coloration (uniform/patched) was mainly associated with chroma. Orange males showed an additional variation in hue values in relation to pattern, with uniformly coloured birds showing a lower (redder) hue than patchy birds. Therefore, four easy-to-distinguish colour categories (yellow, patched orange, uniform orange and red) may conveniently and accurately be used

Table 3. Results from three ANOVAs in which the variation in mean hue, chroma and lightness of the plumage colour of male Common Crossbills in relation to qualitative colour categories (red, orange, and yellow) and pattern (uniform and patched) is analysed.
Resultats de les tres ANOVAs en els quals s'analitza la variació en el to, contrast i lluminositat mitjans de la coloració del plomatge de mascles de trencapinyes en funció de categories de qualitatives de color (groc, taronja i vermell) i patró (uniforme i pigallat).

	F	d.f.	p
Hue			
Colour	75.92	2	< 0.001
Pattern	1.65	1	0.20
Colour x Pattern	3.62	2	0.03
Lightness			
Colour	4.45	2	0.01
Pattern	0.76	1	0.39
Colour x Pattern	2.20	2	0.11
Chroma			
Colour	2.08	2	0.13
Pattern	11.49	1	< 0.001
Colour x Pattern	0.36	2	0.70

Table 4. Hue, lightness and chroma values (mean ± SE) of the three qualitative colour categories and the two colour patterns used to describe the plumage colour of male Common Crossbills (see Table 3).
To, lluminositat i contrast (mitjana ± EE) de tres categories qualitatives de color i dos patrons de color utilitzats per descriure la coloració del plomatge dels mascles de Trencapinyes (vegeu la Taula 3).

	Hue	Lightness	Chroma	N
Yellow	71.25 ± 1.77	46.07 ± 0.51	—	22
Orange	58.45 ± 0.68	44.58 ± 0.20	—	144
Red	46.23 ± 1.39	44.27 ± 0.37	—	53
Uniform	—	—	17.34 ± 0.28	101
Patched	—	—	15.54 ± 0.28	118

to describe the plumage coloration of male Crossbills (Figure 1).

When handling birds, all observers able to discriminate between simple colours and patterns should be capable of differentiating and assigning our proposed categories. These categories are clear enough to avoid biases due to variation in colour sensitivity or observer subjectivity. Although our method is restricted to the human visible spectrum, this limitation is not that problematic when describing carotenoid-based coloration. Most of these pigments show little reflectance in the UV part of the spectrum (Goodwin 1973, Gross 1987, Moss & Weeden 1999; but see Mays *et al.* 2004) and recent data show that the reflectance of the UV peak (300–400 nm) is highly correlated with the peak of the yellow-red spectrum (500–700 nm) (Senar & Quesada 2006, Senar *et al.* 2008).

In recent years, Crossbills have gained popularity within the scientific community as a model species in studies on evolutionary processes and sympatric speciation (e.g. Knox 1992, Benkman 1993, Questiau *et al.* 1999, Edelaar *et al.* 2003,

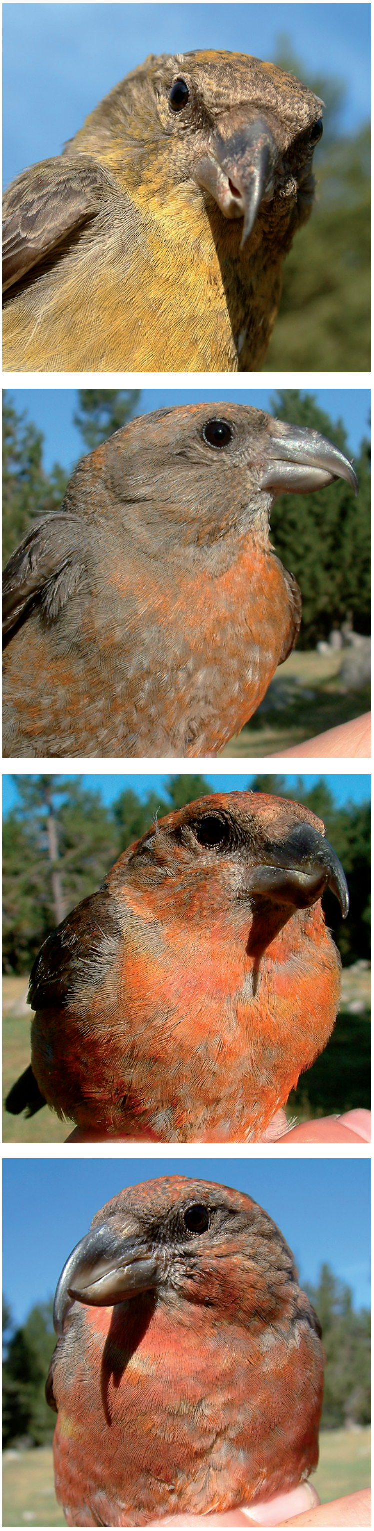
A
B1
B2
C

Figure 1. Visual colour categories proposed to describe the plumage coloration of male Crossbills: yellow (A), patchy orange (B1), uniform orange (B2) and red (C).
Categories visuals de color proposades per descriure la coloració del plomatge de mascles de Trencapinyes: groc (A), taronja pigallat (B1), taronja uniforme (B2) i vermell (C).

Summers *et al*. 2007, Förschler & Kalko 2009). However, most of these studies are concentrated on behavioural and morphological aspects of the species. Further research on plumage coloration might contribute considerably to our understanding of the puzzle of Crossbill evolution, especially if these studies are performed with wide-ranging cooperation between researchers and amateur ornithologists throughout Europe (Edelaar *et al*. 2003). The important methodological constraints to a broader cooperation might be solved with the application of our easy procedure for colour assessment. The implementation of our validated visual method might allow amateurs and professionals alike to join forces in the future in a large-scale cooperation programme aimed at the collection of reliable data on colour and the use of available databases with long data series.

In a more general sense, our results suggest that visual colour inspection may in fact be more objective and useful than currently thought.

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Resum

Coloració del plomatge dels mascles de Trencapinyes *Loxia curvirostra*: avaluació visual validada per colorimetria

En aquest article presentem un mètode senzill i fiable per avaluar les diferents tipologies i patrons de coloració del plomatge dels mascles de Trencapinyes *Loxia* spp. En una mostra de 219 mascles de Trencapinyes *Loxia curvirostra* capturats al Prepirineu, es van comparar les diferents tipologies qualitatives de coloració obtingudes per inspecció ocular dels individus (colors grocs, taronges i vermells, distingint addicionalment entre colors homogenis i tacats), amb dades quantitatives obtingudes amb un colorímetre (valors de lluminositat, to i intensitat). Es va trobar una bona correspondència entre l'avaluació visual i els valors colorimètrics. Aquests resultats ofereixen als amateurs, ornitòlegs de camp i investigadors interessants en l'espècie, una alternativa adequada, senzilla i barata per mesurar les variacions en el color d'aquesta espècie. Des de un punt de vista més general, els nostres resultats suggereixen que les valoracions del color visuals poden ser més objectives i útils del que fins ara s'havia pensat.

Resumen

Coloración del plumaje de los machos de Piquituerto Común *Loxia curvirostra*: evaluación visual validada por colorimetría

En este artículo presentamos un método sencillo y fiable para evaluar los distintos tipos y patrones de coloración del plumaje de machos de Piquituerto *Loxia spp*. En una muestra de 219 machos de Piquituerto Común *Loxia curvirostra* capturados en el Pre-Pirineo, comparamos las diferentes categorías cualitativas de coloración asignadas en el campo mediante inspección ocular de los individuos (coloración amarilla, naranja o roja, distribuida de forma homogénea o parcheada), con los datos cuantitativos obtenidos con un colorímetro (valores de luminosidad, tono e intensidad). Encontramos una buena correspondencia entre nuestro sistema de evaluación visual y los valores colorimétricos. Estos resultados ofrecen a amateurs, ornitólogos de campo e investigadores interesados en la especie una alternativa objetiva, sencilla y barata para medir las variaciones de coloración de esta especie. Desde un punto de vista más general, nuestros resultados sugieren que las valoraciones visuales de color pueden ser más objetivas y útiles de lo que se pensaba hasta ahora.

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