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Cite this article: Endler JA, Gaburro J, Kelley LA. 2014 Visual effects in great bowerbird sexual displays and their implications for signal design. *Proc. R. Soc. B* **281**: 20140235. http://dx.doi.org/10.1098/rspb.2014.0235

Received: 28 January 2014
Accepted: 7 March 2014

Subject Areas:
behaviour, evolution

Keywords:
bowerbird, sexual display, visual effects, illusions, holding attention, constraints

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Electronic supplementary material is available at http://dx.doi.org/10.1098/rspb.2014.0235 or via http://rspb.royalsocietypublishing.org.

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Visual effects in great bowerbird sexual displays and their implications for signal design

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It is often assumed that the primary purpose of a male's sexual display is to provide information about quality, or to strongly stimulate prospective mates, but other functions of courtship displays have been relatively neglected. Male great bowerbirds (*Ptilonorhynchus nuchalis*) construct bowers that exploit the female's predictable field of view (FOV) during courtship displays by creating forced perspective illusions, and the quality of illusion is a good predictor of mating success. Here, we present and discuss two additional components of male courtship displays that use the female's predetermined viewpoint: (i) the rapid and diverse flashing of coloured objects within her FOV and (ii) chromatic adaptation of the female's eyes that alters her perception of the colour of the displayed objects. Neither is directly related to mating success, but both are likely to increase signal efficacy, and may also be associated with attracting and holding the female's attention. Signal efficacy is constrained by trade-offs between the signal components; there are both positive and negative interactions within multicomponent signals. Important signal components may have a threshold effect on fitness rather than the often assumed linear relationship.

1. Introduction

Many animals produce complex courtship displays that contain multiple components [1]. It is often assumed implicitly that they function independently and that their primary function is to provide information about quality to prospective mates [2,3], or to strongly stimulate the potential mate by taking advantage of sensory biases [4], but interactions and additional functions have been largely neglected. Male display traits may have ancillary functions such as attracting attention [5], enhancing signal conspicuousness [6], modifying information content or facilitating female assessment [7]. For example, jungle fowl (*Gallus gallus*) wattles enhance the efficacy of a feeding signal that females use in mate choice, but are not targets of choice [8]. Although they are not under direct female selection as indicators of male quality, these traits can enhance the efficacy of quality signal components [5,6]. The role of such ornaments that enhance signal efficacy rather than content [6] is relatively unexplored and this applies particularly to traits involved in multicomponent displays, where components can overlap, interact and involve multiple sensory modalities. Here, we present an example of interacting signal components that primarily affect signal efficacy rather than affect signal content, and whose interactions result in a constraint on signal design.

Bowerbirds (Ptilonorhynchidae) produce a multicomponent sexual display that includes an extended phenotype [9,10]. Males construct and decorate bowers for the sole purpose of attracting mates, and species vary in their bower structure and decorations [9]. Species vary in the bower traits favouring mating success, which may include the number of coloured decorations [11], avenue form [12] or bower paint [13,14]. Females may also choose mates based on physical traits such as vocal mimicry [15] and courtship movements [16]. Different components of male displays may serve different functions; for

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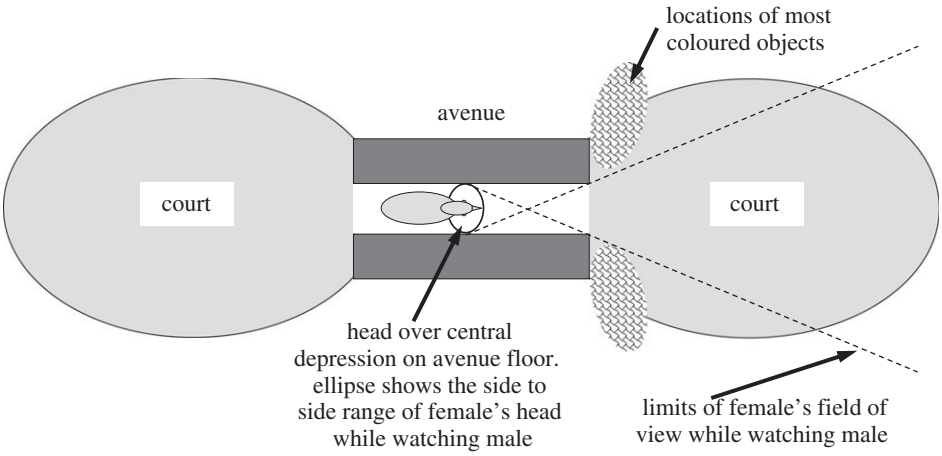

Figure 1. Diagram of a typical great bowerbird bower. A female stands in the centre of the avenue with her head over the central depression in the avenue floor. She has a limited field of view (FOV) of the court, where the male displays (see electronic supplementary material, figure A3). Courts are covered with uncoloured objects and most coloured objects are placed near the avenue entrance or beside the avenue.

example, the white bones at the entrance of male spotted bowerbird (*Ptilonorhynchus maculatus*) bowers may attract females to the bower, while glass objects may stimulate the female once in the bower [17]. However, little is known about how the multiple display traits produced by the male function in mate choice in other bowerbird species.

Male great bowerbirds (*Ptilonorhynchus nuchalis*) construct bowers with a 0.6–1 m long avenue consisting of two parallel densely thatched stick walls and floor, opening at both ends to similar-sized courts (figure 1). The courts are areas of cleared ground covered with uncoloured objects, primarily stones, bleached bones and bleached snail shells [18,19]. During courtship, the female stands in the middle of the avenue and looks out onto a court. The geometry of the bower and the female's predetermined position during the display (figure 1) provide opportunities for males to manipulate female perception [18]. Males arrange the objects on their courts to create a forced perspective illusion for the female viewing the male's display from within the bower, and the quality of forced perspective predicts male mating success [18,19]. Courts are also decorated with coloured objects known as ornaments or decorations. During sexual displays, the bower-owning male stands at the side of the avenue entrance, picks up a decoration and displays it to the female before dropping or tossing it across the court and picking up a new decoration.

The female's predetermined viewpoint from within the bower is important for the forced perspective illusion [18], but the importance of this view for other aspects of the male's display has not been investigated. For example, the female's restricted view may allow males to control what the female sees, when she sees it, and her visual state during the display. Male display movements can influence female choice in satin bowerbirds (*Ptilonorhynchus violaceus*) [20], but the significance of presenting and tossing objects in front of the female in great bowerbirds is unknown. Males also have the opportunity to manipulate other aspects of the females' visual environment, because the bower walls dominate the female's field of view (FOV) when in the avenue.

Here, we quantify two new aspects of courtship displays that use the female's predetermined viewpoint, the rapid and diverse flashing of coloured objects in and out of the female's FOV and the red avenue-induced chromatic adaptation of the female's eyes that alters her perception of the colour of displayed objects. We discuss the potential functions of these display components in the context of signal design and mate choice.

2. Material and methods

We recorded the geometry of active bowers in two great bowerbird populations in north Queensland, Australia. Nine bowers were measured at Mary Valley Station and Nature Reserve (15.04° S, 143.77° E) including part of adjacent Artemis station in 2008. In 2009–2011, 61 samples from 27 active bowers were measured at Dreghorn Station (20.25° S 147.73° E; [19]). Approximately 700 km apart, both study sites are in eucalyptus woodland, which is typical for the species' geographical range [9]. Both locations are far from urban centres and therefore have a distribution of available bower objects more similar to those that they evolved with compared with those in cities. We measured the female's FOV and the location, type and colour of all objects at each bower each bower using our previous methods [18,19,21]. The data for both courts of a given bower were pooled before analysis; both courts are used for male displays and they typically do not differ significantly [19].

Bowerbird behaviour at Dreghorn was recorded during three consecutive breeding seasons (2010: $n = 18$; 2011: $n = 16$; 2012: $n = 17$) by motion-activated video recorders placed 1.5–2.5 m away from one court (details in reference [21]). Recordings were used to obtain the frequency and sequence of colours of objects used in male displays, the time females spent in the avenue watching a male display on the court and the number of copulations, which we use as a proxy for mating success, because most females only mate with one male [22]. We placed the sequences of objects and nuchal crest displays per courtship display bout into a transition matrix for an adjacency pattern analysis [23]. The rows and columns of the transition matrices were object colours, object groups or their pooled classes (figure 2*a*), including the pink nuchal crest. Off-diagonals were counts of object changes. We measured sequence novelty by the inverse Simpson diversity of the off-diagonals; the greater this diversity, the more varying and novel the display. We also measured novelty by comparing the numbers of observed off-diagonals (object changes) and diagonals (object runs) with the random expected. A higher proportion of off-diagonals indicates fewer cases of the same object being used in two successive waves at the female.

In 2011, we experimentally tested whether males actively keep their decorations by the side of the bower entrance, so that they are not visible to females when inside the bower. Numbers and locations of all coloured objects in each of 16 active bowers at Dreghorn were recorded, and then placed on the court so that

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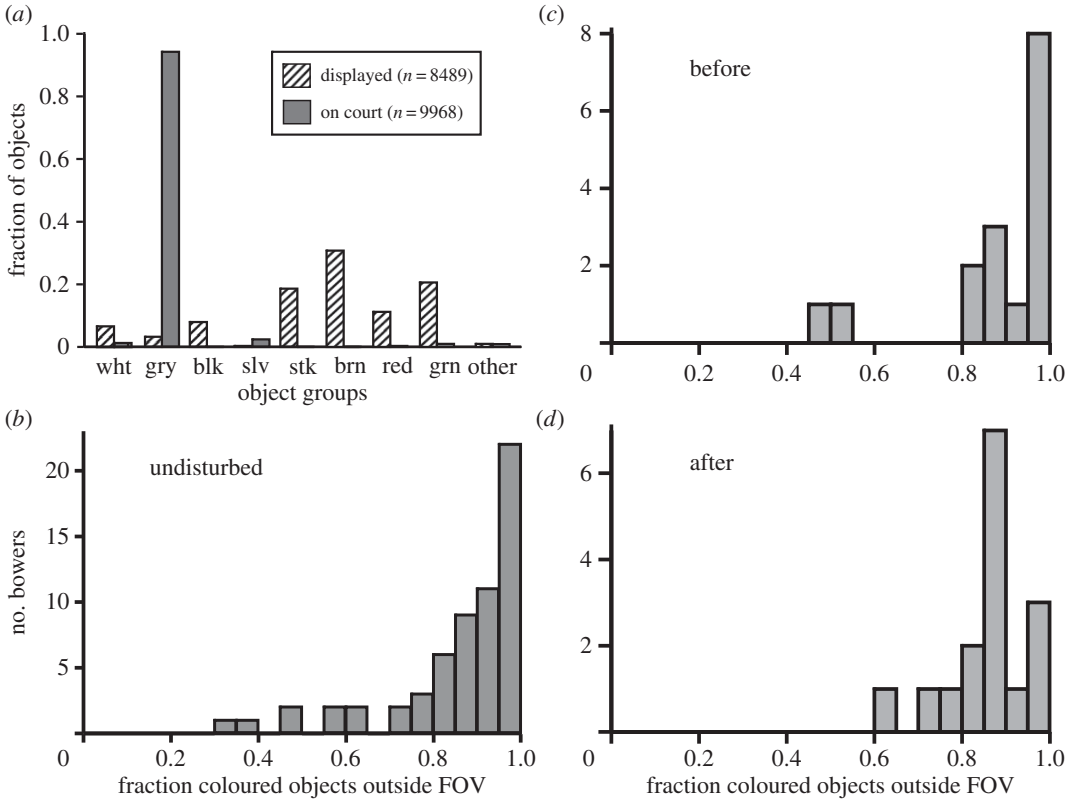

Figure 2. (*a*) Distribution of object groups on bower courts and displayed by males towards females at Dreghorn 2010–2012. Codes: wht, bright white (plastic and quartz); gry: (bones, stones, bleached snail shells, etc., collectively called gesso); blk, black; slv, metal; stk, sticks (too thin to identify colour reliably); brn, brown; red, red; grn, green; other, blue, purple or other miscellaneous coloured objects. (*b*) Distribution of fraction of a bower's coloured objects outside the female's field of view (FOV) at Mary Valley and Dreghorn before any manipulations. (*c*) Distribution for Dreghorn experimental bowers before manipulation. (*d*) Distribution 3 days after all coloured objects were moved inside the FOV.

they were fully within the female's FOV. The numbers of coloured objects inside and outside the FOV were recorded again 3 days later. The samples before and 3 days after the disturbance were compared for each bower using Barnard's exact test [24] on the 2×2 table resulting from pooled data from both courts. All tests were two-tailed.

To determine how females perceive the light environment within the bower, reflectance spectra of the avenue walls and coloured objects were taken at Dreghorn in 2011, using our previous methods [25]. Reflectance spectra were taken in two rows of five samples each near the top and near the bottom of both inner avenue walls; 10 samples at bowerbird eye level and 10 samples near the avenue floor. We also analysed avenue stick spectra collected at different locations during a previous study ([25] and unpublished data 1998–2012). We sampled stick reflectance spectra from 20 to 30 upper and lower inner walls and floor sticks from 178 bowers at 23 locations that were spread across the entire distribution of great bowerbirds from Broome to Cape York and Townsville (see electronic supplementary material). Direct comparison with the upper and lower walls at Dreghorn is not possible because, although we sampled all parts of the inner avenue in the geographical survey, we did not label the transects separately; consequently, comparisons between the species dataset and Dreghorn have to be made with the average of upper and lower Dreghorn wall transects. Bower locations were categorized as 'city' bowers if they were located within suburbs of Townsville or Darwin or 'bush' bowers if they were not located in or near a city. We also recorded the number and colour of all decorations on every bower.

Irradiance (ambient light) measures and mean object class reflectance measurements [25] were used for the bower wall analyses. Chromatic adaptation effects were calculated for the bowerbird V-type eye [25,26] using the Von Kries correction [26,27], and plotting the bowerbird eye responses for each object in LSMU colour space [26]. LSMU colour space is a plot of the relative differences in light-adapted cone captures between middle wavelength-sensitive (MWS) and ultraviolet-sensitive (UVS) cones as the MU axis and relative differences between LWS (long) and SWS (short) cones as the LS axis, hence the name LSMU. As a consequence, hue and chroma are the polar coordinates of each stimulus in this space; hue is the angle clockwise from the top of the LS axis (in human terms, going from red clockwise through yellow, green, blue and UV and back again) and chroma is the distance from the grey point (origin). Two calculations were performed for each object class: (i) eye chromatically adapted to the light outside the bower, and (ii) eye adapted to avenue wall radiance calculated as bower irradiance times upper wall reflectance. Each light environment will be associated with a different grey point when there has been enough time for differential cone bleaching [27]; two light environments are associated with a geometrical shift in all positions in LSMU space, including the grey point (the origin).

In order to estimate the fraction of the female FOV that was filled by the avenue walls (i.e. influencing light adaptation), hemispherical photographs (180° solid angle) were taken at 12 active bowers at Dreghorn and four at Mary Valley. Photos were taken within the avenue at the female head position, looking towards the avenue entrance (one photo per entrance) and looking directly at the avenue wall from the same position. We also analysed video footage of successful courtship displays (i.e. displays that ended in copulation) at nine Dreghorn bowers to investigate the female's viewing behaviour during displays. We measured general viewing direction using the location of the female's head relative to the bower using three categories: head (bill facing within 20°) along the axis of the bower avenue towards the entrance, head facing a bower wall and head between these two angles. We also quantified how often the female moved her head during the display.

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Analysis of mating success per bout was carried out by GLMM using a bimodal family and cloglog link, using R [28] and the *lmer* function in the lme4 package [29]. Full models were reduced by sequentially removing components with function *drop1* until no more components could be removed and the AIC was minimized. There were 1075 observations, 122 date-times and 26 bowers.

3. Results

(a) Presentation of coloured objects

The numbers of coloured objects on bowers were log-normally distributed. The log means and standard deviations were Mary Valley 1.53 ± 0.32 (nine bowers), Dreghorn 1.12 ± 0.41 (61 bowers) and both localities pooled 1.17 ± 0.42 (overall mean of 14.8 coloured objects, s.d. range 5.7–38.7). The distributions of object colour classes displayed or on the bowers at Dreghorn are shown in figure 2*a*. When not being actively displayed, almost all coloured objects were found outside the FOV (figure 2*b*). At Mary Valley, 78% of bowers had 80% or more of their coloured objects outside the FOV and at Dreghorn 79% of bowers had 80% or more outside. For the years 2009–2011 at Dreghorn, 60%, 88% and 85% of the bowers, respectively, had 80% or more objects outside the FOV.

In the years 2010–2012, an average of 5.1 coloured objects (s.d. range 2.2–11.6) were displayed per courtship display bout ($n = 1075$ bouts). During the same bouts, nuchal crests were displayed 2.9 (s.d. range 1.2–6.8) times, and the items tended to alternate between nuchal crests and coloured objects. The displayed objects were mostly sticks, green, red and brown objects. Including nuchal crests, 88% of display items were coloured, and disregarding nuchal crests 82% of objects were coloured. By contrast, 2% of objects on the court were coloured; 98% of court objects were uncoloured. The colour diversity (3.28 ± 1.03) and colour transition diversity (1.53 ± 1.06) per bouts are much smaller than the potential maxima because most displays alternated between the nuchal crest and only one or two different object colours. This is shown by the fraction off-diagonals in the transition matrices; displays had a median (of all bouts) colour transition fraction of 0.91 (i.e. 91% of transitions were between different colours rather than repeats), median colour class was 0.80, and median object class 0.86. Colours and object groups were rarely used twice in a row within bouts.

Females observed males from within the avenue over times that varied from a few seconds to 17 min; these durations were close to lognormally distributed with a geometrical mean of 1.24 min. Female observation bouts that resulted in mating were significantly longer than those that did not (2.40 versus 1.17 min, Kruskal–Wallis test, $p = 0.01$; figure 3). Mating success per male display was predicted jointly by the duration of the display bout (figure 3), the number of objects displayed and the interaction between duration and the object transition diversity (table 1). There were significant correlations between observation duration and the counts of colours, colour classes and colour diversity (all $p < 0.01$) as well as sequence diversity ($p = 0.039$; see electronic supplementary material, figure A1). This indicates that females spent longer observing displays where males presented objects in a variety of colours and had many changes between colours during a display bout. Repeating the analysis using the means of variables for each bower per year to predict the number of copulations at each bower for that year shows no relationships with any variables (all $p > 0.05$). Instead, in each case, mating success per bower is much higher above a threshold value for each trait (example in the electronic supplementary material, figure A2).

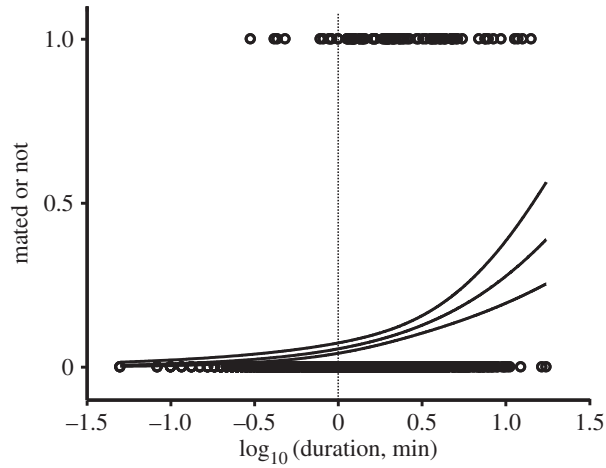

Figure 3. Relationship between mating success during a female's observation bout and the duration of time the female was inside the avenue during that bout. Open circles are bouts. The lines are from a GLMM (table 1) with standard errors. The vertical dotted line is at 1 min, the time required for the principal chromatic adaptation process in opsins.

Table 1. Results of a GLMM relating display characteristics to mating success. Minimum model derived by reduction of a full model including all possible variables. Variables: *Lduration*, $\log_{10}$ duration of display bout (minutes), *Lobnudisp*, $\log_{10}$ number of objects displayed, including nuchal crest; *octrdiv*, object class transition diversity; *bower*, bower number; *dateno*, combined year and date; colon indicates an interaction; asterisks indicate significance level.

random effects and variances				
Dateno	2.3859	1.5446		
Bower	1.6025	1.2659		
fixed effects	**estimate**	**s.e.**	***z*-value**	**Pr(>|*z*|)**
(intercept)	−1.70567	0.57494	−2.967	0.0030**
Lduration	2.03430	0.76126	2.672	0.0075**
Lobnudisp	−2.85741	0.63601	−4.493	7.0×10^{-06}***
octrdiv	−0.04832	0.15239	−0.317	0.75
Lduration:octrdiv	0.90804	0.23006	3.947	7.9×10^{-05}***

When coloured objects were placed, so that they would be visible to females in the bower, males put most of the objects back out of sight within 3 days (figure 2*c*,*d*). Comparing the numbers on each bower inside and outside the FOV before the manipulation and 3 days later, we found that there was no significant difference in the fraction of coloured objects outside the FOV after the sequential Bonferroni correction (before Bonferroni, 16 $p > 0.12$ and one $p = 0.04$). The overhead video recordings showed males displaying by the avenue entrance at either edge of the female's FOV. As a consequence, only the male's head, part of his neck and objects held in his beak were inside the female's FOV. When combined with the female's limited view from within the bower, the overall effect is that coloured objects and nuchal

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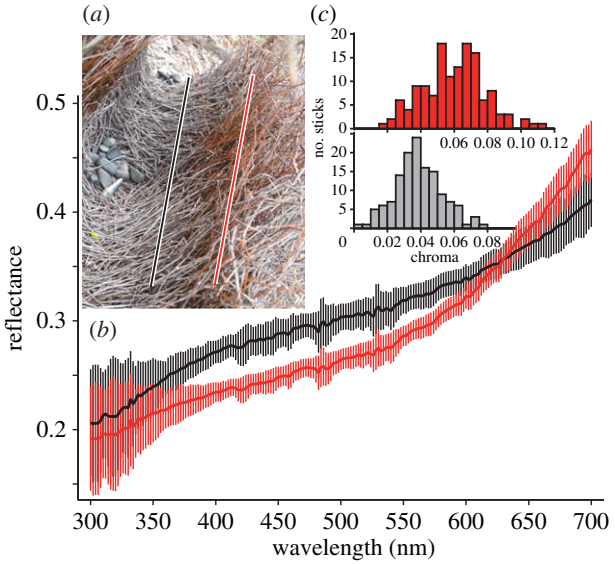

Figure 4. (*a*) Photograph of bower walls, showing wall transect locations at bowerbird eye level (red line; upper wall) and below wing level (black line; lower wall). (*b*) Mean and s.d. of bower mean spectra of transects. (*c*) Distribution of tetrahedral chroma of transects. Higher chroma indicates greater differences between wavelengths ('purity' for humans). Visual backgrounds outside the avenue are generally less than 0.02. (Online version in colour.)

crests are typically seen only briefly against the grey court background when displayed to the female.

(b) Colour enhancement by light adaptation

When standing in the bower avenue, the bower walls occupy most of the female's retina (electronic supplementary material, figure A3). At Dreghorn, when the eye faces an avenue entrance 84 ± 5% of the FOV is taken up by the avenue, and it is 88 ± 5% when the eye faces the avenue walls. At Mary Valley, the fraction when facing the court is 91 ± 1%, owing to more bowers having a closed roof (electronic supplementary material, figure A3). Reddish sticks (figure 4) make up the inner avenue walls and floor. Sticks that are comparatively redder are positioned so that their upper parts show but their lower parts are partially obscured by shorter, less red sticks (figure 4*a*). As a consequence, the reflectance spectra at eye level rise faster with wavelength (redder) than the spectra lower down the walls or floor (figure 4*b*) and degree of redness or tetrahedral chroma [25,26] is stronger at eye level than lower down (Wilcoxon test, $p = 0.0005$; figure 4*c*). Bowers at Dreghorn had significantly lower chroma (0.048 ± 0.13; average of upper and lower walls) than the average of bowers over the entire geographical range of great bowerbirds, at both bush bowers (0.086 ± 0.027; Wilcoxon test, $p < 0.0001$) and city bowers (0.138 ± 0.024; Wilcoxon test, $p < 0.0001$). City bowers were also significantly more chromatic than bush bowers (Wilcoxon test, $p < 0.0001$). Given that Dreghorn avenue walls and floors are less chromatic than 93.8% of bowers at other locations, our calculations of light adaptation on the basis of the Dreghorn data underestimate the degree of light adaptation in most great bowerbird bowers.

When watching a male display, female head movements occurred approximately every 1.6 s (log s.d. range: 1.2–2.1 s) and females spent the majority of their time (mean and s.d.: 65 ± 10%) with their head angled between the axis of the avenue and the walls, 16 ± 10% of the time facing (beak pointed) along the avenue axis, and 19 ± 9% of the time facing a wall. Given the nearly continuous and 180° head movement range and left–right alternation in which the eye looks outside the avenue, the entire retina is mostly (approx. 86%) exposed to the reddish light from the avenue for most of the time. The exposure to reddish light for a minute or more results in chromatic adaptation: differential cone bleaching hence reduction of the sensitivity of the LWS, and to a lesser degree, the MWS photoreceptors, relative to the SWS and UVS cones.

The perceptual effects of the female's chromatic adaptation to the reddish avenue wall light, compared with light adaptation to conditions outside the bower, are shown in figure 5. Chromatic adaptation to the wall results in the wall stimulus moving towards the achromatic (grey) point, and all stimuli to move in roughly the same direction in colour space. The upper wall, at eye height, provides a stronger change in colour perception than the lower wall and floor (difference approx. 0.06, figure 5), but the qualitative effects are the same. The actual degree of perceptual change (position on each line in figure 5) will depend upon the time in the avenue, the actual percentage of the FOV that is reddish, the red chroma and the time looking in various directions. When a female first enters the avenue, her eye will be adapted to the exterior light (stars in figure 5). The longer the time and the redder the light (figure 5 shows means), the further down the line the object will go, and perception will be altered purely for biochemical–optical reasons. Note that these calculations are based upon walls with lower chroma compared with the average of all other parts of the geographical range, so the effects would be stronger, i.e. the line will be longer at most other populations (electronic supplementary material, figure A4).

The error ellipsoid suggests that a female looking at the walls and gesso objects on the court will not distinguish gesso colours and regard them all as grey, because these objects are inside the same error ellipsoid. The most striking effect of this chromatic light adaptation is that the chroma of the nuchal crest is greatly increased, and that red, green and purple objects move closer to the axes, meaning that they stimulate fewer cones, possibly leading to stronger colour sensations. In human terms, green objects will seem more green and purple objects will seem more purple. Red objects will seem more red in the sense of less red–orange, but will become less chromatic (figure 5). We found no relationship between wall chroma or any other aspect of male display and mating success ($p > 0.05$).

The redness inside the avenue should affect what objects the male displays during courtship because it affects some colours more than others; he should not use colours that are close to or inside the noise ellipsoid in figure 5, for example, red fruit. Including all bowers across the great bowerbird range, there is no relationship between the fraction of ornaments that are red and the chroma of the red wall ($n = 178$). However, only 44% of the bush bowers had any red objects, possibly owing to a lack of availability. Excluding bowers with no red objects yields a highly significant negative regression of fraction of red display objects on the degree of avenue chroma ($t_{97} = 5.93$, $p < 0.0001$, $R^2 = 0.27$ see diagrams in the electronic supplementary material, figure A5); bowers with redder internal walls have fewer red decorations present on the bower. There is no relationship between the proportion of green objects and wall chroma ($t_{176} = 0.27$, $p = 0.79$), but there is a significantly

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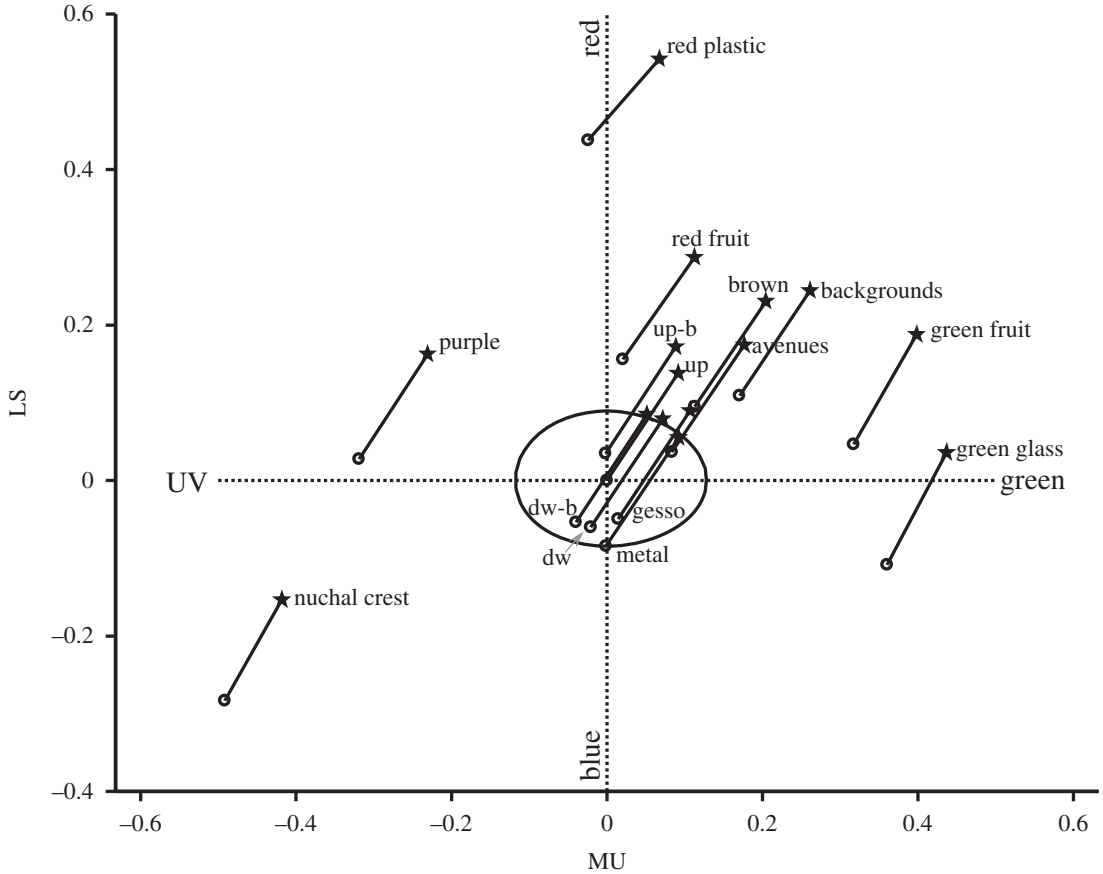

Figure 5. Objects and visual backgrounds in LSMU colour space showing the shift of position (colour) between being adapted to lighting conditions outside the bower (stars) and lighting conditions inside the avenue (circles), which is reddish from the avenue walls. The origin is the achromatic point for the mean lighting conditions within the avenue (using mean upper wall light). Stimuli far from the origin, but on each axis, will have colours with the pure hues indicated. The ellipsoid centred on the avenue-adapted grey point is the Vorobyev–Osorio model-based noise ellipse. Points inside the ellipsoid are not distinguishable. Note how avenue wall light adaptation shifts the positions towards the lower left, and main display objects towards the axes. Up, upper avenue wall transect, all bower mean; up-b, upper transect, most chromatic bower mean; *dw*, lower transect, all bower mean; *dw-b*, lower transect most chromatic bower mean; *avenues*, mean spectra of avenue twigs of bowers from many localities [25]. If the chromatic adaptation was to the light coming off the lower transect, then the origin would be at the position marked *dw* rather than at the lower end of the *up* line; and all lines would be shorter. Most other localities in the range of great bowerbirds have more chromatic avenues (compare *avenues* with *up* and *dw*).

positive relationship with more rare colours (not green or red; $t_{176} = 5.92$, $p < 0.0001$, $R^2 = 0.17$).

4. Discussion

Male great bowerbirds use the female's predetermined viewpoint to produce the forced perspective illusion [18], to provide flashes of colours against a grey background, and with coloured avenue walls, to alter her perception of the colours. Chromatic adaptation and display colours interact, and interact in opposing ways for different colours.

Males actively keep coloured objects outside the female's FOV until used in displays: when moved into the female FOV, males moved them outside within 3 days. This rapid recovery of the original configuration is as fast as recovery from forced perspective modification [18,21], indicating that the hidden location of decorations is very important to the birds. The movement of decorations in and out of the FOV will result in colour flashes, and these may hold the female's attention more successfully than if the colours were seen on the court continuously. The colour of displayed objects generally contrast with the uncoloured visual background of the court [25], increasing salience further. Males tended to alternate between high-contrast-coloured objects (e.g. green fruit, pink nuchal crest) with low-contrast-coloured objects with a large retinal sweep (brown sticks). This minimizes chromatic adaptation to each object's colour, and the long sticks trigger motion detection over a larger area of the retina, and hence ornament display maximizes salience, and consequently may enhance the novelty and surprise in the display.

While the absolute number, types and sequences of displayed objects predict mating success at the level of the bout, it is difficult to separate cause and effect, because displaying each object takes time. We do not know whether the presentation of many objects of diverse colours keep the female in the avenue longer, or whether more time in the court allows more time for more object displays by the male, and hence more diversity. The colour and type of decorations present at the bower is a predictor of mating success for several bowerbird species [12,30]. Here, we have shown that, in this species, the display presentation sequence is also important, but only at the individual bout level. This suggests that these visual signals function primarily in signal salience rather than conveying signal content [5,6].

Chromatic adaptation from the reddish avenue walls and floor may improve the efficacy of this signal, but also

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induces design constraints. For most display bouts, the time females spend observing male displays is more than sufficient for chromatic light adaptation of the female's eyes to the reddish light coming off the walls. The mean time of all observation bouts by females is about a minute, and courtships that result in mating average 2.4 min. In various experiments with human and animal observers, almost all chromatic light adaptation takes place within 2 min, but about 80% takes place in 45 s to 1 min and up to 50–60% occurs within a few seconds [31–33]. As successful display bouts are usually longer than a minute, females that mate are chromatically adapted and probably perceive colours differently than at the start of the bout. The perceptual effects are likely to make the colours of displayed objects appear stronger and hence contrast more with the visual background. This contrast may be enhanced further by movement of the nuchal crest and of coloured objects in the male's beak. In addition to affecting female perception of colour, chromatic adaptation can also affect the ability to discriminate among colours [31], and interact strongly with eye movements [32,34], which may affect mate assessment and attractiveness [35]. These potential knock-on effects highlight the many unexplored avenues in the interaction between visual mechanisms and sexual displays [36].

The avenue chroma at Dreghorn bowers was lower than at 93.8% of other bowers throughout the species' range, so the visual effects of chromatic adaptation will be much stronger in most other populations. The effect is to bring the perception of red fruit as well as brown decorations closer to or even inside the error ellipsoid (electronic supplementary material, figure A4); they may appear weakly red or even indistinguishable from the grey colours of the court. This suggests that in order to maximize visual contrast of waved objects during display, red fruits should be used less often in locations and bowers where the avenue walls are more chromatic. Although red fruits decline in visual contrast, red plastic is still very chromatic (far from the error ellipsoid), so there is still large colour contrast using red plastic even with highly chromatic avenue walls, and both are found in cities. There is a particularly strong enhancement of the nuchal crest with more chromatic avenues. More chromatic avenues do result in green fruit with less chroma, but they are still double the radius of the error ellipsoid (about 1 JND; see electronic supplementary material, figures A4 and B). The reduction in chroma may be more than made up for by the movement to the MU axis, the reduction from three to two cones stimulated may make the green fruit colour appear more intensely green than when seen outside the bower. As predicted, we found that more chromatic bowers had fewer red objects and more objects of other colours, apart from green, which remained unchanged.

We found no relationship between the redness of the interior walls and any aspect of mating success. It is frequently assumed that because a trait is under natural selection that we should be able to relate it to fitness. This is reasonable if we are considering secondary sexual traits that are used as indicators of direct (e.g. parental care) or indirect (genetic quality or compatibility) benefits during mate choice [2]. However, a trait may be subjected to natural selection but not be seen to predict fitness for seven reasons: (i) its major function is to draw or hold the potential mate's attention [7], and other traits are used in choice as indicators of mate quality. This may select against variation, and therefore yield no relationship between trait value and fitness. (ii) The preference function may be in the form of a threshold; the trait has to be above (or below) a certain value to be effective, but variation beyond the threshold is irrelevant (e.g. alerting and species recognition signals). (iii) It may be the result of chase-away sexual selection in which traits that were formerly useful in mate choice become fixed in the population and no longer indicate quality [37]; now it acts like a threshold or is simply present as an appendix to mate choice. (iv) Its major function is as an amplifier [38] or a secondary enhancer [39] of the targets of mate choice; it makes the signal easier to receive, assess or discriminate. (v) It may be one of many traits involved in choice and so contributes at a level below detectability without a large sample size or specialized analysis, as for individual quantitative trait loci [40] or because selection is for genetic dissimilarity, which also involves many loci [41]. (vi) The variation in the trait in the population measured may not be detectible by the sensory or perceptual system as a simple consequence of Fechner's law or other neural mechanisms [42]. For example, movements that are two slow or too fast will not be discriminable. (vii) If the population is near an optimum, or there is frequency-dependent selection, and the population is at or near the equilibrium, then the existing range of variation may not reveal any selection [43]. In any case, we must not assume a simple relationship between trait value and fitness. These kinds of traits that are necessary for mating are still subjected to natural selection, but the relationship between fitness and trait value may not be linear; the function may range from logarithmic or sigmoid to threshold, or even have an optimum.

It is possible that both the flashes of colour and the reddish bower walls act as amplifiers as they both improve signal design by increasing visual contrast and saliency. The increased efficacy of the signals may mean that the female has to visit fewer bowers, or the same bower fewer times, before selecting a mate than if these efficacy enhancers were absent. Chromatic adaptation is more likely to increase signal efficacy than affect preferences as it can simply increase visual contrast and make discrimination on the basis of other traits easier. Experimental manipulations that remove or add red coloured sticks to bower walls are needed to determine whether the chromaticity of the walls makes a fitness difference or merely improves signal salience or discriminability. The reddish sticks are actively chosen and placed differentially on the inner avenue. They do not serve in structural support, and the fact that there is a negative relationship between red ornaments, and the degree of redness of the inner avenue suggests that their use is not a result of a general preference for red objects. In any case, the interaction between the avenue reddish light and the display objects enhances some colours and dilutes others, constraining the overall display form. A general preference for red, which favours red walls and display objects, cannot increase indefinitely because it will eventually lead to a loss of red object saliency.

Could these signals indicate quality indirectly? The presentation of a diverse array of coloured objects may act as a proxy for foraging ability or general cognitive ability [44]. The waving of decorations during the display may provide a direct and accurate representation of the male's vigour [39], but appropriate colours have to be chosen in order to make the movements most conspicuous. Females may also gain information about a potential mate if he modifies the

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intensity of his display in response to female movements, as in satin bowerbirds [20]. While it seems that the presentation of objects to females is an important part of male display, further work is needed to disentangle the relationships between display components. The lack of effect in some traits and a threshold effect in others on individual mating success suggests that these traits function as important parts of signal design rather than content [6]. The emphasis on good gene indicators (signal content) in the literature has led to the neglect of other properties that may promote mating success, such as holding female attention and the evolution of the signal design itself. The study of mate choice and animal signalling is multidimensional with multiple strategies as well as multiple sensory modes [1], and we must not neglect the functions of signal components that do not reflect possible mate quality, or the effects of interactions between different signal components.

Acknowledgements. We thank Natalie Doerr, Michael Jennions and Sonia Kleindorfer for excellent discussions. We are most grateful to the Smith family for access and hospitality at Dreghorn Station, the manager and owners of Mary Valley and Artemis stations for access and L. Endler for help in fieldwork. We thank David Wilson for collecting some of the avenue data. This research was carried out with an EPA-Queensland Parks and Wildlife Service permit (WISP01994004) and ethics approval from Deakin University (A22-2010) and James Cook University (A1318).

Data accessibility. Data will be made available 1 year after publication on Dryad: doi:10.5061/dryad.8rd4v.

Funding statement. Financial support was provided by the ARC, NSF, Deakin University and *Evolutionary Ecology* Editor-in-Chief fees from Springer to J.A.E.

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Addendum

Cite this article: Endler JA, Gaburro J, Kelley LA. 2014 Addendum: Visual effects in great bowerbird sexual displays and their implications for signal design. *Proc. R. Soc. B* **281**: 20140864.
http://dx.doi.org/10.1098/rspb.2014.0864

Received: 9 April 2014
Accepted: 10 April 2014

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Addendum: Visual effects in great bowerbird sexual displays and their implications for signal design

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We inadvertently left out one acknowledgement in our paper [1] and we add it now in this addendum:

We thank Natalie Doerr for an excellent job of setting up and running the bowerbird cameras and other aspects of fieldwork during the 2012 season.

In addition, we neglected to reduce the number of significant figures in table 1 from the original R output. If interested, please round off each number to three significant figures.

Reference

1. Endler JA, Gaburro J, Kelley LA. 2014 Visual effects in great bowerbird sexual displays and their implications for signal design. *Proc. R. Soc. B* **281**, 20140235. (doi:10.1098/rspb.2014.0235)

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