

Female Canaries (*Serinus canaria*) Associate more with Males that Contrast Strongly against the Background

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Abstract

Male birds with bright plumage colors which entail production costs and increased predation risks should be able to emphasize the handicap function of their ornaments when they present themselves against a contrasting background. Contrast with the background may accentuate the signal's costliness and make the male more conspicuous to predators. Both effects should contribute to increase male attractiveness. It is therefore conceivable that the extent to which the male plumage contrasts against the background modifies female choice behavior as it improves the discrimination of mates. We tested this hypothesis in domesticated canaries (*Serinus canaria*). In the first experiment, yellow females could choose between two yellow males presented in front of a yellow and a white background, respectively. In the second experiment we replaced the yellow males with white ones. In experiment 1 females associated significantly more with yellow males which contrasted strongly against the white background. In experiment 2 there was at least a trend for preferred associations with the white male in front of the yellow background. We found no support that male properties per se were chosen. We could further clarify that females associated with the contrasting male and not with a particular background color. Thus, our study demonstrates that not only inherent properties of the sender but also the interaction of bird color with the signaling environment may influence mate choice.

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Introduction

It is widely accepted that sexual selection imposed by female choice is one of the dominant factors explaining the evolution of bright and colorful plumages in birds (see reviews by Darwin 1871; Butcher & Rohwer 1989; Andersson 1994). Depending on production costs plumage colors can function as

condition-dependent handicaps, indicating qualities like genetic health (Lozano 1994; von Schantz et al. 1999), parasite resistance (Hamilton & Zuk 1982) or foraging abilities (Endler 1980; Hill & Montgomerie 1994). In addition, vivid coloration entails further costs in that it attracts not only conspecifics but also predators. In this sense, plumage colors function as handicaps which signal the ability to survive despite increased risks of predation (Zahavi 1975).

Irrespective of the type of cost associated with a brightly colored plumage, males which present themselves against a contrasting background should be able to emphasize the handicap function of their coloration. First, as the subjective impression of brightness and color of a signal is not just a one-to-one translation of its physical intensity and reflected wavelengths, contrast to the background may determine how signal color is perceived by the receiver (e.g. Brou et al. 1986; McFadden 1992; Luo et al. 1995). Thus, contrast with the background may accentuate the signal's costliness, making the sender more attractive. Secondly, background contrast makes a colorful male even more conspicuous to predators. Thus, by presenting itself against a contrasting background a male should even better demonstrate its abilities to evade predation. It is therefore conceivable, that the extent the male plumage contrasts against the background modifies female choice behavior as it improves the discrimination of high-quality males.

We tested whether the contrast between plumage color and its background affects mate choice in domesticated canaries (*Serinus canaria*). We chose domesticated canaries for two reasons: first, as there are breeds of different colors, we were able to run with the same test individuals two sets of trials which differed by the color of the stimulus birds. Thus, in the first experiment, yellow females could choose between two yellow males presented in front of a yellow and a white background, respectively. In the second experiment, we replaced the yellow males with white ones. Secondly, as we expected that in both experiments females choose the male which contrasts more against the background, our experimental design allowed us to differentiate between female preferences for a particular male or only for a particular background color.

Although male attractiveness of canaries has so far only been studied in relation to song characteristics (Vallet & Kreutzer 1995; Beguin et al. 1998), we consider it possible that plumage color may additionally influence female choice behavior. At least, the yellow plumage color, which is produced by carotenoids and thus presumably entails some costs (Hill 1999, 2000), should be indicative of genotypic and phenotypic male qualities as was found for other yellow-colored cardueline and emberizine species (Sundberg & Larsson 1994; Sundberg 1995; Figuerola et al. 1999; Harper 1999, McGraw & Hill 2000).

Methods

Study Subjects, Test Apparatus, and Spectroradiometry

Subjects were domesticated, adult (one or more years of age) canaries of an outbred form of heterogeneous genetic background. They were obtained from

commercial breeders or other research institutions and kept in aviaries with food ad libitum. Groups of males (17 yellow and nine white) and females (19 yellow) were held in visual and auditory isolation, so that stimulus and test birds had no previous experience of each other before the trials. Experiments were carried out from mid-October to mid-December 2000, thus starting more than a month after canaries had finished their annual molt. At that time of year, males hardly sang in the aviaries and never did so in the test chambers, so that we could exclude vocalization as a bias of female behavior. We kept males at a constant 12:12 h (L:D) photoperiod. Females experienced first the seasonal decrease in daylight (below 12 h) and were then exposed to a photostimulatory long day-lighting regime [(14:10 h; L:D), modified from LeBoucher et al. (1994)] 10 d before experimentation began to encourage mate choice to occur.

We used the pairwise choice apparatus outlined in Fig. 1. To present males in front of backgrounds which contrasted differently with canary plumage colors, we wallpapered one male chamber with naturally colored white cotton clothes, the other with cotton clothes dyed yellow with commercial cloth dye. Thus, in the white-chamber yellow canaries contrasted strongly against the background, whereas in the yellow chamber they did not (Fig. 2b). Background contrast of the white plumage was vice versa (Fig. 2c).

We measured plumage reflectance with a portable diode-array spectrometer (USB 2000; Avantes, Eerbeek, The Netherlands) which provided stable readings between 220 and 800 nm. As a light source, we used a Deuterium-Halogen lamp (Top Sensor Systems DH-2000) which supplied a continuous spectrum from 215 to 1500 nm. We measured reflectance in relation to a white standard reference tile (Top Sensor Systems WS-2) and calibrated the spectrometer software to the white standard and to the dark current once per bird. For each individual male we obtained reflectance of the crown, the back, the rump, the breast and the wing coverts by taking the average of five reflectance spectra measured at randomly chosen locations within each body region, lifting and replacing the probe between each measurement. Spectral data were processed with our own software which smoothed spectra with the Hanning algorithm set for a width of 5-nm intervals and calculated reflectance for each 5-nm interval.

The yellow plumage strongly reflects near-ultraviolet wavelengths (UVA, Fig. 2a) which are visible for canaries (Das et al. 1999) but not for humans. As we were not able to produce a yellow background with similar UV-reflectance as the yellow canary plumage, we decided to cover the chamber fronts with UV-blocking glass screens, so that no UV-radiance coming from the stimulus birds could reach the test bird's eye. Thus, we could maintain a fairly low background contrast of yellow males in the yellow test chamber and avoided any potential effects of the otherwise contrasting UV-signal on female behavior.

We quantified plumage coloration to analyze color variation in stimulus birds. We restricted color analyses in terms of intensity (brightness) and spectral shape (hue, chroma) to the 400–700 nm spectral window which was relevant for our experimental setup. We objectively computed a spectrum's brightness as the area under the spectral curve of the entire spectrum. Yellow plumage spectra change

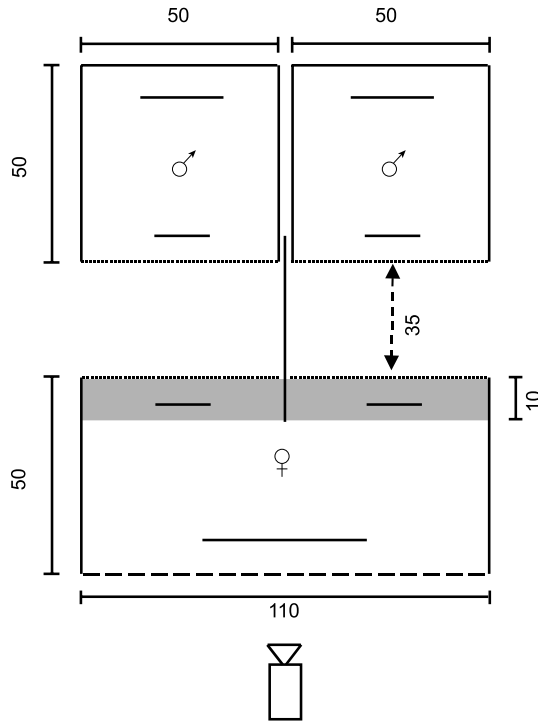


Fig. 1: Plan of the test chambers (measures in cm). Height of each chamber cell is 50 cm. Dotted lines indicate glass screens impermeable for UV. Dashed line indicates wall made of wire nettings. Solid lines indicate walls made of plywood. Plywood walls and bottom of male chambers were wallpapered with either white or yellow dyed cotton clothes. Each background color was permanently fixed to a particular chamber. The shading indicates the female response area. Bars within compartment cells indicate perches. Behavior was recorded with a video camera placed behind the female chamber. Each compartment was uniformly illuminated with halogen bulbs

immensely around 500 nm (Fig. 2a). Therefore, we divided reflectance between 500–700 nm by total reflectance (400–700 nm) to obtain an estimate of chroma ($R_{500-700}/R_{400-700}$) and computed the spectral position of maximum slope as an estimate of hue (Endler 1990). These color estimates should have high relevance for canaries, as their middle-wave-sensitive cone type has a sensitivity maximum at 505 nm (Das et al. 1999). We averaged color parameters over all plumage regions to obtain one value of hue, chroma and brightness for each individual of the yellow males. As the spectral curves of the white plumage are relatively flat above 400 nm (Fig. 2a), we only calculated brightness values for the white males.

We quantified morphological variation within stimulus birds by measuring wing length as the average of two to five measurements to the nearest 0.5 mm, tarsus length as the average of two to five double measurements to the nearest 0.05 mm, and body weight as the average of two to four measurements at the beginning of a trial to the nearest 0.1 g.

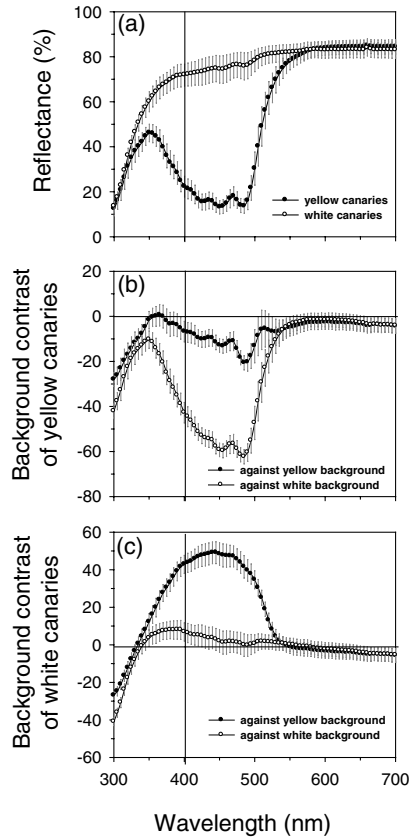


Fig. 2: (a) Average spectral reflectance functions (mean \pm SD) of yellow ($n = 17$) and white ($n = 9$) male canaries. Spectral contrast functions (mean \pm SD) of yellow (b) and white (c) canaries were computed by subtracting the average plumage reflectance function of each male from the mean reflectance function of the yellow and white background ($n = 3$ for each color) at each 5 nm interval. Glass screens used in the experimental setup cut off wavelengths in the UV, i.e. shorter than 400 nm (denoted by vertical bars)

We did not make any effort to match the stimulus males within a trial for similarity in color and morphology. Moreover, we assumed that background contrast was the predominating variable in male differences. However, we did explore the bias of male color and morphology on the outcome of the experiments (see below).

Experiment 1

We released a female into the test chamber and left her alone for 60 min. Female behavior during this acclimatization period was recorded by a video camera. The acclimatization period was reduced to 45 min after testing the first eight of 19 females. After we recorded behavior once for each test bird, we

further reduced the acclimatization period to 30 min which appeared to be sufficient time for females to get used to the test chambers. After the acclimatization period, we covered the glass screens with plywood walls and placed one yellow male in each stimulus chamber. We allowed males 15 min to recover from handling. We removed the plywood covers and started the trial after another 15 min in which birds could accustomize to the presence of the opposite sex. Then, female choice behavior was recorded for 60 min by the video camera. Stimulus males could not see each other. Outside the response area (see Fig. 1), the female could normally see both males. Inside the response area, the female could only see the male of the respective chamber. Thus, the female had to leave the response area when she wanted to approach the other male. We had the impression that in each trial, birds became aware of the presence of the opposite sex, however we never noticed males or females singing or performing obvious display behavior. Therefore, we classified females which entered the response area and – to be more conservative – sat on a perch (not on the floor) to associate with the respective male.

The time a female associated with each male was calculated as the cumulative time spent perched in each response area (left or right). Because females, when left alone, did not sit more time on perches than on the chamber's floor (see Results), we considered a female to respond to the males during the 60-min choice period, when she spent more time in the response area than expected by chance. As the response area is one-fifth of the entire area of the female chamber, we assumed a female to respond when she was perched more than 12 min in the response area irrespective of left or right, or more than 6 min in front of either the left or right male. Per trial we assigned to each female, a stimulus pair sampled at random from a pool of 17 yellow males. All males were used more than once, however each time with a different male partner. In total, we performed 29 trials with 19 different females. A total of 12 females responded to males during their first trial. Six females did not respond until their second or third trial. One female did not respond at all. Thus, we based our analysis on 18 successful trials of 18 different females. During the successful trials each of the 17 males was used two or three times and at least once in front of each background. Repeatedly tested females encountered a particular male only once. We placed male chambers, and thus the different backgrounds, at random left and right to avoid position effects. Each male and female was tested only once per day.

Experiment 2

Test procedure of experiment 2 was the same as in experiment 1, except that we used throughout an acclimatization period of 30 min for the females and did not record their behavior when alone. We used the same 19 females of experiment 1 as test birds, however we replaced the yellow stimulus males with white ones. We used the same balanced sampling regime as in experiment 1 to assign stimulus male pairs to females from a pool of nine white males. In total, we performed 29 trials. Among the 16 females which responded, five had to be tested repeatedly

(two to three times) until they responded to the stimulus males. During successful trials white males were presented three or four times, balanced for background type. Owing to the low number of white stimulus birds, we could not avoid using one male pair a second time, however with reversed backgrounds.

Statistical Analyses

Differences in time within a particular response area were tested with the Wilcoxon matched-pairs test. Data for pairwise comparisons were the times a female spent in the left or right response area expressed as the percentage of total time in the entire response area. Differences of observed vs. expected frequencies of female preferences were tested with the Chi-square test.

To test if the males per se seriously bias female behavior, we ranked males by increasing magnitude of their color and morphology values (i.e. yellower, more chromatic, brighter and larger males had higher ranks), starting with rank 1 and ending with rank 17 (yellow males) and nine (white males), respectively. We correlated rank differences within male pairs with the ratio of time spent in front of the higher ranked male divided by time in front of the lower ranked male. This approach took into account, that stimulus males were not matched for similar differences in color and morphology, and assumed that the more males differed from each other the more the females would tend to affiliate with the larger, brighter or more colorful male. Significant correlations would indicate strong effects of other factors than background contrast on female behavior.

To check if females responded to males and not instead to a particular background color (yellow or white), we tested the proportion of time females were perched in front of the background color which they approached most in experiment 1 against the proportion of time they were in front of the same background during experiment 2. If females had a preference for a particular background color, they should spend approximately equal amounts of time in front of the same background in both experiments. The outcome of the test should then be non-significant.

Results are presented as mean \pm SD. All tests were two-tailed. We rejected the Null-hypothesis at a significance level of $p < 0.05$.

Results

Experiment 1

During the acclimatization period, i.e. when left alone, females spent about equal proportions of time on the floor ($45 \pm 42\%$) and on perches ($55 \pm 42\%$, Wilcoxon matched-pairs test: $Z = 0.62$, $p = 0.53$, $n = 19$). Females sat $90.5 \pm 19.8\%$ of their perch sitting time on the back perch and only $9.5 \pm 19.8\%$ of their time on the perches in the response area.

In the successful trials females spent on average 27.7 ± 13.7 min in the response area which is more than twice as much as expected by chance. Of the 18

trials, 13 females responded more to the yellow male in the white chamber and five responded more to the yellow male in the yellow chamber ($\chi^2 = 3.56$, $df = 1$, $p = 0.059$). When in the response area, females stayed on average more than twice as long in front of those males that contrasted strongly against the background (Fig. 3, Wilcoxon matched-pairs test: $Z = 2.46$, $p = 0.014$, $n = 18$).

Experiment 2

In the successful trials females spent, on average, 25.9 ± 13.4 min in the response area. Of the 16 trials, 12 females responded more to the white male in front of the yellow background and four responded more to the white male in front of the white background ($\chi^2 = 4.0$, $df = 1$, $p = 0.046$). When in the response area, females did not significantly spend more time in front of a particular test chamber, however tended to stay almost twice as long in front of the male that contrasted more strongly with the background (Fig. 3, Wilcoxon matched-pairs test: $Z = 1.81$, $p = 0.07$, $n = 16$).

Fifteen of the females used appeared in both experiments. Of those, nine spent in experiment 2 more time in front of that male chamber which they less approached in experiment 1. Proportion of time spent in front of that male chamber to which females affiliated most in experiment 1 differed significantly from the proportion of time females spent in front of the same male chamber during experiment 2 (Wilcoxon matched-pairs test: $Z = 2.73$, $p = 0.006$, $n = 15$).

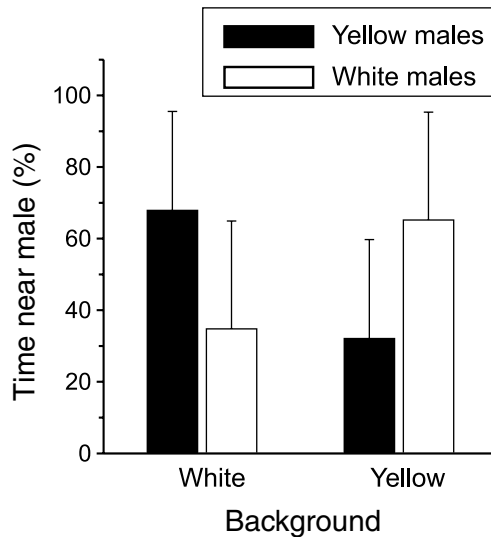


Fig. 3: Proportion of time (mean \pm SD) female canaries spent within the response area close to yellow males in experiment 1 (filled bars) and to white males in experiment 2 (open bars) during trials lasting 1 h. In both experiments females had to choose between two males presented in front of a yellow and a white background. $n = 18$ in experiment 1, $n = 16$ in experiment 2

This indicates that females preferred neither a particular background color nor any other non-color-related cage-specific effects.

Effects of Males per se on Female Behavior

Table 1 gives an overview over the variation of color and morphology within stimulus males. Color parameters of yellow-plumaged males were correlated with each other, i.e. yellower males were more chromatic but less bright (Spearman rank correlation, hue vs. chroma: $r_s = 0.61$, $p = 0.01$; hue vs. brightness: $r_s = -0.49$, $p = 0.04$; chroma vs. brightness: $r_s = -0.51$, $p = 0.04$; $n = 17$). However, neither any of the morphological variables nor measures of relative body size (wing length/body weight and tarsus length/body weight) were significantly correlated with hue, chroma or brightness (Spearman rank correlation, $|r_s| < 0.36$, $p > 0.16$, $n = 17$). In the white males, again, neither absolute morphological measures nor variables of relative body size were significantly correlated with brightness (Spearman rank correlation, $|r_s| < 0.5$, $p > 0.67$, $n = 9$).

In both experiments, correlations of rank differences in color and morphology with the ratio of time in front of the higher ranked male divided by time in front of the lower ranked male were for all variables not significant (Spearman rank correlation, Experiment 1: $|r_s| < 0.23$, $p > 0.4$, $n = 18$; Experiment 2: $|r_s| < 0.31$, $p > 0.25$, $n = 16$), indicating a low impact of the males per se on female behavior.

Discussion

Experiment 1 showed that female canaries associated significantly more with yellow males that contrasted strongly against the white background. In experiment 2, we found at least the trend, that females spent more time in front of the white males that were presented in front of a yellow background. These

Table 1: Variation of characters among stimulus males within each experiment. Brightness measures were calculated for an illuminant of $100 \mu\text{mol}/\text{m}^2\text{s}$

Male characters	Yellow males (n = 17)		White males (n = 9)	
	Mean \pm SD	CV (%)	Mean \pm SD	CV (%)
Brightness ($\mu\text{mol}/\text{ms}$)	50.79 \pm 2.75	5.4	70.37 \pm 3.76	5.3
Hue (nm)	505.89 \pm 3.41	6.7	–	–
Chroma ($R_{500-700}/R_{400-700}$)	0.89 \pm 0.017	1.9	–	–
Wing length (mm)	82.5 \pm 2.34	2.8	81.0 \pm 3.18	3.9
Tarsus length (mm)	18.75 \pm 0.74	3.9	18.75 \pm 0.54	2.9
Weight (g)	21.5 \pm 2.13	9.9	21.0 \pm 2.17	10.3
Wing/weight	3.89 \pm 0.36	9.3	3.88 \pm 0.29	7.5
Tarsus/weight	0.89 \pm 0.07	7.9	0.9 \pm 0.07	7.8

results are unlikely to be due to a preference for a particular background color as we found no support for constant female-background affiliations. It is also unlikely that females chose contrasting males because they did not see the less contrasting ones. We had the impression that all females noticed stimulus males irrespective of background color because of the close distance of presentation. In both experiments, all females but one perched at least once in front of the less-preferred male. Therefore, our study suggests that female canaries preferred the males which contrasted strongly against the background, and that background contrast critically influenced female choice behavior even after the males had already been detected.

As the birds did not show any obvious display behavior we cannot be sure that females simply showed the tendency to flock with conspecifics regardless of sex. However, if females simply wanted to flock, it would have been probably more likely that they chose the background where they were safest from predators. This would have been yellow in both experiments. Obviously, they did not, so that we may assume that it was mate choice that was occurring.

We found no evidence that male properties per se affected female behavior. However, the experiments do not imply that background contrast overrides entirely inherent male traits during mate choice. Stimulus males did not differ in coloration and morphology beyond their natural variability, i.e. we did not manipulate male traits under investigation as was done in many other mate choice studies (e.g., Andersson 1982; Sætre et al. 1994; Swaddle & Cuthill 1994; Siitari et al. 2002). Thus, it is very likely that the numbers of sampled males would be simply too small to show any significant female preferences for particular male traits even with equally colored backgrounds.

Why should females prefer males which contrast strongly against the background? Contrast against the background makes the plumage more conspicuous. Contrasting males therefore increase their handicap of being more visible to potential predators, which may increase their attractiveness to females (Zahavi 1975). On the other hand, background contrast accentuates the color of the plumage and therefore may improve the discrimination of quality levels from the quality-indicating trait (Guilford & Dawkins 1991; Rowe 1999). In our study, we found significant female choice for the contrasting male with yellow-colored stimulus birds. This suggests that the emphasis of signal production costs may be a very important clue for mate choice. Expression of a yellow plumage when based on dietary carotenoids is costly as it depends on the amount of pigments deposited in the feathers. Latter increases with foraging abilities (Endler 1980; Hill 1992; Hill & Montgomerie 1994), physiological capabilities to metabolize the ingested pigments (McGraw & Hill 2001; McGraw et al. 2001) and genetic health which reduces the need of carotenoid-consuming immune responses (Lozano 1994; von Schantz et al. 1999). Thus, the yellow canaries should be more handicapped than the white ones, whose plumage is devoid of carotenoids. In other cardueline and emberizine bird species the expression of a yellow plumage was found to be associated with parasite resistance (Sundberg 1995; Figuerola et al. 1999; Harper 1999; McGraw & Hill 2000), immune stress (Figuerola et al.

1999) and parental efforts (Sundberg & Larsson 1994). Thus, the yellow plumage in canaries should be more informative about male quality than the white one. This may explain why females did not clearly choose the contrasting male in the experiment with white stimulus birds. Accentuation of the white plumage against a contrasting background possibly did not increase male attractiveness to the same extent as it might be the case with the yellow plumage. However, our experiments do not provide direct evidence for this assumption which would require further testing.

Overall, our study suggests that not only male properties per se but also the interaction of bird color with the signaling environment may influence mate choice. Males can only exploit context-dependent female preferences if they have behavioral control over whether or not to manipulate their conspicuousness. There is evidence from at least five bird species (*Rupicola rupicola*, *Corapipo gutturalis*, *Lepidothrix serena*, *Pipra filicauda*, *Pipra erythrocephala*) that males are able to increase the contrast within their coloration pattern as well as that of their plumage against the background by selecting particular light environments during display (Endler & Théry 1996; Heindl & Winkler 2003; own data). Alternatively, it is conceivable that males will search for the suitable display site first which in turn may affect the evolution of the suitable color signals and signaling behavior.

We are aware that our study only provides a first approach into the complex field of context-dependent signal appearance and mate choice decisions. Canaries have UV-sensitive cone types (Das et al. 1999), and thus are likely to include reflected UV-wavebands into color perception. The fact, that we had to cut off the UV-waveband of light, may have caused species recognition problems as males could have looked a bit odd to females. Although there is no reason to assume that canaries are worse to recognize as such against a yellow background or vice versa, future experiments should allow females to perceive the full spectrum of male colors. Furthermore, our study simulated a very artificial situation, in that we presented males whose coloration was either extremely similar or extremely different from that of the background. Females will usually neither view mating partners against the background colors we used in our experimental setup, nor will they probably ever face a situation where they have to discriminate between males that differ in such a degree of background contrast as they did in our experiments. Further experiments will be required to explore whether the effects of context-dependent plumage appearance on mate choice decisions can still be maintained with stimulus males which differ much less in background contrast, e.g. when presented against a blue vs. a white background simulating blue sky and white clouds. Similarly, it would be interesting to test whether males not able to invest in costly ornaments can compensate for their lack of attractiveness. Under signaling conditions which accentuate the appearance of the content-carrying trait they may outcompete high-quality but less contrasting males. Finally, experiments which let displaying males choose among different signaling conditions produced by different backgrounds and/or light conditions, would give insights into whether male canaries actively manipulate how they are perceived by females.

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Literature Cited

- Andersson, M. 1982: Female choice selects for extreme tail length in a widowbird. *Nature* **299**, 818–820.
- Andersson, M. 1994: *Sexual Selection*. Princeton University Press, New York.
- Beguín, N., LeBoucher, G. & Kreutzer, M. 1998: Sexual preferences for mate song in female canaries (*Serinus canaria*). *Behaviour* **135**, 1185–1196.
- Brou, P., Sciascia, T. R., Linden, L. & Lettvin, J. Y. 1986: The color of things. *Scient. Am.* **255**, 80–88.
- Butcher, G. S. & Rohwer, S. 1989: The evolution of conspicuous and distinctive coloration for communication in birds. *Curr. Ornithol.* **6**, 51–108.
- Darwin, C. 1871: *The descent of man and selection in relation to sex*. Murray, London.
- Das, D., Wilkie, S. E., Hunt, D. M. & Bowmaker, J. K. 1999: Visual pigments and oil droplets in the retina of a passerine bird, the canary *Serinus canaria*: microspectrophotometry and opsin sequences. *Vision Res.* **39**, 2801–2815.
- Endler, J. A. 1980: Natural selection on color patterns in *Poecilia reticulata*. *Evolution* **34**, 76–91.
- Endler, J. A. 1990: On the measurement and classification of colour in studies of animal colour patterns. *Biol. J. Linn. Soc.* **41**, 315–352.
- Endler, J. A. & Théry, M. 1996: Interacting effects of lek placement, display behavior, ambient light, and color patterns in three neotropical forest-dwelling birds. *Am. Nat.* **148**, 421–452.
- Figuerola, J., Munoz, E., Gutierrez, R. & Ferrer, D. 1999: Blood parasites, leucocytes and plumage brightness in the Cirl Bunting, *Emberiza cirius*. *Funct. Ecol.* **13**, 594–601.
- Guilford, T. & Dawkins, M. S. 1991: Receiver psychology and the evolution of animal signals. *Anim. Behav.* **42**, 1–14.
- Hamilton, W. D. & Zuk, M. 1982: Heritable true fitness and bright birds: a role for parasites? *Science* **218**, 384–387.
- Harper, D. G. C. 1999: Feather mites, pectoral muscle condition, wing length and plumage coloration of passerines. *Anim. Behav.* **58**, 553–562.
- Heindl, M. & Winkler, H. 2003: Interacting effects of ambient light and plumage color patterns in displaying Wire-tailed Manakins (Aves, Pipridae). *Behav. Ecol. Sociobiol.* DOI 10.1007/s00265-002-0562-3).
- Hill, G. E. 1992: Proximate basis of variation in carotenoid pigmentation in male house finches. *Auk* **109**, 1–12.
- Hill, G. E. 1999: Mate choice, male quality, and carotenoid-based plumage colouration. In: *Proceedings of the 22 International Ornithology Congress, Durban* (Adams, N. J. & Slotow, R. H., eds). BirdLife South Africa, Johannesburg, pp. 1654–1668.
- Hill, G. E. 2000: Energetic constraints on expression of carotenoid-based plumage coloration. *J. Avian Biol.* **31**, 559–566.
- Hill, G. E. & Montgomerie, R. 1994: Plumage colour signals nutritional condition in the house finch. *Proc. R. Soc. Lond. B* **258**, 47–52.
- LeBoucher, G., Kreutzer, M. & Dittami, J. 1994: Copulation-solicitation displays in female canaries (*Serinus canaria*): are oestradiol implants necessary? *Ethology* **97**, 190–197.
- Lozano, G. A. 1994: Carotenoids, parasites, and sexual selection. *Oikos* **70**, 309–311.
- Luo, M. R., Gao, X. W. & Scrivener, S. A. R. 1995: Quantifying color appearance. 5. Simultaneous contrast. *Color Res. Appl.* **20**, 18–28.

- McFadden, S. 1992: Discrimination of colors presented against different colored backgrounds. *Color Res. Appl.* **17**, 339—351.
- McGraw, K. J. & Hill, G. E. 2000: Differential effects of parasitism on the expression of carotenoid- and melanin-based ornamental coloration. *Proc. R. Soc. Lond. B* **267**, 1525—1531.
- McGraw, K. J. & Hill, G. E. 2001: Carotenoid access and intraspecific variation in plumage pigmentation in male American Goldfinches (*Carduelis tristis*) and Northern Cardinals (*Cardinalis cardinalis*). *Funct. Ecol.* **15**, 732—739.
- McGraw, K. J., Hill, G. E., Stradi, R. & Parker, R. S. 2001: The influence of carotenoid acquisition and utilization on the maintenance of species-typical plumage pigmentation in male American Goldfinches (*Carduelis tristis*) and Northern Cardinals (*Cardinalis cardinalis*). *Physiol. Biochem. Zool.* **74**, 843—852.
- Rowe, C. 1999: Receiver psychology and the evolution of multiple-component signals. *Anim. Behav.* **58**, 921—931.
- Sætre, G. P., Dale, S. & Slagsvold, T. 1994: Female pied flycatchers prefer brightly coloured males. *Anim. Behav.* **48**, 1407—1416.
- von Schantz, T., Bensch, S., Grahn, M., Hasselquist, D. & Wittzell, H. 1999: Good genes, oxidative stress and condition-dependent sexual signals. *Proc. R. Soc. Lond. B* **266**, 1—12.
- Siitari, H., Honkavaara, J., Huhta, E. & Viitala, J. 2002: Ultraviolet reflection and female mate choice in the pied flycatcher, *Ficedula hypoleuca*. *Anim. Behav.* **63**, 97—102.
- Sundberg, J. 1995: Parasites, plumage coloration and reproductive success in the yellowhammer, *Emberiza citrinella*. *Oikos* **74**, 331—339.
- Sundberg, J. & Larsson, C. 1994: Male coloration as an indicator of parental quality in the Yellowhammer, *Emberiza citrinella*. *Anim. Behav.* **48**, 885—892.
- Swaddle, J. P. & Cuthill, I. C. 1994: Female zebra finches prefer males with symmetric chest plumage. *Proc. R. Soc. Lond. B* **258**, 267—271.
- Vallet, E. & Kreutzer, M. 1995: Female canaries are sexually responsive to special song phrases. *Anim. Behav.* **49**, 1603—1610.
- Zahavi, A. 1975: Mate selection – a selection for a handicap. *J. theor. Biol.* **53**, 205—214.

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