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Great Bowerbirds Create Theaters with Forced Perspective When Seen by Their Audience

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Summary

Birds in the infraorder Corvida [1] (ravens, jays, bowerbirds) are renowned for their cognitive abilities [2–4], which include advanced problem solving with spatial inference [4–8], tool use and complex constructions [7–10], and bowerbird cognitive ability is associated with mating success [11]. Great bowerbird males construct bowers with a long avenue from within which females view the male displaying over his bower court [10]. This predictable audience viewpoint is a prerequisite for forced (altered) visual perspective [12–14]. Males make courts with gray and white objects that increase in size with distance from the avenue entrance. This gradient creates forced visual perspective for the audience; court object visual angles subtended on the female viewer’s eye are more uniform than if the objects were placed at random. Forced perspective can yield false perception of size and distance [12, 15]. After experimental reversal of their size-distance gradient, males recovered their gradients within 3 days, and there was little difference from the original after 2 wks. Variation among males in their forced-perspective quality as seen by their female audience indicates that visual perspective is available for use in mate choice, perhaps as an indicator of cognitive ability. Regardless of function, the creation and maintenance of forced visual perspective is clearly important to great bowerbirds and suggests the possibility of a previously unknown dimension of bird cognition.

Results and Discussion

Male bowerbirds in the avenue species group build structures in the form of an avenue defined by two parallel walls of sticks [10] (Figures 1A and 1B; Figure S1 available online). During courtship, a female stands within the avenue and watches the male display over the court [10] (Figure 1A and Movie S1). Great bowerbird females (Ptilinorhynchus [= Chlamydera] nuchalis) have a small field of view (46 ± 6°, 19 bowers; Figure S1) because they view males through a long channel (Figure 2A) within a long avenue [10] (our data: 61 ± 11cm; Figure 1B). This predefined viewpoint makes the creation of forced visual perspective by great bowerbird males, for female viewers, possible and practical because forced perspective requires a predefined (forced) field of view [12–14].

An observer’s eye receives a two-dimensional projection of the objects in the scene [12, 13], making a mosaic of patches on the retina. Retinal patch size is proportional to the angle subtended on the viewer’s eye (φ) by the object, which is jointly dependent upon the object size and distance to the viewer (Figures 1C and 1D; Figures S1–S3). Visible width (w) is the width of an object measured horizontally perpendicular to the viewer’s line of sight, and visible depth (d) is measured parallel to the line of sight; w and d result in visual width and depth angles φw and φd, respectively, corresponding to lateral and vertical directions on the retina.

In natural scenes, the angles (φ) subtended on the viewer’s eye by objects of similar size decline with distance (Figure 1C), and this is used by the brain to estimate object size and distance [12, 14, 15]. Retaining this relationship in constructed scenes and images makes them look more natural [12–14]. Altering the natural relationship between φ and distance is called forced perspective, and it can make some objects, and entire scenes, appear larger or smaller than they are [12, 14–18]. In scenes where object size declines with distance, the more rapidly decreasing φ appear to correspond to larger scenes or objects [15–18]. This is used in gardens, buildings, theaters, movie sets, and amusement parks to give the illusion of greater size [16–18]. When object size increases with distance, the φ decrease more slowly than normal, or remain constant (Figure 1D) and the visual pattern (φ distribution) is more regular than random. The scene may appear smaller, depending upon the gradient. To avoid the variable meanings of perspective in different sets of literature, we define forced perspective simply from geometric optics [14] as a geometric pattern projected to a predetermined viewpoint with abnormal relationships between object size and object visual angles. Forced perspective works only from the appropriate viewpoint.

Great bowerbird courts consist of gray to whitish objects (pebbles, bones, shells, etc.; Figures 1A and 1B, Figure 2B, Figure S6) on which are placed colored objects, some of which are used by displaying males [10]. We will collectively call these gray and white objects the gesso, because, as in painting, males place colored objects upon gesso. In two Queensland populations separated by 700 km (Mary Valley: 15.04° S, 143.77° E; Dreghorn: 20.25° S, 147.73° E), the gesso objects are arranged in order of increasing size with distance from the avenue (Figures 2A and 2B); regressions of object visible width (w) on distance from the avenue center (x, Figure S4) were positive for all bowers at both sites and were significantly (p < 0.05) positive in 79% of Mary Valley bowers (14 bowers, 7 to 66 degrees of freedom [df]) and 95% of Dreghorn bowers (19 bowers, 185 to 405 df; Figure 3A), with very similar results for visual depth (d). Bowers vary in their slopes, suggesting individual variation in the ability to create geometric patterns. Photographs of bowers throughout the species range suggest that this pattern is widespread and variable within and among locations.

From the female’s viewpoint within the avenue, the increasing gesso object size with distance is an example of forced perspective (Figure 1D). The consequence is a more uniform distribution of visual angles (φ) than random or than
normal perspective (Figure 2A). If bowerbirds were to create forced perspective with no variation in $\phi$, they would place objects with visible width $w$ and depth $d$ at viewing distance $x$ according to $w = 2 \sqrt{(h^2 + x^2) \tan (\phi/2)}$ and $d = \phi (h^2 + x^2)/(h-x\phi)$, where $h$ is the female's eye height (Figures S2 and S3). This, plus errors in placement of objects, predicts the positive regressions of $w$ and $d$ on $x$ that we observed. The result of this male behavior is a female view of the gesso with low variation in $\phi$: a significantly even visual background pattern.

The critical test for forced perspective is whether $s$, the standard deviation of $\phi$, is smaller than random expectation (the same objects placed at random). Permutations of $x$ and $w$ within each bower (Figure S5) show that all bowers at Mary Valley and 95% of the bowers at Dreghorn showed some variance reduction ($p < 0.50$ or better). 64% of the bowers at Mary Valley and 95% of the bowers at Dreghorn showed significantly ($p < 0.05$) less variation in $\phi$ than if the gesso objects were placed at random. Effect sizes ($\bar{s}$) for

Dreghorn are shown in Figure 4A and show the variation in the degree of forced perspective among bowers. A very similar result was obtained for permutations of $x$ and $d$. Results were the same when the north and south courts of each bower were tested separately. Almost all males constructed female views of their courts with forced perspective; visual angles $\phi_w$ and $\phi_d$ have much lower standard deviations than if the objects were placed at random on the court.

To test for maintenance and repair of the forced perspective, we reversed the size-distance gradient (Figures 2C and 2D) of all objects on the courts in 15 Dreghorn bowers and recorded subsequent changes after 3 days and 2 wks (Figure 3, Figure 4, Table 1, Figure S6). Three days after the reversal, most bowerbirds returned their courts to positive slopes (Figure 3C) and positive effect sizes $\bar{s}$ (Figure 4C). The bowers were back to their original perspective after 2 wks (Figure 3D, Figure 4D, visits 1 and 4 in Table 1). Control bowers did not change sign, but the slopes changed slightly (shaded bars in Figure 3 and Figure 4; repeat measurement error is less than one histogram bar width), most likely because the birds continually shift object positions (Figure S6). Individual bowers were consistent in the quality of their forced perspective over 2 wks. The correlation between visits 1 and 4 for mean $\phi$ was highly significant ($\phi_w r = 0.82, p < 0.0001$; $\phi_d r = 0.76, p = 0.0002, 17$ df), indicating consistency in the scale (patch size) of the forced perspective.

The visit 1–4 correlations for $s$ were significant only for width ($\phi_w r = 0.77, p = 0.0001$; $\phi_d r = 0.36, p = 0.13$), indicating that
males consistently differed in the quality of their forced perspective (degree of patch regularity) with respect to visible width (horizontal size) but not visible depth.

To test the possibility that the repair of the gradients was incidental to males putting each gesso object back in its original location, we compared the locations of unequivocally recognizable objects at visit 1 (V1, original) with visits V3 or V4. X is the distance from the avenue along the avenue axis, and Y is the distance perpendicular to the X axis. If objects were replaced at their original locations, then the correlation between V1 and either V3 or V4 would be high (r = 0.9 for 5 cm location error, 0.7 for 9 cm) and roughly equal for X and Y directions (rX = rY). If relocation were imperfect, then rY ≥ rX because the courts are longer than they are wide, making maximum random errors smaller in Y. If males gradually transfer the objects to their original locations, then both rX and rY should increase with time. Alternatively, if males simply repair the gradient, then rX should be high but not as high as in object relocation, because exact location of each object is unimportant; only size and distance matter. For gradient repair, rY should be low or zero, because Y direction is irrelevant. The results reject object replacement (Table 2, Figure S7). X correlations are moderate and either remain the same or decrease with time. Y correlations are significantly smaller than rX, not significantly different from zero in the experimentals, and one is significant in the controls, owing to objects not touched by the birds during the sampling period. All rY decrease with time, because males continually move the gesso objects on their bowers (Figure S6) and random movement yields decreasing position correlation unless corrected by males. This is consistent with gradient-specific behavior in the X direction, but random placement and movement in Y, and inconsistent with location replacement.

Like humans, bowerbird art varies; there is among-individual variation in both mean and standard deviation of ϕ, and individual styles remain stable over two weeks. This could arise from variation in males’ abilities or variation in local gesso availability, or both. If a bowerbird placed his bower in an area where there was a small range (variance) in potential gesso object sizes, then he would not be able to produce size gradients as steep as another male in an area with a greater available size range. We do not have availability data, but a simple test would be to regress the slope of the gradient against the variance of object size on the assumption that the observed size variance on a bower represents local availability. However, this results in a classical artifact [19], because the size data appear in both the gradient and the variance. As when using the opportunity for sexual selection (I S) as a measure of the intensity of sexual selection [20], the variance in object size can give only an upper limit to the gradient and is not a good predictor. Another approach is to examine the bowers and their neighbors by using spatial autocorrelation; local availability differences may result in near neighbors having more similar variances than distant neighbors. Tests of the Dreghorn bowers at visit
1 using Moran's I [21] indicate the highest similarity among groups of 4–6 bowers and significant similarity (Z-scores > 1.96) within groups of 9–11 bowers. The peak at 4–6 bowers is suggestive because the bowers are spaced evenly, males frequently steal objects from neighbors, and object availability is a function of what is present at several neighboring bowers and what is found in the environment [22]. The 9–11 bower similarity scale may correspond to local differences in fundamental availability: half the bowers are found in the riparian region of the Burdekin river and the other half in the riparian region along a small tributary of the Burdekin; differences on this scale could arise from local geology and drainage (stone size), local density of snail populations (shells), and other local habitat differences. There are therefore four possible nonexclusive causes of consistent variation among bowers: (1) variation in ability to construct the gradient, (2) variation in the ability to steal ornaments [22] with high variation, (3) variation in the ability to resist theft of ornaments [23] leaving high variance, and (4) local variation in availability of objects unrelated to behavior. Only the last possibility does not involve male quality attributes, unless one assumes that some males select bower sites with more variation in object size when they first establish their bowers.

It is not clear how much cognition is needed to create the size-distance gradients. Males might explicitly place small objects close to the avenue entrances and larger objects farther away. This could result from complex cognition, be created through a simple inherited decision rule, or be the result of trial and error. Video recordings show that males spend 78% of their time at their bowers on bower maintenance, which involves moving gesso and other objects on their courts and avenue. They frequently show a cycle of looking at the court from the female’s avenue viewpoint and then moving court objects, and this is repeated throughout the day. Forced perspective could therefore be created by trial and error, in which the male moves the objects

Table 1. Friedman Test Probabilities for Differences in Slopes among Visits within Experimental Bowers

<table>
<thead>
<tr>
<th>Visit</th>
<th>V1 and V2</th>
<th>V2 and V3</th>
<th>V3 and V4</th>
<th>V1 and V4</th>
</tr>
</thead>
<tbody>
<tr>
<td>w (n = 15)</td>
<td>0.0001</td>
<td>0.0001</td>
<td>0.20</td>
<td>0.80</td>
</tr>
<tr>
<td>d (n = 15)</td>
<td>0.0001</td>
<td>0.0001</td>
<td>0.20</td>
<td>0.20</td>
</tr>
</tbody>
</table>

Visits are abbreviated as follows: V1, original bower; V2, immediately after reversal; V3, 3 days after reversal; V4, 2 wks after reversal. p < 0.05 indicates a significant change in the slopes of w or d on x between visits.
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Table 2. Correlations between Object Locations between Visits

<table>
<thead>
<tr>
<th></th>
<th>Experimental Bowers (n = 59)</th>
<th>Control Bowers (n = 32)</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>$r_x$</td>
<td>$r_y$</td>
</tr>
<tr>
<td>V1 and V3</td>
<td>0.501***</td>
<td>0.164</td>
</tr>
<tr>
<td>V1 and V4</td>
<td>0.526**</td>
<td>0.079</td>
</tr>
<tr>
<td>Z</td>
<td>0.61</td>
<td>2.42</td>
</tr>
</tbody>
</table>

Shown are $r_y$, correlations between X values (measured along avenue axis from avenue entrance) at visits 1 and 3 (V1 and V3) or visits 1 and 4 (V1 and V4) and $r_x$, correlations between Y values (measured perpendicular to the avenue axis; positive is left from inside avenue). $Z$ are test values and significance levels for differences between pairs (rows or columns) of correlation coefficients. Sample sizes are much lower than the gradient data because objects are continually moved within courts, moved to the other court, and/or stolen by other birds (up to 50% turnover per court in 2 wks); we included only objects that were easily identifiable in all visits.

*p < 0.05, **p < 0.01, ***p < 0.001, ****p < 0.0001.

until the court looks “good” from the avenue. Trial and error could reinforce a preexisting decision rule or formulate the rule. These possibilities require a value judgment by the male about the regularity of the view, which is essential in an aesthetic sense [24], but if constructed only by trial and error or a spatial rule (small objects close), this might not require a direct sense of perspective. It is noteworthy, however, that standard (linear) perspective was not invented by humans until the 15th century; before that it appears to have resulted from trial and error [14, 25]. Was there a significant evolutionary transition in humans (which also allowed the Renaissance) and bowerbirds that allowed the evolution of perspective? Assuming that bower building occurred in bowerbirds before the 15th century, why did perspective evolve in bowerbirds before it did in humans?

Great bowerbird courts produce forced perspective when the female views them from within the avenue; the image of the court projected on her retina, when viewed from within the avenue, has a more regular pattern than expected by chance. We do not yet know the consequences. The regular visual background (Figure 2A) may make the displaying male more conspicuous than if he was seen against an irregular background (Figure 2C). We do not know if this forced perspective produces the same illusions as it produces in humans, but pigeons perceive at least three illusions that are well known in humans: the Ponzo [26], Ebbinghaus-Titchener [27], and Müller-Lyer [28] illusions. If similar to humans, the regular pattern would make the court look smaller than it is and less deep, perhaps making the visible parts of the displaying male and his colored ornaments appear larger. The regular pattern created by the gesso might generate Ebbinghaus-Titchener effects when combined with colored objects or the male’s nuchal crest, which are displayed on or over the gesso and have the required similar sizes. Females use a fixed position within the avenue during the male’s display, restricting their head motion to mostly side-to-side and rotational movements (see Movie S1), yielding predictable motion parallax. Depth and size cues given falsely by the forced visual perspective will conflict with motion parallax cues; this may yield perceptive or illusion effects similar to the reversed perspective effect in humans [29]. The forced perspective of the Middle Ages (most notably in Byzantine art and Russian icons) draws the viewer’s attention to the person in the foreground; it might do the same for a displaying bowerbird, facilitating his mating with the female viewer. The effects of visual signal geometry would repay further study. Whatever the perceptual effects in bowerbirds, the geometry is clearly very important to them, because they repair defects in their designs within a few days and the regular pattern has to be viewed from a particular place to be seen (Figure 2).

The regularity of the pattern itself (small variance in $\phi$, larger $\delta$) is available to be used as a male quality indicator [30]. As for the among-individual variation in style, there are six possible sources of variation: (1) cognitive ability needed to construct forced perspective directly (other cognitive behavior increases mating success in satin bowerbirds [11]), (2) ability to create forced perspective by trial and error, possibly by regular pattern template matching or a sensory bias [31], (3) experience and age needed to learn to construct the bower [10], and gradient, (4) ability to steal ornaments with a high size variance, permitting better gradients, (5) ability to prevent theft of larger and smaller objects to retain high size variance, and (6) ability to choose bower sites with higher object variance. Some or all of these could affect the quality of a male’s forced perspective, but this requires further research. For whatever reason, the behavior of bowerbirds leads to their audience viewing a scene with forced perspective, which depends upon viewing the pattern from a predetermined angle and distance, something unknown aside from humans.

Experimental Procedures

Nineteen active bowers were found and measured at Dreyhorn (V1). Measurement was performed by computer-assisted analysis of scaled photographs. Fifteen had their size-distance gradients (both courts) reversed by moving existing gesso objects such that larger ones were closer and smaller ones farther away from the avenue, with random left-right movements. The inverted gradients were measured (V2). All courts were measured again 3 days (V3) and 2 wks (V4) later. See Supplemental Information for details.

Supplemental Information

Supplemental Information includes bower viewing geometry, definition of the variables; the relationships between visual angle, height of eye, distance to object, and object size; sample calculations; example photographs of an experimental and control bower court over time; plots of the positions of objects tracked among visits; tests for left or right position replacement; a movie of a male displaying to a female; detailed Supplemental Experimental Procedures; and a Supplemental Discussion. These can be found with this article online at doi:10.1016/j.cub.2010.08.033.

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References


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Inventory of Supplemental Information

Supplemental Experimental Procedures

Supplemental Discussion

Supplemental Figures

Figure S1. Basic Bower and Object Geometry
Relates directly to Figure 1 and first paragraphs of text.

Figures S2 and S3. Derivations of Visible Width and Visible Depth Angles, Respectively
Relate directly to Figures 1 and 2, and these terms are used throughout the text.

Figure S4. Example Regression of $w$ on $x$
Relates directly to Figure 3.

Figure S5. Example Distribution of Visual Angle and Corresponding Permutation Test
Relates directly to Figure 4 and text.

Figure S6. Example Photographs of the Course of the Experimental Court Geometry Sampling for an Experimental and a Control Bower Court
Relates directly to Figures 4 and 5 and throughout the text.

Figure S7. Demonstration that Males Do Not Replace Objects Where They Were before the Experiment
Relates directly to Table 2 and the text.

Supplemental Reference
Supplemental Experimental Procedures

Experiments were carried out at Dreghorn Station where 15 of the 19 active Dreghorn bowers were chosen at random for gradient reversal. There were only 4 controls because we wanted to keep the experimental sample size as large as possible given the unknown effect size and variation among bowers. Bowers were recorded by JAE four times for both courts: visit v1 (undisturbed), v2 (reversed gradient if experimental), v3 (3 days later), and v4 (2 weeks later). V2 is actually part of v1, but includes the manipulation (in 15 bowers) and the second set of measurements after the manipulations. Each visit took 3 days.

At a court, two 80cm dowels marked at 1cm intervals were placed at the edges of the field of view with one dowel end touching the center of the avenue wall and a part of the dowel touching the opposite wall (Figure S1 A). A T-shaped dowel assembly marked at 1cm intervals was placed inside the avenue with the crossbar touching the avenue wall ends and a screw marking the avenue entrance center. The distance from the screw to the center of the central avenue depression was read off this dowel. The 'tail' of the T gives the avenue axis and the screw serves as a geometric reference point (Figure 2B). The court, entrance and dowels were photographed together, or sometimes with two photographs for subsequent joining. Photograph numbers contained no information about whether the bower was was experimental or control, or which court or visit it was from; cross references to this data were kept separately in a notebook along with the direct measurements.

If the bower was experimental, and it was visit 2 (manipulation), the gesso objects were reorganized by picking them up and moving them within the court such that larger objects were placed closer to the avenue entrance and the smaller objects more distally, random left-right, but retaining the original court outline (Figure 2D). The reorganized court was photographed with the dowels again. The controls were unmanipulated because the birds constantly rearrange their objects. After photography, the dowels were removed and the other court received the same treatment.

MATLAB software (available upon request) was written (by JAE) and used to measure (by LCE) the gesso object distances \((x)\) along the object view axis determined by a line between the avenue and object centers, width measured perpendicular to the axis \((w)\) and depth along the view axis \((d,\) Figure S1 B). The program rescaled the image using the dowel centimeter marks and converted pixel distance to cm before storing the data; this corrects for camera height and position. The software operator (LCE) had only photograph numbers, and never had a close look at the courts during photography (the courts are under dense shrubs), to prevent unconscious bias in object measurements. Only objects on the top layer of gesso were measured; to be included the object had to be at least \(3/4\) uncovered by another object. If there were large numbers of unobscured objects in the photo, then only the
objects in a band continuing the avenue width (8-10 cm) to the far end of the court were measured; these are in the center of the female's field of view. Objects partially or wholly within the measurement area were measured.

For each bower, court, and visit, the set of $x, w,$ and $d$ of gesso objects were used to calculate regressions of $w$ on $x$ (example in Figure S4) and $d$ on $x$. The north and south court data were homogeneous ($P>0.05$) and were pooled for the analysis presented here. Therefore there were 15 experimentals and 4 controls.

For each bower, the set of $x, w,$ and $d$ (for both courts pooled) were used to calculate the visual angles $\phi_w$ (using $w$) and $\phi_d$ (using $d$) of each gesso object, using a typical eye height above the gesso ($h$) of 30cm (variation of $h$ over 10cm makes no qualitative difference to the results). See figure S2-S3 for the geometry and derivations of $\phi_w$ and $\phi_d$ from $x, w, d$ and $h$, and an example $\phi_w$ distribution. The distributions of log($\phi$) were not significantly different from normal (Lilliefors test, each bower $P > 0.05$ after the sequential Bonferroni correction), consequently the analysis of $\phi_w$ and $\phi_d$ used log($\phi_w$) and log($\phi_d$). The observed mean ($m$) and standard deviation ($s$) was recorded for both log($\phi_w$) and log($\phi_d$) for each bower and visit. Small $s$ indicate forced perspective (regular visual angles); a perfectly regular pattern would have $s = 0$. Larger $m$ indicates a larger scale (grain) of the visual pattern.

For each bower, 20,000 permutations were made of $x$ and $w$, and of $x$ and $d$. After each permutation the $\phi_w$ or $\phi_d$ of the permuted measurement data were calculated and a permuted standard deviation $\sigma$ was calculated for all objects for that permutation. The probability ($P$) of obtaining the observed or a smaller $s$ by random placement of the measured objects was obtained by the proportion of $\sigma \leq s$ (example in Figure S5). A small $P$ indicates that the observed variation in $\phi$ is significantly smaller than random, or that the visual angles are more regular than expected, demonstrating the presence of forced perspective.

The effect size $\delta s$ (strength) of the perspective in a given bower measured by $s$ was calculated as $(\sigma_m-s)/SE$, where $\sigma_m$ is the mean value of all permuted $\sigma$ and SE is the standard deviation of the permuted $\sigma$, which is also the standard error of log($\phi$). This is roughly equivalent to a standard normal deviate for $s$ because there were 20,000 permutations, but we tested for significance directly from the permuted $\sigma$ distribution. Stronger forced perspective is indicated by larger positive $\delta s$ and standard forced perspective (i.e. that used by architects to make buildings look taller) is indicated by negative $\delta s$.

The tests for differences between correlation coefficients used to test the hypothesis that bowerbirds replace objects where they were before the manipulation can be found on pages 575-582 of Sokal and Rohlf (1995).
Supplemental Discussion

Given that Great Bowerbirds create scenes with forced perspective, is what they produce art? The definition of art as a human activity is problematic and controversy rages. For a thorough discussion of definitions and their problems see http://plato.stanford.edu/entries/art-definition/.

We suggest an operational definition of art, which allows testable hypotheses: Visual art can be defined as the creation of an external visual pattern by one individual in order to influence the behavior of others, and an artistic sense is the ability to create art. Influencing behavior can range from attraction to and voluntary viewing of the art by others to viewers mating with the artist; bowerbirds and humans do both. Our definition equates art with conventional signals which are not part of the artist's body. In this sense, bowerbirds are artists and their viewers judge the art enough to make decisions based upon it, implying an aesthetic sense.
Bower geometry and parameters

Figure S1. Basic Bower Geometry
Bowers consist of an avenue surrounded by twin parallel walls of twigs with a court at each end (one court shown). In many bowers the walls arch over to make a tunnel (Figure 1). (A) A female views a male displaying on the court, usually from the opposite half of the avenue, anywhere between positions 1 and 2. Her field of view is restricted to an angle $F$, determined by the maximum excursion of her head between the walls during the male's display. For any one head position the actual field of view will be smaller than $F$, and it will be still smaller if the female is closer to the opposite avenue end (position 1) than the center (position 2). (B) Objects on the court, or color pattern elements in the male's plumage, at a distance $x$ from the female's eyes, have a visual width $w$ and depth $d$ which subtend (object tangent) visual angles $\phi_w$ and $\phi_d$ (not shown) on the female's eye. The distributions and relationships between $w$, $d$, and $x$ determine the visual perspective ($\phi$ distributions).
**Geometry of Bowerbird Perspective**

**Visual Width Angle $\phi_w$ and the width needed to keep $\phi_w$ constant**

Let $\phi_w$ be the angle horizontally subtended on the female’s eye, $x$ be the horizontal distance to the object or color pattern patch, and $w$ the object’s width along an axis perpendicular to the eye-object axis. Then

$$\phi_w = 2 \text{ArcTan}(w/2x)$$

In order to keep $\phi_w$ constant with $x$:  

$$w = 2 x \tan(\phi_w/2)$$

However, the proper $x$ to use is in fact the distance from the eye to the object, not the horizontal distance (as implicitly shown above). To correct for this, instead of $x$, use the hypotenuse of the triangle resulting from $x$ and the height of her eye above (or below) the object $h$:

$$\phi_w = 2 \text{ArcTan}[w/(2 \sqrt(h^2+x^2))]$$

In order to keep $\phi_w$ constant with $x$, males should use objects with

$$w = 2 \sqrt(h^2+x^2) \tan(\phi_w/2)$$

**Figure S2, Derivation of Visible Width Angle**
**Visual Depth Angle \( \phi_d \) and the depth needed to keep \( \phi_d \) constant**

\( \phi_1 \) and \( \phi_2 \) are the angles subtended by the eye and object relative height on the near and far edges of the object, respectively, other symbols as before.

\[ \phi_d = 180 - \phi_2 - (180 - \phi_1) = \phi_1 - \phi_2 \] (angles in degrees)

\[ = \text{ArcTan}(h/x) - \text{ArcTan}(h/(x+d)) = d (h^2 + x(d+x)), \]

therefore, in order to keep \( \phi_d \) constant with \( x \) a male should use

\[ d = \phi_d (h^2 + x^2)/(h-x \phi_d) \]

Note how \( d \) increases faster with \( x \) than does \( w \).

**Figure S3. Derivation of Visible Depth Angle**

Although \( d \) should increase with distance slightly faster than \( w \), the \( d \) regression slopes were neither significantly nor consistently higher than the \( w \) regressions in either locality. This could result from most gesso objects having aspect ratios less than 2, making it difficult for birds to adjust both \( w \) and \( d \) by varying orientation. In addition, we ignored object height (some objects protrude 1-4cm above the gesso surface), which would lead to an underestimate of the relationship between \( d \) and \( x \). This may also explain the difference between recovery of the visual angles \( \phi_w \) and \( \phi_d \).
Figure S4. Example Calculation of the Regression of $w$ on $x$ for a Single Bower
Regression results are $w = -0.214 + 0.047x$, 77df, $P<0.0001$, $r^2 = 0.20$. 
Figure S5. Example of $\phi$ and $\sigma$ Distributions from a Single Bower

(A) Distribution of visual width angles $\phi_w$ at one bower. (B) observed standard deviation ($s$) of $\phi_w$ from the bower in (A) and distribution of $\sigma$ resulting from 20,000 permutations of that bower's $x$ and $w$. The resulting probability is $P<0.0001$, indicating that this bower has very regular (low $s$) $\phi_w$. 
Example of the appearance of an experimental court during the experiment (bower and court chosen at random). V1 shows the court before manipulation, V2 is the same court immediately after gradient reversal. V3 is the same court 3 days later. V4 is the same court 2 weeks later. Note the continual movement of objects, and the recovery of the gradient. Note particularly the small objects closer to the avenue (at right) and the larger objects at the opposite side of the court in V1 and V4.

Example of the appearance of a control court during the experiment, V1 and V4 only. Note the lack of consistency of locations of almost all objects which are recognizable.

**Figure S6. Photos of the Appearance of an Experimental and a Control Court**
Figure S7. Correlation between Original Position (at Visit 1) and Return Visits Three Days (Visit 3) and Two Weeks (Visit 4) after the Gradient Reversal

X is the distance (cm) from the avenue entrance and Y is the distance (cm) to the left (positive) and right (negative) from the axis through the avenue centre for easily identifiable gesso objects which were not stolen by other birds during the study. Data are homogeneous among bowers and courts. Male great bowerbirds do not replace each object in the same place it was originally. A weaker hypothesis is that males have left or right preferences for each object. We asked how often objects moved by us left to right or right to left relative to the avenue axis (Y direction) during our gradient reversal were moved back to their original side or remained in (including being moved within) the new side after the reversal. Objects which were displaced to the other side remained (21) or moved back to the original side (15) with equal frequency ($\chi^2 = 1.0$, $P = 0.32$; v1-v3 and v1-v4 homogeneous, $P = 0.22$). Objects which remained on the same side during the gradient reversal were slightly more likely to stay on the same side than change sides (34:20, $\chi^2 = 4.6$, $P = 0.03$), but the larger numbers remaining arises because some objects were not moved at all by the birds, making the objects moved left or right by us more informative. We therefore reject the hypothesis that males have fixed locations or L-R zones for each object and also reject the hypothesis that males place objects randomly by size and distance from the avenue.
Supplemental Reference

Errata:

Page 1, results and discussion, line 7
"Ptilinorhynchus" should be spelled
"Ptilonorhynchus"