

Male great bowerbirds create forced perspective illusions with consistently different individual quality

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Males often produce elaborate displays that increase their attractiveness to females, and some species extend their displays to include structures or objects that are not part of their body. Such “extended phenotypes” may communicate information that cannot be transmitted by bodily signals or may provide a more reliable signal than bodily signals. However, it is unclear whether these signals are individually distinct and whether they are consistent over long periods of time. Male bowerbirds construct and decorate bowers that function in mate choice. Bower display courts constructed by male great bowerbirds (*Ptilonorhynchus nuchalis*) induce a visual illusion known as forced perspective for the female viewing the male’s display over the court, and the quality of illusion is associated with mating success. We improved the quality of the forced perspective to determine whether males maintained it at the new higher level, decreased the perspective quality back to its original value, or allowed it to decay at random over time. We found that the original perspective quality was actively recovered to individual original values within 3 d. We measured forced perspective over the course of one breeding season and compared the forced perspective of individual males between two successive breeding seasons. We found that differences in the quality of visual illusion among males were consistent within and between two breeding seasons. This suggests that forced perspective is actively and strongly maintained at a different level by each individual male.

Males often produce elaborate displays that increase their attractiveness to females or to enhance their ability to compete with rivals for mates (1). Such displays are typically produced directly by males using visual ornamentation such as color (2) or physical behavior such as song (3), but males can also extend their displays to include structures or objects that are not part of their body. Such “extended phenotypes” (4) are taxonomically widespread, occurring in birds, mammals, fish, crustaceans, insects, and spiders (5). The physical and cognitive skills required to construct these signals, along with their independence from the male’s body, may allow information to be communicated to females that cannot be transmitted by bodily signals alone.

The production of an external trait requires not only that males collect the resources required from the environment, but also that they actively maintain these signals despite interference from rival males and environmental decay (6). As a result, constructed sexual traits may signal mate quality more reliably than body traits because they may represent a large time and energy investment in construction, maintenance, and defense. Defense is particularly important because extended phenotypes are more easily disrupted than bodily ornaments. Some extended phenotypes also require aspects of learning and memory and may therefore reflect the cognitive ability of the owner (7, 8). As a result of these factors an extended phenotype constructed by a male may also vary more over time than a bodily ornament. To our knowledge, the long-term consistency of extended phenotypes constructed by an individual has only been examined in species where the male construction directly benefits the female, such as nests (9, 10). It is unknown how individually consistent extended phenotypes are in species where males do not contribute anything apart from genetic material to their offspring.

Male bowerbirds (Ptilonorhynchidae) construct and decorate bowers where female mate choice occurs (11). Males can directly affect the mating success of other males by destroying their bowers and stealing their decorations (6, 12–14). Decoration count is positively correlated with mating success in some species (15, 16). Thus, the bower is an extended phenotype (5).

Males that have artificially enhanced numbers of decorations suffer an increase in the rate of marauding until their original decoration number is restored (6, 12, 17). Conversely, when the number of decorations a male displays is artificially decreased, the male restores his original decoration count by stealing from rivals and foraging from the environment (12, 14, 18). Males may also modify their own displays to avoid interference from rival males; when given a choice of “free” decorations, male spotted bowerbirds (*Ptilonorhynchus maculatus*) do not increase their decoration numbers beyond what they normally have (12). Therefore, males do not necessarily signal at the maximum level available and individuals maintain their displays at different levels. Similarly, artificially increasing the size of male African cichlid (*Cyathopharynx furcifer*) mating craters also results in males restoring their craters to their original size within 24 h, despite a female preference for large craters (19). Such manipulation experiments are useful for determining the importance of a trait that may be sexually selected.

Typically, bowerbird and cichlid extended phenotypes involve signals with quantity or size attributes and may simply reflect accumulation in the face of attrition. In contrast, great bowerbirds (*Ptilonorhynchus nuchalis*) create an advanced extended phenotype that involves complex geometry in addition to accumulation (20). Males build bowers that consist of an avenue, two courts, and colored objects. The avenue consists of two 0.6-m parallel walls, floor and partial ceiling made of densely thatched sticks, and opens onto two courts (Fig. 1A). The courts are flat areas covered with stones, bones, bleached shells, and other gray-to-white objects. We refer to these objects as “gesso,” a term used in art where an uncolored background is used as a base upon which colors are painted (21). Similarly, on bowers, the court objects create an uncolored background upon which colored objects (called ornaments or decorations) are displayed; less than 4% of displayed objects are uncolored gesso objects; the remaining 96% are colored objects. Females stand with their head in the center of the avenue and view males displaying colored ornaments and his nuchal crest over one of the two courts (see online movie in ref. 20). The uncolored court objects are arranged in a gradient so that object size increases as distance from the avenue entrance increases. This size-distance gradient creates a forced perspective illusion of an even textured pattern for a female viewing the court from within the bower. This arises because

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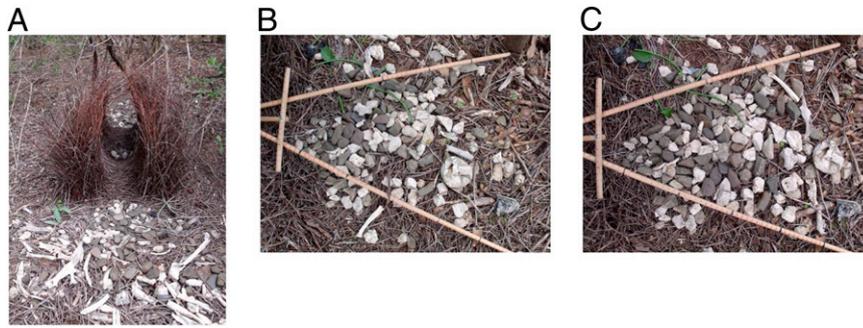


Fig. 1. Photographs of experimental manipulation. (A) Bower with the court in the foreground. A few pale objects mark the avenue floor depression in the center of the avenue, from which we calculate the fields of view. (B) Top view of the unmanipulated court. (C) Top view of the court after improvement. Bower avenue entrance is *Left* in photos B and C (marked by a vertical dowel), and the *Upper* and *Lower* dowels define the maximum female field of view from the center of the avenue.

smaller objects nearer to the avenue entrance subtend similar visual angles on the female's eye (ϕ) to larger objects further away (for a full description of the geometry behind this illusion, see ref. 20). The quality of forced perspective is a good predictor of mating success (22). The relatively even pattern resulting from the reduced variation in ϕ might be a target of female choice, but it also provides a more even pattern against which males display decorations, making them easier to see. The forced perspective may also facilitate other illusions, including those that alter the apparent size of displayed ornaments and illusions that may hold the female's attention, making mating more likely (22). For brevity we will use "geometry" to refer to both the gradients and their visual effects (illusions).

Male great bowerbirds vary in their ability to make geometric patterns, and experimental reversal of the size–distance gradients resulted in the original court geometry being restored within 3 d (20). We determined the stability of court geometry constructed by individual males within one breeding season and between two breeding seasons to assess whether illusions were individually distinct and whether any differences were consistent over extended periods of time. We also tested for consistency in geometry by experimentally improving gradients to determine whether males retained the improved geometry, whether geometry degraded over time due to random factors, or whether males restored the original court geometry.

Results

Bower court geometry was assessed using three measures: slope, variation in visual angle, and effect size (20, 22). The slope (b) of each gradient on each court was calculated by regressing the visible width and visible depth of each court object against distance from the female's viewing location in the middle of the avenue. Better gradients have larger b . Court objects subtend visual angles (ϕ) on the female's eye when she sees them from within the avenue. The regularity of the pattern she sees is related to the SD (s) of ϕ , a smaller s_ϕ is associated with a more regular pattern. The s_ϕ were compared with random permutations of the same objects placed at random. The regularity effect size (δs) was calculated by comparing the actual perspective quality with 20,000 permutations of what the bird could make with the objects available on the court (20).

Variation Among Bowers. There were significant levels of among-male variation in court geometry before, during, and after our experimental manipulation (all $P < 0.0001$). Bowers varied in all parameters, from weak to strong slope (visible width b_w 0.0537 ± 0.040 ; visible depth b_d 0.0413 ± 0.029), large to small visual angle variation ($s_{\phi w}$ 0.368 ± 0.076 ; $s_{\phi d}$ 0.396 ± 0.059), and weak to strong effect size (δs_w 4.20 ± 1.75 ; δs_d 3.86 ± 2.08), (means \pm SD,

SD of log-angles for s_ϕ). These distributions are similar to those of the previous (2009) field season (20).

Quality of the Manipulation and Bowerbird Responses to Manipulated Gradients.

The experimental manipulation (period 1 versus 2) improved the gradient slopes b_w and b_d (Fig. 2A and Table 1). We improved the evenness (reduced s_ϕ) for $s_{\phi d}$ but not for $s_{\phi w}$ (Fig. 3B and Table 1). The intrinsic negative relationship between visible width and depth of objects (23) meant that we could not minimize the variation in both width and depth for this bower parameter. We significantly improved the effect size δs for both visible width and depth (δs_w and δs_d , Fig. 3A and Table 1). The experimental treatments of the previous gradient reversal experiment are shown for comparison (Fig. 2B and ref. 20).

All males restored their court geometry within 3 d of the manipulation (period 2 versus 3, all $P < 0.03$ except b_d $P = 0.069$ and $s_{\phi w}$ $P = 0.86$). We did not manage to improve $s_{\phi w}$, so it is unsurprising that it did not change. All males returned every aspect of the geometry of their courts to the premanipulation values within 3 d (period 1 versus 3), and it remained similar to the premanipulation condition 10 and 90 d after the manipulation (Figs. 2A and 4 and Table 1). As expected, the controls did not change during the same time period (all $P > 0.08$ and most $P > 0.5$). The time scale in which geometry was restored is similar to our previous experiment where we reversed the gradients (Fig. 2B and ref. 20). Males that originally had higher quality patterns (more even perspective or smaller s_ϕ) restored a larger proportion of their original geometry by day 3 compared with males with lower quality patterns ($s_{\phi w}$ $t_{(23)} = 2.54$, $P = 0.018$, $r^2 = 0.22$; $s_{\phi d}$ $t_{(23)} = 2.67$, $P = 0.014$, $r^2 = 0.24$). There was no relationship between original quality and relative restoration of geometry for slope or effect sizes (all $P > 0.13$).

Consistency of Court Parameters over Time. Males in our study population were not banded, but great bowerbirds retain bower sites for long periods of time (10 y or more) (11), so it is very likely that the bowers had the same owners over the two years of this study. Individual bowers were consistent in their court parameters over the course of the breeding season (Figs. 3 and 4 and Table 1), indicating consistent and strong differences in individual performance. Repeatability for bowers ranged from 0.365 to 0.537 (Table 1). Both gradient slopes (b) and illusion pattern regularity (s_ϕ) were consistent within bowers between successive breeding seasons (Fig. 4A and Table 2). Repeatability ranged between 0.18 and 0.40 (Table 2), lower than within years. Interestingly, the effect sizes (δs) significantly increased between years, suggesting that males were better at producing forced perspective in 2010 than 2009 (there was also a barely nonsignificant increase in b_w). The only manipulation between these samples was

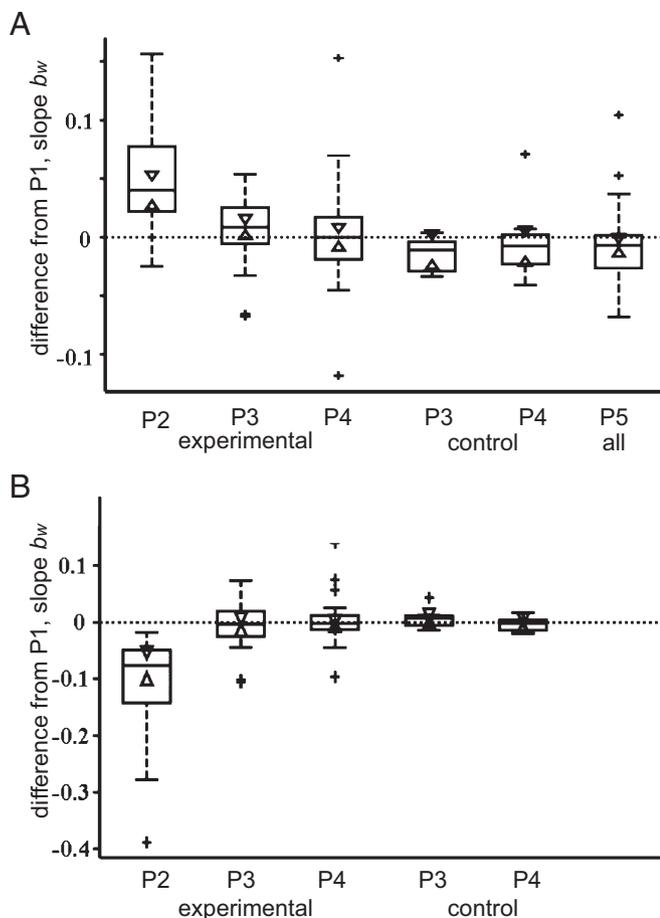


Fig. 2. Differences between the original undisturbed visual width gradient slope (b_w) and its value for the same court and bower at various times after the experimental manipulations of court objects. (*A, Upper*) (2010) Results of the gradient improvement experiment. (*B, Lower*) (2009) Results of the previous gradient reversal experiment (data from ref. 20) for comparison. Positive difference at a given time indicates that a given bower's slope increased at that time compared with what it was before the experiment. Horizontal dotted line at 0 indicates no change. Box plots show the distribution of these differences for all bowers. Times on the horizontal axis are for immediately postcourt improvement (P2; experimental bowers only) and 3 (P3), 10 (P4, 2010), or 14 (P4, 2009) and 90 (P5) days after improvement or reversal. The last box in *A* shows the differences for both experimental and control bower groups pooled. On each box the central line is the median difference, edges are the 25th and 75th percentiles, whiskers go to extreme nonoutliers, and + signs are outliers. If the line between the triangular markers overlaps the dotted zero line, then the median is not different from zero (no change from before the experiment). If the between-marker lines on different boxes overlap, then their medians are not different. Statistical test results appear in Table 1.

the gradient reversal experiment in 2009 (20). Given that bower geometry was restored within 3 d and that courts are reconstructed each year (when the bower is often moved) our previous manipulation is highly unlikely to have affected court geometry between years and would not explain the improvement in gradients over the prereversal values. Unfortunately we do not yet have more than these 2 y of data so we cannot say whether or not this reflects a steady improvement in the production of forced perspective.

Bower Movement and Gradient Quality. We found a median movement (2007–2011, 26 bowers) of 55 m and 93% of bowers moved less than 100 m, with a maximum (outlier) of 258 m. The median nearest neighbor (between bower) distance is 519 m with a minimum of 390 m (31 bowers), so all movements between years were

within the male's home range, defining home range by the midpoints to nearest 6 neighbor bowers, given that they steal from neighbors (6). There was no relationship between the distance bowers moved and the quality of perspective parameters, nor was there any relationship between the movement and the residuals from the consistency axis; after sequential Bonferroni correction, none of the relationships for b , δs , or s_{δ} were significantly different from zero (and almost all $P > 0.2$).

Discussion

It is clear that court geometry is very important to male great bowerbirds because bower owners returned their courts to their original state within 3 d after we improved the gradient. Individuals varied significantly in their court parameters and these differences were consistent during the course of the breeding season and between two breeding seasons. We conclude that great bowerbirds consistently vary in their ability or tendency to make gradients and therefore forced perspective illusions.

These results demonstrate that males maintain characteristic illusions even when they have the materials available to produce better ones. When we improved the gradients and perspective, the birds reduced them to their previous inferior values within 3 d, a short time for an animal with a breeding season of around 4 mo (11). There are a number of possible explanations.

The consistent variation that we found among males in their illusion quality, along with evidence that forced perspective promotes mating success (22) fulfills two of the three basic requirements for sexual selection via the Fisher process: (*i*) consistent differences among males, (*ii*) association between the differences and mating success, and (*iii*) the differences are heritable (24). We do not yet know if the bower parameters are heritable, but if so, the simplest form of sexual selection can proceed (1) even if perspective quality does not indicate cognitive or other beneficial male qualities.

The repeatable differences observed in court geometry may be a result of inherent individual differences in cognition, construction, or learning behavior. Gradients may be constructed using simple methods such as trial and error or rule of thumb, or may require a more complex form of cognition. Individuals may also possess a mental template for visual patterns, similar to neural templates used in learning birdsong (25). Males continually manipulate court objects and then view them from within the avenue and they may match the viewed patterns they make with an internal template of regularity. Individual differences in any of these techniques would result in individual differences in court geometry. For example, males may vary in their pattern regularity templates or in how well they match a template. We do not know whether the skills used to create gradients or illusions are demanding in terms of cognitive ability or other skills, but individual differences in these attributes will also result in significant and consistent variation in bower geometry.

Variation in learning ability and experience may also contribute to individual variation among males and their gradients. Juvenile males spend time at the bowers of mature males when learning how to construct bowers and how to display to females, and juveniles may also learn how to construct court geometry during this time. An adult may build bowers for up to 20 y (11) and gradually learn what patterns result in higher mating success. Improvement over time is known for other kinds of bowerbird display traits (26, 27). Ontogenetic improvement is weakly supported by the increasing effect size over the 2 y of this study. If making perspective involves learning and males steadily improve over time, then the quality of the forced perspective may reflect age rather than, or in addition to, cognitive or other abilities.

Learning by juveniles from adults brings up the possibility that bower geometry is culturally transmitted (28). Social learning and culture may play a role in the sexual displays of bowerbirds (29), particularly given that juvenile males spend time at the bowers of

Table 1. Changes in response to experimental manipulation and court consistency over time

Court variable	Effectiveness (1 vs 2)		Recovery (1 vs 3)		Consistency (1,3,4,5)		
	z	P	z	P	Bower P	Time P	Repeatability
Slope, b_w	-9.27	<0.0001	-1.10	0.51	<0.0001	0.14	0.493
Slope, b_d	-2.35	0.049	2.21	0.98	<0.0001	0.62	0.469
SD ϕ , $s_{\phi w}$	0.67	0.78	0.16	0.99	<0.0001	0.43	0.537
SD ϕ , $s_{\phi d}$	-3.06	0.006	-0.60	0.82	<0.0001	0.95	0.444
Effect, δs_w	6.74	<0.0001	1.41	0.34	<0.0001	0.15	0.444
Effect, δs_d	12.0	<0.0001	0.93	0.62	<0.0001	0.52	0.365

GLMMs and Tukey test results (Tukey tests for effectiveness and recovery columns only) for differences in court variables within 25 bowers, to test the effectiveness of the gradient improvement (period 1 vs. 2), the recovery of the original gradient (period 1 vs. 3), and the consistency over the breeding season (all periods excluding 2) along with measures of repeatability (R).

mature males and that mature males visit each other's bowers when marauding. It is currently not known whether the bowers and court geometry of juveniles are more similar to those of their tutors compared with other males. If this is the case, then cultural lineages may diverge at random and generate variation among bowers, although this is more likely to lead to among-population variation rather than within-population variation.

Another possible function of the variation in bower geometry is honest signaling in a good genes sexual selection system. To be an accurate signal of good genetic quality a signal must have a cost or constraint that prevents all individuals in a population from

converging on a single form (1). Males could cheat (produce better geometry), but do not, as our results demonstrate. Sand crater cichlids also decrease the size of experimentally enlarged breeding craters (19). In both species, males were given display structures that were more attractive to females (better illusions or larger craters), but they did not maintain them. The return to previous individual levels may reflect individual variation in the ability to create and maintain the geometry, but if this is fixed, at least for a given breeding season, then one or more of these constraints will maintain the variation, even if the costs of construction and maintenance of gradients are negligible. In great bowerbirds, signal honesty may be enforced by skill or cognitive constraints rather than costs, but this does not explain why males restored their original court geometry after it was experimentally improved. However, there may also be costs in defending the geometry against other males, although these will be lower than the costs of maintaining the quantity of objects.

Males may vary in their ability to prevent stealing or disruption of court objects by other males, or they vary in the tendency to maraud neighbors' bowers (12–14, 30). We have observed stealing of objects in our video recordings over 15 y but the only form of disruption we have seen is destruction of the avenue walls, not rearranging the court objects (see also ref. 18). The stealing rate of 0.15–0.21 objects per day (18) is far less than that needed to return gradients to their previous lower values within 3 d because each court has several hundred objects. Even one or two per day would not be sufficient to seriously affect the effect size (δs) of the perspective, which is most sensitive to disturbance. The low level of stealing also means that this behavior is unlikely to explain the consistent variation that is present among males in their court geometry during the course of the 3-mo breeding season.

Whereas stealing is unlikely to have a large impact on gradient quality, males with artificially enhanced gradients might suffer increased levels of bower destruction. However, this seems unlikely to explain our results given that other aspects of male displays are not socially controlled in this population. Males supplemented with decorations do not limit the number of decorations they display and the incidence of bower marauding by rivals remains unchanged (6). Male–male policing has been shown to maintain the honesty of decoration numbers in spotted and satin bowerbirds (12, 17), but not in great bowerbirds (6). It therefore seems unlikely that costs of defense are maintaining variation in geometry.

The availability of potential court objects does not affect the quality of court geometry because groups of adjacent bowers have similar size distributions of objects but very different levels of perspective (20). The fact that the distance the bower was moved between years had no effect on the perspective parameters is further evidence that object availability is not important. Object availability and the ability to avoid or minimize theft or destruction from other birds appear to have negligible effects on perspective quality in great bowerbirds. Males that produce high

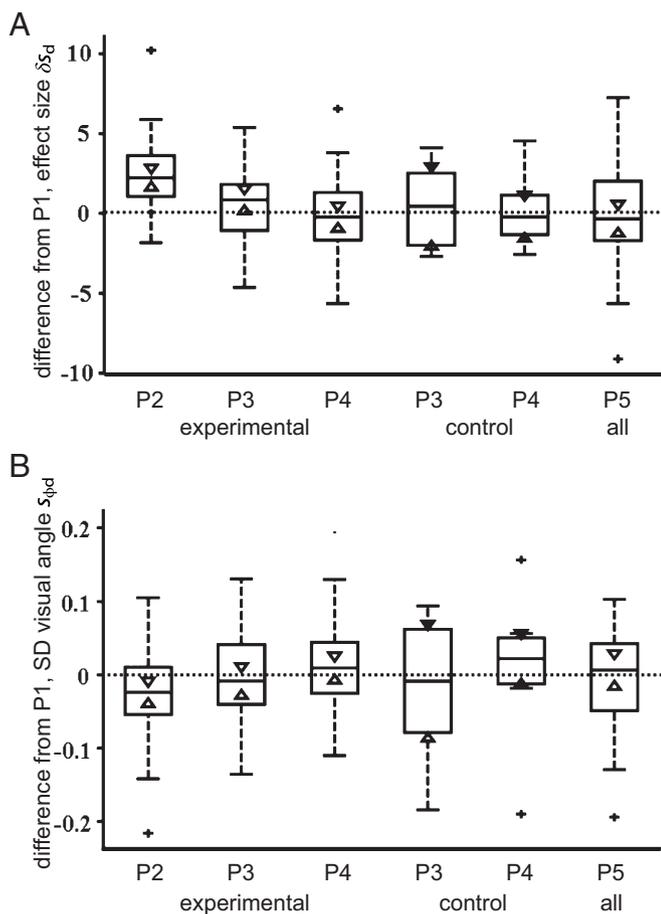


Fig. 3. Effects of court improvement on effect size and visual angle SD. (A, Upper) Differences from the original undisturbed visual depth effect size (δs_d) and (B, Lower) visual depth angle SD ($s_{\phi d}$) at various times after the experimental manipulations. Statistical test results appear in Table 1.

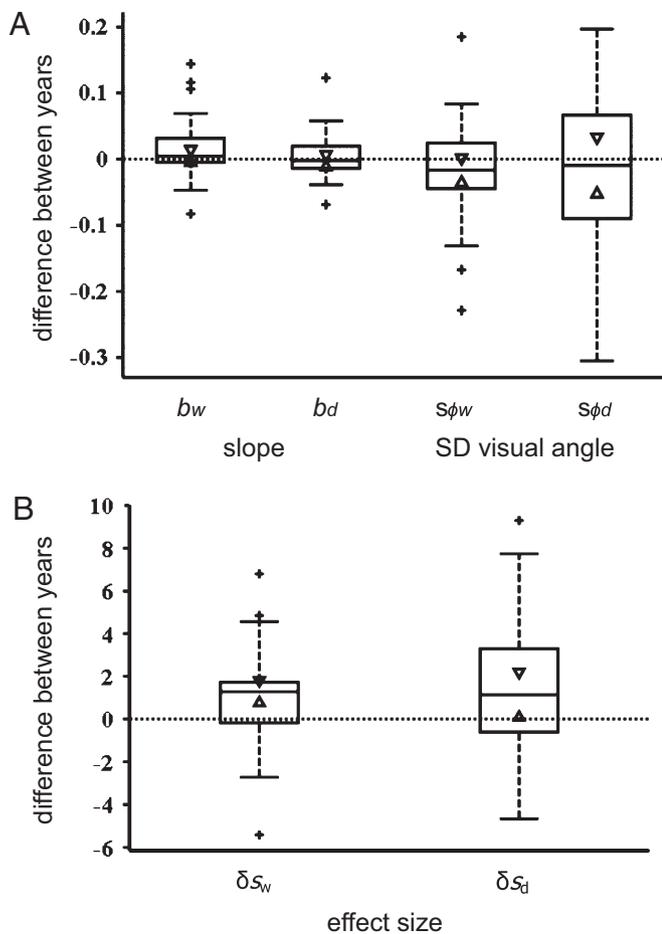


Fig. 4. Differences in court geometry between years within bowers. *A* (Upper) shows the difference between years in slope and visual angle SD; *B* (Lower) shows the difference in effect size. A positive difference means an increase in parameter quality between 2009 and 2010. Statistical test results appear in Table 2.

quality patterns (low s_{ϕ}) enjoy higher mating success than rival males (22), and we found that these males also restore this signal component more efficiently after modification. Males may preferentially restore this aspect of geometry first as it is a target of female choice (22). These findings also suggest the possibility that males with high quality geometry are more efficient (i.e., faster) at constructing geometry compared with males that have bowers with lower quality geometry.

Table 2. Differences in bower geometry between breeding seasons

Court variable	Bower	Time	Repeatability
Slope, b_w	<0.0001	0.06	0.40
Slope, b_d	<0.0001	0.43	0.39
SD ϕ , $s_{\phi w}$	<0.0001	0.31	0.40
SD ϕ , $s_{\phi d}$	<0.0001	0.21	0.18
Effect size, δs_w	<0.0001	0.01	0.30
Effect size δs_d	<0.0001	0.023	0.30

GLMM for differences between years for 17 bowers (period 1) that were active in both 2009 and 2010, with *P* values for bower and time generated by MCMC simulation. Time *P* > 0.05 indicates consistency between years. Repeatability measures are given in the right hand column.

Court geometry (and therefore perspective quality) of individuals was consistent over the course of a breeding season and between two breeding seasons, indicating that males actively maintain their courts at a certain level. The consistency of constructed extended phenotypes has only previously been quantified in species where the male construction provides direct benefits to the female, e.g., nests. Species where nest building appears to be under tight genetic control show little variation in nest building (31), but in other species nests show lower repeatability within individuals, which may be due to a number of environmental or physiological factors (9, 10). Our results show that, in a species where males contribute only genetic material to their offspring, a sexually selected constructed phenotype is consistent within individuals both within and between years.

We have provided a unique demonstration of long-term, stable quality variation in an extended phenotype and sexual signal that depends upon geometric pattern rather than size or magnitude and provides no direct benefit to females. These results provide evidence that extended phenotype signals can respond to sexual selection and evolve in ways similar to conventional (bodily) phenotypes, and that the geometric design of signals is as important as their magnitude.

Materials and Methods

This research was carried out with an Environment Protection Authority-Queensland Parks and Wildlife Service permit (WISPO1994004) and ethics approval from Deakin University (A22-2010) and James Cook University (A1318). We monitored 25 bowers of male great bowerbirds (*P. nuchalis*) in the Dreghorn population in central Queensland, Australia (20.25°S, 147.73°E) from August to December 2010. In August, after assessing the undisturbed gradients, we experimentally improved the gradients of both courts of 21 bowers and left 4 bowers undisturbed as simultaneous controls; all bowers also serve as their own temporal controls. If the bower was experimental, the objects on each court were reorganized by moving small objects relatively closer to the avenue entrance and larger objects relatively further away to create a smoother and steeper size–distance gradient (Fig. 1). We used only objects that were already present on the court and retained the original court shape and size. The manipulation experiment was carried out at the commencement of the breeding season (before females are assessing suitable mates) to minimize any potential impact on male mating success. Courts were photographed for measurements before manipulation, immediately after manipulation (excluding control bowers), and then 3, 10, and 90 d postmanipulation; these are called periods 1, 2, 3, 4, and 5, respectively. The experimental and measurement protocols were identical to our previous experiment (20) except that we improved the gradients rather than reversing them, period 4 was on day 10 rather than day 14, and we measured again during a new period 5 on day 90.

Measurements of gradients were performed using computer-assisted analysis of scaled photographs in MATLAB (20). All measurements were performed blind with no identifying information available on the photographs other than the photo number assigned by the camera when the photo was taken. For each visible object, the object’s coordinates and view axis distance (*x*, in centimeters) were determined by a line between the female’s viewing location (the middle of the avenue depression) and the center of the object, with object width (*w*, in millimeters) measured perpendicular to the view axis and depth (*d*) along the axis. For each bower at each time point, regressions of *w* on *x* and *d* on *x* were carried out to measure the slope of each gradient (*b*) on each court. Better gradients have a larger *b*. We also calculated the visual angles for width (ϕ_w) and depth (ϕ_d) of each gesso object and analyzed their logarithms (20).

To test for the presence of forced perspective, we tested whether the observed visual angle SDs (s_{ϕ}) of gesso objects were smaller than the SDs σ generated by 20,000 permutations of the same gesso objects placed at random (17). A smaller s_{ϕ} indicates a more even pattern (a perfect honeycomb pattern would have $s_{\phi} = 0$). Both s_{ϕ} and mean (ϕ) were calculated on $\log(\phi)$ because ϕ was close to log normally distributed on the bowers. The probability of obtaining the observed s_{ϕ} by random placement of objects was obtained by $1 - (\text{proportion of } \sigma > s_{\phi})$ (20). A small probability indicates that the observed variation in ϕ is significantly smaller than random and that visual angles are more regular than expected, demonstrating the presence of forced perspective. Smaller s_{ϕ} indicates higher quality forced perspective. Effect sizes were calculated to estimate the perspective quality relative to

what the bird could make with the gesso items available on the court. Effect size was calculated as $\delta s = (\sigma_m - s_{\phi})/SE$, where σ_m is the mean of all permutations of σ , and SE is the SD of all σ ; SE is also the SE of ϕ (20). The quantity s_{ϕ} measures the absolute variation in visual angles (how uneven the pattern is as seen by a bird within the avenue), whereas δs measures how good the forced perspective is compared with what it could be, given what gesso the bird actually has on its bower courts. Females can compare s_{ϕ} but not δs , and the two are not necessarily correlated.

We used b , s_{ϕ} , and δs of each court of each bower at each time point to establish (i) the initial variation among males in both gradient and forced perspective quality, (ii) whether our experimental manipulation improved forced perspective, (iii) whether or not the gradients changed after manipulation and whether the amount of change was related to the original geometry quality, (iv) how consistent gradients of individual males were within one breeding season, and (v) how consistent bowers were between two successive breeding seasons; we monitored the same population of bowerbirds the previous year (20).

We analyzed the changes using generalized mixed linear models (GLMM) in R (32) using the package lme4 (33) with Markov chain Monte Carlo (MCMC) simulations (package LanguageR) (34) to obtain parameter estimates, credible intervals, and P values. The GLMM model included bower and court (court nested within bower) as a random variable and visit as a fixed effect. Post hoc Tukey tests (package multcomp) (35) tested the effectiveness of the manipulation on bower geometry (period 1 versus 2), whether the geometry had changed 3 d later (period 2 versus 3), and if geometry was changed, whether this change restored the geometry to its original values within 3 d (period 1 versus 3).

We calculated the consistency of the gradients during the course of the breeding season using all data but excluding period 2 (experimental manipulation). We also determined how consistent individuals were between breeding seasons (2009 and 2010) by using the first set of measurements (period 1) taken each year. Repeatability was calculated from the MCMC estimates of the random effects (bower + court – within-bower divided by total random variance estimate). The residuals of each model were tested for normality using the Cramer–von Mises test (package nortest) (36), and transformations were carried out if normality assumptions were not met (powerTransform function in package car) (37). This was successful for all

tests except for the between-years tests of slope and the effect size of depth. The lack of normality in the between-years tests was due to a single outlier in each of the slope measures and eight outliers for effect size in visible depth, out of 67 data points for each variable. These outliers were negative but were associated with nonsignificant slopes or effect sizes. When these values were set to zero, the residuals were successfully transformed to normality. All final Cramer–von Mises tests were nonsignificant at $P > 0.1$ or higher. The equivalent nonparametric tests using all data produced the same outcomes, indicating that our analysis is robust.

We tested whether there was any relationship between the quality of the original bower geometry and the degree to which the original geometry was restored by period 3. We regressed the original (period 1) geometry values against the relative amount of change in geometry between periods 2 and 3.

We also tested whether the local availability of objects or bower movements between years contributed to variation in gradient quality by examining the effects of bower movements. Most males move their bowers between years (breeding seasons) and when moving their bowers, males carry most of the court objects and colored ornaments to the new site (18, 38), so gradients may be consistent within males among years due to reuse of court objects. In addition, the new bower site may have a different distribution of available potential court objects than the previous site. This suggests that moving bowers might have an effect on the quality of the gradients, as well as the consistency of geometry measures among years. We examined this by testing for (i) a relationship between movement distance between 2 y and the perspective parameters at the second year and (ii) a relationship between the residuals from the consistency axis and the amount of movement of that bower. The consistency axis is the principal axis of the correlation between 2009 and 2010 data. If movement between locations causes a change in the bower, then these relationships should differ significantly from zero. For example, if moving a bower alters the objects available to a male such that he can make a better or worse gradient than before, then the relationship between movement distance and the residuals from the consistency axis should be significantly positive.

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