

RESEARCH ARTICLE

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# The carotenoid-continuum: carotenoid-based plumage ranges from conspicuous to cryptic and back again

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## Abstract

**Background:** Carotenoids are frequently used by birds to colour their plumage with green, yellow, orange or red hues, and carotenoid-based colours are considered honest signals of quality, although they may have other functions, such as crypsis. It is usually assumed that red through yellow colours have a signalling function while green is cryptic. Here we challenge this notion using the yellow and green colouration of blue tits (*Cyanistes caeruleus*), great tits (*Parus major*) and greenfinches (*Carduelis chloris*) as a model.

**Results:** The relationship between colouration (chroma, computed using visual sensitivities of conspecifics) and detectability (contrast against natural backgrounds as perceived by conspecifics and avian predators) followed a similar curvilinear pattern for yellow and green plumage with minimum detectability at intermediate levels of carotenoid deposition. Thus, for yellow and green plumage, colours at or close to the point of minimum detectability may aid in crypsis. This may be the case for blue and great tit green and yellow plumage, and greenfinch green plumage, all of which had comparably low levels of detectability, while greenfinch yellow plumage was more chromatic and detectable. As yellow and green blue tit colouration are strongly affected by carotenoid availability during moult, variation in pigment availability between habitats may affect the degree of background-matching or the costliness of producing cryptic plumage.

**Conclusions:** Increasing carotenoid-deposition in the integument does not always lead to more conspicuous colours. In some cases, such as in blue or great tits, carotenoid deposition may be selected through enhanced background-matching, which in turn suggests that producing cryptic plumage may entail costs. We stress however, that our data do not rule out a signalling function of carotenoid-based plumage in tits. Rather, it shows that alternative functions are plausible and that assuming a signalling function based solely on the deposition of carotenoids in the integument may not be warranted.

## Background

Carotenoids are some of the commonest pigments that confer colour to bird plumage, being responsible for many yellow, orange and red, but also greenish hues [1]. As carotenoids cannot be synthesised *de novo* by birds, they need to be ingested with food [1]. Thus, the extent of carotenoid-based colouration could be a sign of the foraging ability of an individual, which may be indicative of its quality and/or condition [1,2]. Moreover, allocating carotenoids to produce colourful plumage could be

traded-off with other important functions such as free-radical scavenging, immune activation, etc. (for a review see [1]). Given the potential of carotenoid-based colouration to convey information about individual quality, it has been often assumed that yellow through red carotenoid-based colours should have a signalling function. For some carotenoid-based plumages the signalling function has been confirmed through careful experimental studies (e.g. [3-7]). In other cases a signalling function has been inferred based on observed correlations between plumage colouration and condition at moult, degree of parasitism, immune-responsiveness, etc. (e.g. [8-13]).

An example of the latter is the yellow ventral colouration of great tits (*Parus major*) and blue tits (*Cyanistes*

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*caeruleus*), that are popular model systems for the study of carotenoid-based ornamental plumages. Although yellow colouration in these species (which is based on the deposition of the carotenoids lutein and zeaxanthin obtained directly from the diet [14]) has been intensively studied, a confirmation of its signalling function is still elusive. In general, for both adults and nestlings the intensity of yellow colouration depends on environmental factors at the time of plumage development such as food availability [15,16], carotenoid content of food [17-20], parasitism [21] and pollution levels [22-24]. Therefore in theory yellow colouration could indicate individual quality. In adult tits, some studies suggest that yellower individuals are better at providing food to offspring [25-27], have higher reproductive output [28] or survival [21], although the only available mate choice study found no difference in yellow colouration between preferred and non-preferred male blue tits [29]. In fledglings, evidence in favour of a signalling function is even scarcer, as parents do not seem to discriminate between nestlings based on their yellow colouration [30], and nestling survival is unrelated to their colour [31]. This has led to doubts about the signalling function of yellow colouration in these species [32].

Alternatively, the deposition of yellow carotenoids may be selected to reduce conspicuousness to avian predators. Predation by birds of prey such as the sparrowhawk (*Accipiter nisus*) is an important source of mortality for adult and fledgling tits [33-35], and due to their good colour discrimination abilities (compared to other potential predators such as mammals or reptiles), birds of prey are thus expected to exert strong selection pressure on cryptic colouration (e.g. [36]). Indeed, crypsis was initially proposed as the main function of yellow tit plumage [37], especially in fledglings which are very prone to being depredated [38], but this idea has not received much attention (although see [31,33]). Crypsis has been the usual explanation for the occurrence of the green, carotenoid-based, back colouration in these and other species [39,40], although there is limited evidence that green plumage is cryptic. The main difference between yellow and green plumage is that in the latter yellow carotenoids are deposited on more heavily melanised (grey) feathers ([41] and unpubl. data). For green plumage it seems clear that a certain quantity of yellow carotenoids has to be deposited in order to achieve a more cryptic plumage against natural backgrounds such as green leaves. However, how conspicuousness covaries with colour intensity is unknown (i.e. to what extent does conspicuousness decrease with increasing carotenoid deposition?). Whether carotenoid deposition has the same effect on yellow plumage is unclear.

If yellow plumage functions as a signal we would expect clear differences between green and yellow plumage

based on signalling theory [42-44]. Specifically, we would predict that more intense colouration (higher deposition of carotenoids, higher production costs) in yellow plumage should lead to higher detectability compared to green plumage. At the same time, yellow plumage should respond more strongly to the experimental manipulation of carotenoid availability during moult than green colour (e.g. [13]).

Here we use blue and great tit carotenoid-based colouration (yellow and green) as a case study to highlight the effects of carotenoid deposition in the plumage on colouration and detectability. To this end we determined the relationship between colouration and detectability for great tits and blue tits, using data on the natural variation in colouration of adults and fledglings, in combination with experimental manipulation of carotenoid availability during moult. Additionally, in order to show the pattern of variation beyond the range of colouration of blue and great tits, we include reflectance measurements of the greenfinch (*Carduelis chloris*) which possesses more intensely coloured green and yellow plumage patches than the tit species, and where yellow colouration is more sensitive than green colouration to carotenoid-availability during moult [13].

## Methods

### Study area and species

Birds were captured using mist nets in Möggingen, SW Germany (47°45'N, 8°59'E), between March and June from 2005 to 2007. The area consists of a matrix of mixed forest, orchards, gardens, and reed beds. Adult and fledgling great tits and blue tits, and adult greenfinches, were measured (see Reflectance Spectrometry below) directly after capture and then released. Some blue tit measurements were made on fledglings that had been taken into captivity as nestlings (aged 12 days) in May 2006 together with their parents which continued raising them until independence in large outdoor aviaries (under licence from Regierungspräsidium Freiburg 55-8852.15/05 and G-06/05, 35-9185.82/3/339). Their colouration was measured five to six weeks after hatching, when the yellow to greenish-grey juvenile plumage, present until the autumn moult into adult plumage, was fully developed. As the intensity of carotenoid-based colouration is determined early in nestling development [18], food provided in captivity most likely did not affect plumage colouration. Some of these fledglings were subsequently used in an experiment designed to manipulate the availability of carotenoids during moult [45-47]. Fledgling blue tits were fed either a semi-synthetic control diet (11 males and 10 females; no added lutein other than that present in mealworms) or a semi-synthetic enriched diet (9 males and 10 females; with higher protein content and 0.05% of wet weight added lutein) during the post-juvenile moult

period (license from Regierungspräsidium Freiburg Nr. Aktenzeichen 55-8852.15/05 and Registriernr. G-06/05, Aktenzeichen 35-9185.82/3/339 respectively). Their plumage reflectance was measured as detailed below the following spring (March 2007).

### Reflectance Spectrometry

Yellow plumage patches measured were the breast of great tits and blue tits and the tail patch of the greenfinch. Their colour is produced by depositing yellow carotenoids (lutein with small amounts of zeaxanthin in the blue tit and great tit, [48,32,14]; and canary xanthophylls A and B in the greenfinch: [48,49]) on white feathers. Olive-green plumage patches (the back in the three species) derive their colour by depositing yellow carotenoids (presumably the same as in yellow plumage) on melanized grey feathers [41]. Despite depositing different carotenoids in the plumage we considered tit and greenfinch carotenoid colouration as a single colour type due to the similarities in absorption profiles of lutein, zeaxanthin and canary xanthophylls (all three show absorption maxima between 440-450 nm, [48], see also the similarity in shape of plumage reflectance spectra in Additional File 1). For comparative purposes we also measured the reflectance of the presumably cryptic brown-grey melanin-based back plumage of other species captured at the study site namely: wren, *Troglodytes troglodytes* (N = 3); chiffchaff, *Phylloscopus collybita* (N = 10); blackcap, *Sylvia atricapilla* (N = 66); blackbird, *Turdus merula* (only females, N = 11); and robin, *Erithacus rubecula* (N = 31).

Reflectance spectra were obtained using an Avaspec 2048 spectrometer connected to a deuterium-halogen light source (Avalight-DHS, Avantes, Eerbeek, Netherlands) through a bifurcated fibre optics cable fitted at the end with a plastic cylinder to standardise measuring distance and shield out ambient light. The probe was held perpendicular to the surface of the feathers and illumination and recording angles were both 90°. Reflectance was computed relative to a WS-2 white standard using the program Avasoft 6.2.1. We took a set of five reflectance readings of different predefined and standardized spots in each body part separated by at least 0.5 cm. Reflectance of the breast was measured on the upper breast (i.e. above the belly) taking two readings on either side and one closer to the centre (but avoiding the dark breast stripe). Measurements on the back were taken following the pattern of five points on a die centred on the middle of the back (the rump was not measured). For the greenfinch we also measured tail colour whereby we only measured the reflectance of the yellow patch on the rectrices.

Reflectance of natural backgrounds present in the study area was measured with the same equipment in spring 2008. We measured leaves, small branches and bark of the main trees and shrubs in the area and samples of leaf-

litter and grasses, totalizing 1954 reflectance spectra belonging to 26 different types of vegetation (76.7 spectra on average per vegetation type, range: 15-235; see Table 1 in Additional File 2 for a complete list). We separated the sample in the two main types of backgrounds present in the environment, namely green backgrounds (green leaves and grasses) and brown backgrounds (branches, bark and leaf-litter). We computed the average green and brown backgrounds for each species in the sample and then we calculated the overall green and brown averages, weighing the contribution of each species by its relative abundance in the study area.

Reflectance values of plumage and backgrounds between 300 to 700 nm (in 1 nm steps) were imported into custom made spreadsheets for further analysis. Average reflectance spectra of plumage and backgrounds are provided in Additional Files 1 and 2 respectively.

### Colour analyses

Our analyses focused on assessing the relationship between the intensity of carotenoid-based colouration and detectability. Thus, these two components needed to be estimated. The intensity of colouration in carotenoid-based plumage colours is most likely dependent on the quantities of carotenoids deposited in the feathers, and yellow plumage colour (mainly measurements of chroma) correlates positively with carotenoid content in several bird species (great tits [32], greenfinches, [49], American goldfinches *Carduelis tristis* [50]). Thus we (the same as potential receivers interested in assessing a particular bird) used plumage colouration as a proxy for carotenoid content and assumed that plumage with higher chroma contained higher amounts of deposited carotenoids. We defined detectability as the combined chromatic and achromatic visual contrast against natural backgrounds as seen by conspecifics and birds of prey [51][52][53][54], [36]. Birds of prey, such as the sparrowhawk, were chosen as model predators because they are one of the most common and important predators of great and blue tits [33,35,55-59]. At the same time compared to other potential tit predators (mammals or reptiles) birds have a highly sophisticated visual system with good colour discrimination abilities [36,60,61] and thus are expected to exert strong selection pressures on the visual appearance of their prey. Note that we only computed detectability for the specific colours under study and make no claim about the detectability of each species as a whole, which probably also depends on other exposed plumage patches and their size, in combination with behaviour and other traits.

### Visual modelling

To quantify variation in carotenoid-based colouration and contrast against natural backgrounds we used a physiological model of avian vision [60]. This model, which

can be used to compute chromatic and achromatic contrasts between different reflectance spectra, relies on the correct estimation of a series of parameters. Chiefly, data on spectral sensitivities of photoreceptors (including the effects of the ocular media and the effects of oil droplets) is used in combination with the spectrum of ambient light to obtain stimulus quantum catches for each photoreceptor [60]. These are used to compute contrast between two stimuli (reflectance spectra) and contrast depends on the signal-to-noise ratio of the photoreceptors which in turn depends on the relative abundance of the photoreceptors in the retina. Values of contrast will thus depend on the illuminant used, knowledge of the spectral sensitivity of the photoreceptors, and the relative abundance of these photoreceptors.

Colour vision in diurnal birds depends on the four types of single cones, sensitive to very short (VS), short (S), medium (M), and long (L) wavelengths. The spectral sensitivities of the four single cones vary interspecifically, but among birds two main groups can be recognized based on the sensitivity maximum of the VS cone [62,63]: birds with U-type eyes (some passerines, parrots, gulls, trogons), showing peak sensitivity in the near ultraviolet and birds with V-type eyes, such as raptors, with peak VS sensitivity in the violet wavelength range [62]. Therefore, we used generalized spectral cones sensitivities of U- and V-type birds (from Appendix 1 in [63]) to compute cone quantum catches for each cone type, employing formula 1 in Vorobyev et al. [60], with standard daylight (D65) as the illuminant. Changes in illuminant used in the calculations have been shown to affect results but these effects are relatively small due to colour constancy [60,11,64], and are unlikely to affect the results. The choice of generalized U-type cone sensitivities instead of blue tit specific values is unlikely to have affected our results since small differences in sensitivities (peak sensitivities between generalized U-type and blue tit specific sensitivities differ by less than 5 nm [63,65]) have been shown to cause minimal differences in contrast [66]. While single cones are used for chromatic tasks in birds, perception of achromatic variation is believed to be mediated by the double cones [67]. We computed double cone quantum catches using the sensitivity spectrum of the double cones of *Leiothrix lutea* [68] and formula 1 in Vorobyev et al. [60] as above.

#### **Quantification of carotenoid-based colouration as seen by conspecifics**

Single cone quantum catches for U-type eyes were transformed into relative cone quantum catches by dividing each value by the sum of all four. When these are plotted in the avian tetrahedral visual space, each reflectance spectrum is defined as one point, with x, y and z coordinates. Tetrahedral coordinates were computed using the formulas in Kelber et al. [69]. Reflectance measurements

from yellow and green plumage patches form more or less discrete cigar shaped clouds in the visual space (see for example figure S2 in [11]). As an estimate of the intensity of carotenoid-based colouration we used Euclidean chroma which is calculated as the Euclidean distance to the achromatic centre (i.e. where all cone types are equally stimulated, [63]). Euclidean chroma (hereafter "chroma") correlates strongly and positively with carotenoid chroma (carotenoid chroma =  $-2.98 - 19.85 \cdot \text{chroma} - 26.05 \cdot \text{chroma}^2$ ;  $R^2 = 0.93$ , all  $p < 0.0001$ ) a variable commonly used to quantify yellow carotenoid-based colouration in birds (computed as  $(R_{700} - R_{450})/R_{700}$ , [70]). Thus similar results are also obtained if we use carotenoid chroma. Note however, that carotenoid-chroma does quickly become saturated at higher carotenoid concentrations (hence the significant quadratic component in the formula above), becoming less sensitive to changes in carotenoid concentrations as shown in simulations [71]. Similar simulations show that higher carotenoid concentrations are needed for Euclidean chroma to become saturated, largely outside the range of colouration of this study (unpubl. data).

#### **Quantification of visual contrast as seen by conspecifics and birds of prey**

Chromatic visual contrast ( $\Delta S$ , also called discriminability) between yellow and green plumage patches of each individual and the average green and brown backgrounds was computed using formulas 2, 3, 4 and 8 in Vorobyev et al. [60] which are based on the assumption that discriminability thresholds are set by the signal-to-noise ratio. In order to estimate the signal-to-noise ratio this formula requires knowledge about the proportions of single cones in the retina. Cone proportions are known for the blue tit [72] but not for great tits, greenfinches or putative avian predators such as the sparrowhawk. Since variability in retinal cone proportions can affect the values of contrast [66] we assessed how this parameter affected our results using all known retinal cone proportions [73]. Our analyses (see Additional File 3 for details) indicate that the shape of the relationship between chroma and contrast was similar for all used retinal cone proportions (Figures 1 and 2 in Additional File 3). Therefore we carried out our computations using cone proportions of the blue tit (0.37:0.71:1:1; VS:S:M:L) as representative for U-type eyes and of the peafowl (0.47:0.89:1.04:1) for V-type eyes (as in [74]).

Achromatic contrast ( $\Delta L$ ) was computed in the same way for conspecifics and predators using double cone quantum catches and followed formula 7 in Siddiqui et al. [75] assuming a Weber fraction of 0.05 for the L cone. As birds probably rely on a combination of chromatic and achromatic contrast cues to detect conspecifics or prey [76,54], and in order to reduce the number of statistical tests, we combined chromatic and achromatic contrast in

a single measurement following Darst et al. [52], that we termed contrast. Chromatic and achromatic contrasts are measured in 'just noticeable differences' (jnd), where values above 1 jnd are assumed to be discriminable by birds under optimal viewing conditions [60]. As all values of contrast in this study exceeded 1 jnd (see Results) it could be argued that avian predators should always be able to detect these colours, and that variation in contrast is largely irrelevant for crypsis [77]. However, more contrasting colours may be detected from further away. Schaefer et al. [54] showed that crows (*Corvus ossifragus*) detected more contrasting artificial fruit from further away than less contrasting (but contrast  $\gg$  1 jnd) fruit, probably due to the differences in chromatic and achromatic contrasts against the background. Similarly, more contrasting lizard and fruit models suffered higher "predation" by birds than less contrasting, but still detectable (i.e. contrast  $\gg$  1 jnd) models [51,78]. Moreover, available evidence indicates that contrast seems to scale in a roughly linear fashion with behavioural measurements of perception. Cazetta et al. [78] found that removal rate of highly contrasting artificial fruit by birds was linearly correlated with chromatic contrast up to high values of contrast ( $> 40$  jnd) beyond which the relationship flattened out. Similarly, but at the low end of contrast values (0-4 jnd), the rate of rejection of artificial eggs from chaffinch (*Fringilla coelebs*) nests followed a linear function of their chromatic contrast [79]. Thus, it is likely that variation in contrast above the 1 jnd threshold contributes to the variation in overall conspicuousness. Finally, a cryptic colour may not necessarily need to match an average background perfectly but rather to be within the levels of contrast found among elements of the background (e.g. [80]). We tried to include this aspect by comparing the contrast between plumage and average backgrounds with the levels of contrast among background elements. In order to do so we computed the contrast between each background (i.e. each plant-type-specific brown and green average) and the global green and brown background averages.

## Results

Taking all three species together the relationship between chroma and detectability followed a curvilinear pattern with minimum detectability at intermediate values of chroma for both yellow and green plumage (Figures 1 and 2). This relationship was very similar for U- versus V-type eyes (although in general contrast was higher for U-type eyes with blue tit cone proportions than for V-type eyes with peafowl cone proportions [74], but see Additional File 3 for an exception) and for both main types of average natural backgrounds. Roughly similar curvilinear relationships were obtained if instead of the global averages we used the average green and brown backgrounds

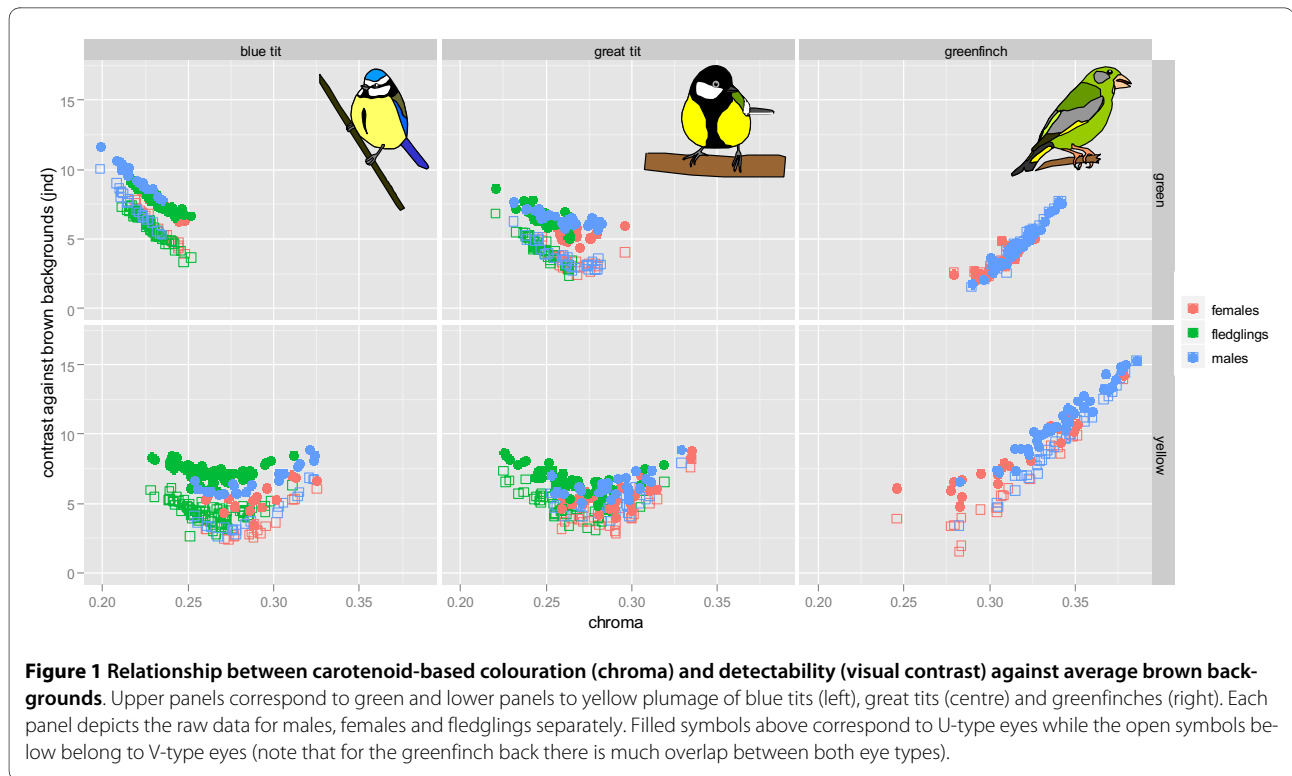
of each plant species separately (Figure 3 and Additional File 4).

For yellow and green plumage patches, as chroma increased (due to increased carotenoid deposition) their detectability to both conspecifics and potential predators decreased until a minimum was reached at intermediate levels of carotenoid deposition. Beyond this point further increase in chroma led to higher detectability. The three species studied here occupied different parts of this 'carotenoid continuum', with blue tits having the lowest, great tit intermediate and greenfinches highest levels of carotenoid deposition. Within each species the range of carotenoid variation was further partitioned by sex and/or age class. This information is detailed in Table 1, Figures 1, 2 and 4 and summarized below.

In blue and great tits, yellow breast colouration was more intense in adults than in fledglings, while there was little sexual dichromatism in adults. Conversely, sexual dichromatism in yellow tail colouration was marked in greenfinches where males had more intense colouration than females. Chromatic differences may or may not lead to differences in detectability depending on the position along the carotenoid continuum (Figures 1 and 2). Thus, while fledgling tits differed significantly from adults in their colouration, the difference in detectability was small (0 - 1.9 jnds depending on the background and eye type). Sex differences in detectability for both tit species were also small (0.25 - 1.3 jnd). In greenfinches on the other hand, the more elaborate ornamentation of males resulted in the increased detectability of this plumage patch compared to females (difference = 2.5 - 3.5 jnds).

The green back colouration of fledgling great tits was less intense than in adults, which showed little sexual dichromatism. For blue tits on the other hand, fledglings showed more intense back colouration than males, and slightly less than females. Unlike great tits, adult blue tits showed sexually dichromatic green back colouration, females being more chromatic. Green back colouration was moderately sexually dichromatic for greenfinches, males being more chromatic than females. Adult female blue tits and fledglings differed little in detectability (-0.7 - 0.1 jnd) which was lower than that of adult males (0.5 - 1.8 jnd), while adult male and female great tits were in general less contrasting than fledglings although differences were small (-0.02 - 1.3 jnd). Among greenfinches, the small differences in colouration between males and females led to small differences in detectability, but only against brown backgrounds (males being more detectable than females, brown backgrounds, 1.3 jnd; green backgrounds, -0.08 - -0.012 jnd).

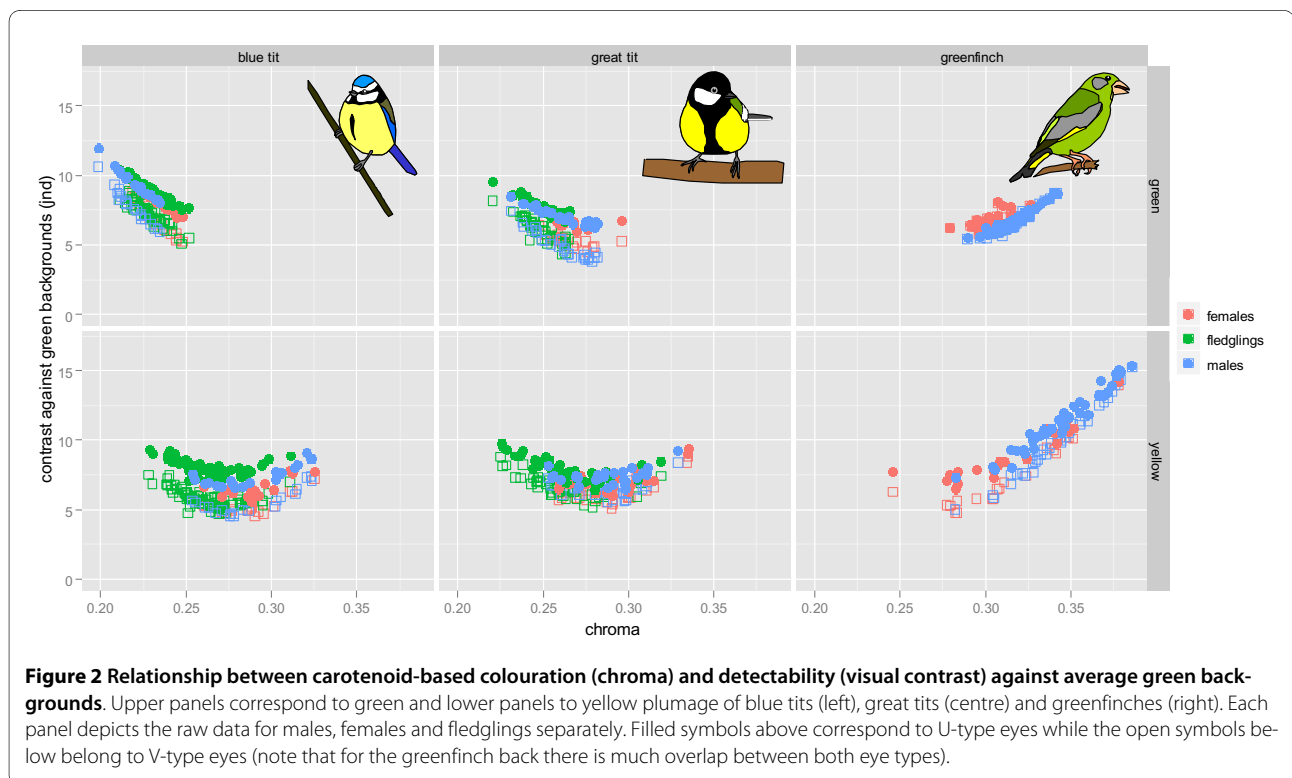
Average levels of contrast between carotenoid-based tit coloration and background were inside the range of within-background contrast (Figure 4). Average levels of contrast of tit carotenoid-based plumage are comparable



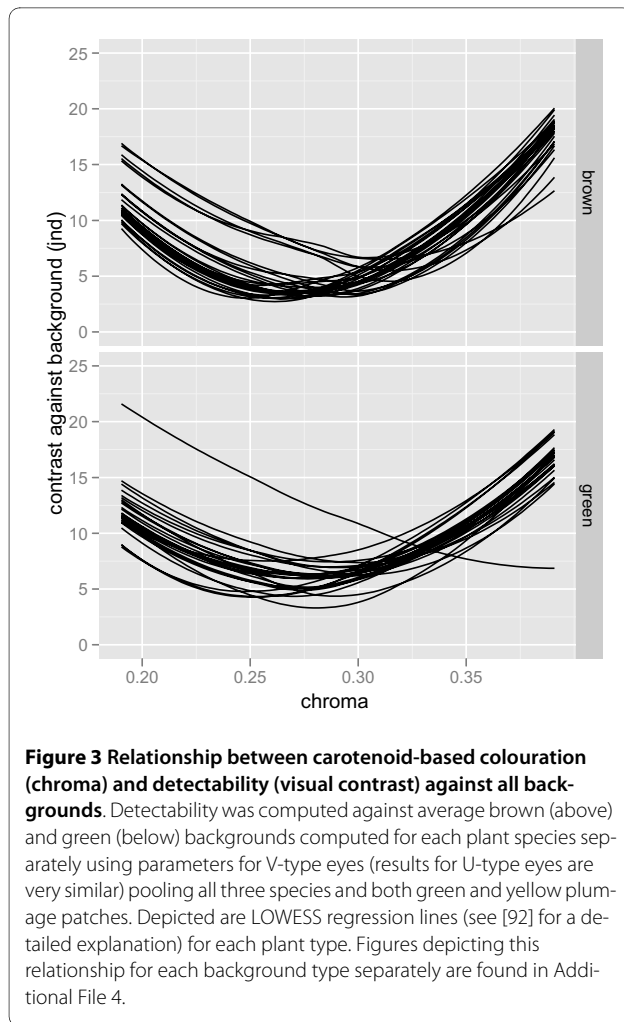
**Figure 1** Relationship between carotenoid-based colouration (chroma) and detectability (visual contrast) against average brown backgrounds. Upper panels correspond to green and lower panels to yellow plumage of blue tits (left), great tits (centre) and greenfinches (right). Each panel depicts the raw data for males, females and fledglings separately. Filled symbols above correspond to U-type eyes while the open symbols below belong to V-type eyes (note that for the greenfinch back there is much overlap between both eye types).

to those of the melanin-based back plumage of other local species (Figure 4), some of which are typically considered highly cryptic (e.g. wren or chiffchaff).

Carotenoid availability during moult strongly affected yellow and green plumage in male and female blue tits (Table 2). Birds fed carotenoid-enriched diet had higher



**Figure 2** Relationship between carotenoid-based colouration (chroma) and detectability (visual contrast) against average green backgrounds. Upper panels correspond to green and lower panels to yellow plumage of blue tits (left), great tits (centre) and greenfinches (right). Each panel depicts the raw data for males, females and fledglings separately. Filled symbols above correspond to U-type eyes while the open symbols below belong to V-type eyes (note that for the greenfinch back there is much overlap between both eye types).



**Figure 3 Relationship between carotenoid-based colouration (chroma) and detectability (visual contrast) against all backgrounds.** Detectability was computed against average brown (above) and green (below) backgrounds computed for each plant species separately using parameters for V-type eyes (results for U-type eyes are very similar) pooling all three species and both green and yellow plumage patches. Depicted are LOWESS regression lines (see [92] for a detailed explanation) for each plant type. Figures depicting this relationship for each background type separately are found in Additional File 4.

chroma than control birds. Control birds were considerably less chromatic than wild-caught birds (compare values in Tables 1 and 2) suggesting that the amount of carotenoids available to them was lower than local carotenoid availability in the wild. Experimental effects on carotenoid-based colouration led to differences in detectability in blue tit yellow and green plumage, in that carotenoid supplemented birds had lower detectability, this effect being particularly strong for the green back plumage (yellow =  $-0.3 - 1.8$  jnd; green =  $-2.1 - 3.5$  jnd).

## Discussion

We found more similarities than differences between yellow and green plumage. For both types of plumage the relationship between carotenoid-based colouration and detectability followed a comparable curvilinear pattern with minimum detectability at intermediate levels of carotenoid deposition (pooling the data from the three species, Figures 1 and 2). While in general yellow plumage patches were more chromatic than green plumage, both had similar levels of low detectability (contrast against

natural backgrounds) in tits. Furthermore, our experiments indicate that, at least for the blue tit, the yellow breast colouration and the green back colouration are both strongly affected by carotenoid availability during moult (Table 2). These patterns were very similar for all types of measured natural backgrounds (Figure 3) and for both types of avian visual systems (Figures 1 and 2).

## Honest yellow signals?

Individual variation in the ability to obtain and metabolise carotenoids is assumed to enforce the honesty of carotenoid-based signalling, thus maintaining the correlation between individual variation in colouration and quality [2]. The curvilinear relationship between carotenoid deposition and conspicuousness indicates that only for colours with levels of carotenoid deposition beyond the point of minimum detectability (Figures 1 and 2) is it likely that increasing carotenoid-deposition will be (mainly) favoured by selection through signalling. This is best exemplified by the yellow tail patch of the male greenfinch which has been demonstrated to fulfill the requirement of heightened condition-dependence of a signalling (indicator) trait since it responds disproportionately to the dietary availability of carotenoids compared to other carotenoid-based plumage patches [13].

Similarly, yellow carotenoid-based colouration in blue and great tits is generally assumed to act as a signal of quality both in adults and fledglings (see Introduction). Indeed, our results (Table 2) and published information [15,17,70,18,19,27] show that yellow has the potential to convey information about carotenoid availability and hence foraging proficiency or quality. However, sensitivity of the yellow colouration to carotenoid availability is not much greater than the (apparently cryptic [40]) olive-green back colour (Table 2), contrary to the central assumption of greater condition-dependence of signalling traits [44,13]. Likewise, average detectability of yellow and green plumage was similar and within or below the range of what are considered classical examples of cryptic brownish plumages (Figure 4). Moreover, for all these plumage patches contrast fell within the range of contrast found among background elements (Figure 4) suggesting that contrast between plumage and backgrounds could be hidden within the contrast of the background itself (also see [80]). While low detectability does not preclude a signalling function, it does imply that it is not necessary to invoke signalling in order to explain carotenoid deposition in these feathers.

## Optimised for crypsis?

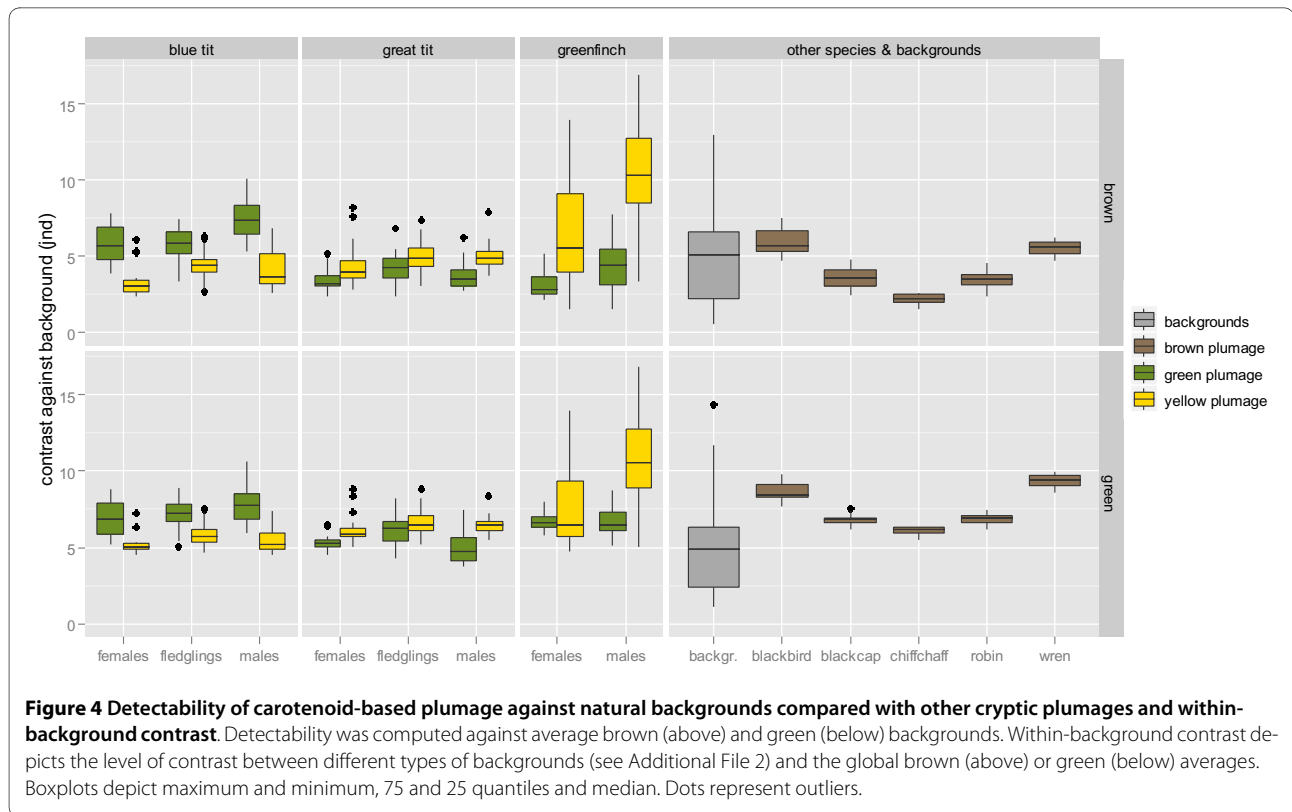
We hypothesise that selection for crypsis is the most likely driving force behind increasing carotenoid deposition at concentrations below the trough of minimum detectability, since increasing carotenoid-deposition will

**Table 1: Sex and age-related differences in carotenoid-based coloration (chroma) and detectability (visual contrast in jnd).**

			males			females			fledglings		
			mean	SE	N	mean	SE	N	mean	SE	N
blue tit	yellow breast	chroma	0.287 <sup>a</sup>	0.005	20	0.288 <sup>a</sup>	0.004	17	0.263 <sup>b</sup>	0.002	71
		Contrast_U_G	7.42 <sup>a</sup>	0.17	20	6.57 <sup>b</sup>	0.15	17	8.02 <sup>c</sup>	0.06	71
		Contrast_V_G	5.53 <sup>ab</sup>	0.20	20	5.26 <sup>b</sup>	0.17	17	5.81 <sup>a</sup>	0.07	71
		Contrast_U_B	6.72 <sup>a</sup>	0.23	20	5.34 <sup>b</sup>	0.22	17	7.27 <sup>c</sup>	0.07	71
		Contrast_V_B	4.26 <sup>a</sup>	0.31	20	3.39 <sup>b</sup>	0.27	17	4.42 <sup>a</sup>	0.09	71
	green back	chroma	0.218 <sup>a</sup>	0.002	20	0.232 <sup>b</sup>	0.002	17	0.228 <sup>b</sup>	0.001	54
		Contrast_U_G	9.58 <sup>a</sup>	0.22	20	8.27 <sup>b</sup>	0.22	17	8.99 <sup>c</sup>	0.10	54
		Contrast_V_G	7.75 <sup>a</sup>	0.27	20	6.91 <sup>b</sup>	0.29	17	7.23 <sup>b</sup>	0.11	54
		Contrast_U_B	9.47 <sup>a</sup>	0.23	20	7.66 <sup>b</sup>	0.21	17	8.08 <sup>b</sup>	0.11	54
		Contrast_V_B	7.34 <sup>a</sup>	0.29	20	5.90 <sup>b</sup>	0.30	17	5.79 <sup>b</sup>	0.13	54
great tit	yellow breast	chroma	0.287 <sup>a</sup>	0.003	27	0.289 <sup>a</sup>	0.004	23	0.262 <sup>b</sup>	0.003	43
		Contrast_U_G	7.40 <sup>a</sup>	0.11	27	7.00 <sup>b</sup>	0.17	23	7.98 <sup>c</sup>	0.11	43
		Contrast_V_G	6.44 <sup>ab</sup>	0.11	27	6.18 <sup>a</sup>	0.19	23	6.61 <sup>b</sup>	0.12	43
		Contrast_U_B	6.28 <sup>a</sup>	0.15	27	5.57 <sup>b</sup>	0.24	23	6.84 <sup>c</sup>	0.13	43
		Contrast_V_B	4.99 <sup>ab</sup>	0.16	27	4.35 <sup>a</sup>	0.28	23	4.97 <sup>b</sup>	0.15	43
	green back	chroma	0.261 <sup>a</sup>	0.003	27	0.264 <sup>a</sup>	0.002	23	0.248 <sup>b</sup>	0.001	43
		Contrast_U_G	7.09 <sup>a</sup>	0.11	27	6.76 <sup>b</sup>	0.08	23	7.78 <sup>c</sup>	0.09	43
		Contrast_V_G	4.99 <sup>a</sup>	0.19	27	5.34 <sup>a</sup>	0.10	23	6.13 <sup>b</sup>	0.13	43
		Contrast_U_B	6.47 <sup>a</sup>	0.09	27	5.55 <sup>b</sup>	0.11	23	6.59 <sup>a</sup>	0.11	43
		Contrast_V_B	3.75 <sup>a</sup>	0.18	27	3.42 <sup>a</sup>	0.13	23	4.26 <sup>c</sup>	0.14	43
greenfinch	yellow tail patch	chroma	0.344 <sup>a</sup>	0.003	41	0.312 <sup>b</sup>	0.007	20			
		Contrast_U_G	11.42 <sup>a</sup>	0.33	41	8.94 <sup>b</sup>	0.44	20			
		Contrast_V_G	10.21 <sup>a</sup>	0.40	41	7.45 <sup>b</sup>	0.55	20			
		Contrast_U_B	11.20 <sup>a</sup>	0.36	41	8.24 <sup>b</sup>	0.53	20			
		Contrast_V_B	9.88 <sup>a</sup>	0.45	41	6.31 <sup>b</sup>	0.72	20			
	green back	chroma	0.316 <sup>a</sup>	0.002	41	0.302 <sup>b</sup>	0.002	20			
		Contrast_U_G	6.79 <sup>a</sup>	0.13	41	6.90 <sup>a</sup>	0.14	20			
		Contrast_V_G	6.69 <sup>a</sup>	0.13	41	6.77 <sup>a</sup>	0.13	20			
		Contrast_U_B	4.56 <sup>a</sup>	0.22	41	3.19 <sup>b</sup>	0.22	20			
		Contrast_V_B	4.53 <sup>a</sup>	0.23	41	3.19 <sup>b</sup>	0.21	20			

Values of contrast are modelled for U- and V-type eyes (represented by U and V respectively) and for average green and brown backgrounds (G and B respectively). Presented are means, standard errors (SE) and sample sizes (N). Means with the same superscript letter are not statistically different (based on t-tests,  $p > 0.05$ ).





**Figure 4 Detectability of carotenoid-based plumage against natural backgrounds compared with other cryptic plumages and within-background contrast.** Detectability was computed against average brown (above) and green (below) backgrounds. Within-background contrast depicts the level of contrast between different types of backgrounds (see Additional File 2) and the global brown (above) or green (below) averages. Boxplots depict maximum and minimum, 75 and 25 quantiles and median. Dots represent outliers.

lead to reduced detectability. Selection for reduced conspicuousness, everything else being equal, should cause plumage colouration to converge towards the optimally cryptic phenotype (i.e. the trough of minimum detectability in Figures 1 and 2). Why then, do not all individuals have optimally cryptic carotenoid-based plumage? Or, in other words, what constrains the development of optimally cryptic carotenoid-based colouration? One possibility is that intraspecific variation in colouration does not lead to significant variation in detectability to predators. This may be the case for the yellow colouration of blue and great tits since their average is close to the optimum and the correlation between colouration and detectability not very strong (Figs 1 and 2). Indeed, our experimental manipulation of carotenoid availability during moult in blue tits had strong effects on chroma for both yellow and green plumage but only in the latter did it translate into large differences in detectability (Table 2). Accordingly, Fitze & Tschirren [31] did not find any relationship between natural variation in yellow ventral colouration of great tit fledglings and survival or recruitment, which could have been expected if coloration correlates with predation risk. More extreme variation in colouration through experimental reddening of the ventral plumage, on the other hand, led to a (slightly) increased risk of capture by sparrowhawks [33]. Most likely, the relationship between predation risk and con-

trast of carotenoid-based plumage colouration will vary markedly in space and time and will also depend on other factors such as the contrast of other colour patches and the behaviour of the birds. One additional factor however, that will constrain the acquisition of optimally cryptic carotenoid-based plumage more directly is the availability of carotenoids which ultimately will determine the colour of the birds.

Carotenoid availability can vary strongly between habitats and this can affect the expression of carotenoid-based colouration. Variation in carotenoid availability has usually been considered in the context of costly carotenoid-based ornamental colours [81-83] but rarely with respect to the development of cryptic carotenoid-based colours (but see [37,84]), perhaps because the expression of naturally selected traits is often (erroneously) assumed to be condition-independent [44]. If in some habitats carotenoid availability is limiting, or if carotenoids are allocated to other important functions such as immune defense [85,86], there may be real constraints involved in producing optimally cryptic carotenoid-based plumage. Costs of developing cryptic plumage are usually neglected [87], but may be an important component in preventing an optimal match between organisms and their backgrounds. Our experiment indicates that both yellow and green blue tit plumage respond strongly to the availability of dietary carotenoids during moult. Thus,

**Table 2: Effects of the manipulation of dietary carotenoid availability on yellow and green plumage coloration (chroma) and detectability (visual contrast in jnd) in blue tits.**

		males						females						ANOVA			
		control			carotenoid suppl.			control			carotenoid suppl.			sex	treat.	s × t	adj. R2
		mean	SE	N	mean	SE	N	mean	SE	N	mean	SE	N				
yellow breast	chroma	0.238	0.003	11	0.281	0.003	9	0.239	0.002	10	0.273	0.004	10	NS	**	NS	0.77
	Contrast_U_G	8.59	0.21	11	7.86	0.08	9	8.48	0.14	10	7.46	0.13	10	NS	**	NS	0.45
	Contrast_V_G	6.93	0.24	11	5.08	0.07	9	6.91	0.15	10	5.18	0.16	10	NS	**	NS	0.72
	Contrast_U_B	7.68	0.22	11	7.37	0.13	9	7.44	0.16	10	6.68	0.13	10	**	**	NS	0.3
	Contrast_V_B	5.50	0.27	11	3.95	0.17	9	5.33	0.17	10	3.67	0.18	10	NS	**	NS	0.6
green back	chroma	0.201	0.002	11	0.224	0.002	9	0.210	0.002	10	0.237	0.002	10	**	**	NS	0.85
	Contrast_U_G	11.63	0.28	11	9.30	0.16	9	10.60	0.13	10	8.25	0.19	10	**	**	NS	0.8
	Contrast_V_G	10.09	0.31	11	6.57	0.25	9	9.27	0.18	10	5.80	0.24	10	**	**	NS	0.83
	Contrast_U_B	11.41	0.30	11	9.27	0.19	9	10.02	0.12	10	7.90	0.20	10	**	**	NS	0.78
	Contrast_V_B	9.60	0.33	11	6.20	0.27	9	8.36	0.17	10	4.93	0.27	10	**	**	NS	0.82

Values of contrast are modelled for U- and V-type eyes (represented by U and V respectively) and for average green and brown backgrounds (G and B respectively). Presented are means, standard errors (SE), sample sizes (N) and significance values for each factor (sex, treatment and their interaction) in ANOVAs (\*\*p < 0.01; NS = not significant, p > 0.05).

lack or excess of carotenoids in the diet may lead to considerable variation in the costs of producing an optimally cryptic plumage or to poor background matching.

Alternatively, environmental variation in carotenoid availability may not necessarily cause mismatches between natural backgrounds and cryptic colouration. Carotenoid-availability, carotenoid-based colouration, and colouration of the natural backgrounds could covary in such a way that more intensely coloured birds are equally cryptic in carotenoid-rich habitats, as less intensely coloured birds in carotenoid-poor habitats [37]. Still untested, this is a plausible hypothesis since the optimal level of carotenoid colouration needed to achieve minimum detectability varied with plant species over a broad range (Figure 3) and differences in the floristic composition and structure of forests are known to affect carotenoid availability [37,88-90]. On a smaller scale, moderate differences between species or individuals in their carotenoid-based colours may lead to similar levels of detectability if birds differ adaptively in their choice of microhabitats. Indeed, differences in foraging microhabitats between great and blue tits may be in part responsible for the differences in back colouration between these two species [40].

## Conclusions

Knowledge on the relationship between colouration and detectability may provide insights into the function of animal coloration. Curvilinear relationships such as shown here for yellow carotenoid pigments may also be found for other types of pigmentary colours (e.g. melanins, psittacofulvins, etc). The shape of the relationship between detectability and colouration may be helpful to determine which level of colour intensity leads to maximum crypsis or conspicuousness. This could, in turn, reveal potential costs and constraints in the development of cryptic or conspicuous plumage. We stress, however, that this is only a first step towards understanding of the function of colours, and careful studies which take into account the detectability of the whole suite of plumage patches and behaviour, are needed to confirm our hypotheses. Meanwhile, and in the same way as we now know that yellow colouration is not always carotenoid-based [91]; our data suggest that assuming all yellow carotenoid-based colours to have a signalling function may be equally flawed.

## Additional material

**Additional file 1 Plumage Reflectance Spectra of blue tits (Figure 1), great tits (Figure 2) and greenfinches (Figure 3).** Depicted are mean reflectance spectra for males, females and fledglings and treatment groups (blue tit only).

**Additional file 2 List of common plants in the study area (Table 1, including relative abundance and number of collected reflectance spectra (N)) and their reflectance spectra (Figure 1).** Depicted are mean reflectance spectra for brown (branches, twigs, leaf-litter) and green (leaves) backgrounds. Red lines represent mean spectra for each plant type separately and blue lines the overall brown and green averages taking into account the abundance of each plant type.

**Additional file 3 Effects of inter-specific variation in cone proportions**

**Additional file 4 Figures representing the relationship between chroma and detectability for each type of background depicting raw data points.**

### Authors' contributions

KD: designed study, collected and analyzed data, wrote the manuscript, MLR: carried out the carotenoid-supplementation experiment, collected data, AP: participated in the design of the study and writing the manuscript. All authors read and approved the final manuscript.

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