



## Comment on "Illusions Promote Mating Success in Great Bowerbirds"

Gerald Borgia *et al.*  
*Science* **337**, 292 (2012);  
DOI: 10.1126/science.1220775

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# Comment on “Illusions Promote Mating Success in Great Bowerbirds”

Gerald Borgia,<sup>1\*</sup> Brian J. Coyle,<sup>1</sup> Jason Keagy<sup>2</sup>

Kelley and Endler (Reports, 20 January 2012, p. 335) claim that male great bowerbirds construct a visual illusion, using display object gradients, that affects mating success. We argue that they provide inadequate statistical support for their hypothesis, inappropriately exclude important data, and do not consider other display traits that explain mating success. We propose a more plausible alternative hypothesis to explain display object patterns.

Kelley and Endler’s (*I*) forced perspective model makes two major predictions: that male mating success is (i) positively related to the slope of the display object size gradient (width,  $Wslope$ ; depth,  $Dslope$ ) on the bower display court and (ii) negatively related to the standard deviation of the visual angles among display objects (width,  $SD\Phi_W$ ; depth,  $SD\Phi_D$ ). (We do not use their term “gesso” because this implies a functional differentiation of display objects that has not been demonstrated.) Their multiple regression models show an overall significant result for the slope and  $SD\Phi$  variables. To meet predictions of their forced perspective argument, however, it is necessary that the regression slopes of variables in the model show the predicted association with mating success. In their regression, the  $Wslope$  variable is nonsignificant, and both  $Wslope$  and  $SD\Phi_W$  have slopes opposite to the predicted direction. Separate regressions of each variable with male mating rate provide a more straightforward test of their predictions and show that for decoration gradients only,  $Dslope$  ( $r^2 = 0.58$ ,  $df = 1,6$ ,  $P = 0.017$ ) is significant, and  $Wslope$  ( $r^2 = 0.017$ ,  $df = 1,6$ ,  $P = 0.33$ ) is not. Neither visual angle variable is significant ( $SD\Phi_W$ :  $r^2 = 0.06$ ,  $df = 1,6$ ,  $P = 0.46$ ;  $SD\Phi_D$ :  $r^2 = 0.16$ ,  $df = 1,6$ ,  $P = 0.18$ ). So, their predictions are confirmed in only one of four cases (Fig. 1).

We disagree with Kelley and Endler’s (*I*) suggestion that depth rather than width variables should more closely match their predictions. They claim to be assessing object size the way females see them, but their measurements are based on photos taken from above the display objects. This is different from the female’s more horizontal perspective from inside the bower that can affect her perception of object depth. For example, this near-horizontal view can prevent females from seeing the depth of rounded snail shells and

stones because the rear edge is hidden by their raised middle portion.

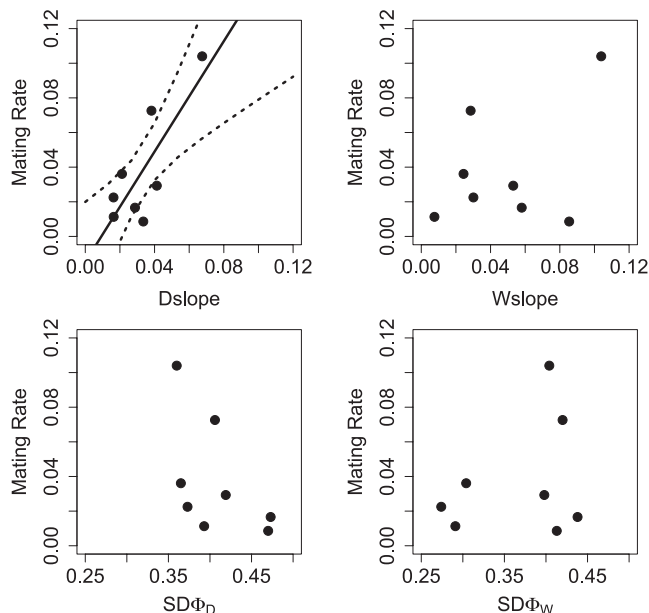
Kelley and Endler (*I*) describe glitches in their video recording system that may have affected estimates of their mating rate variable. They suggest that the lack of a correlation of recording time with matings and courtships indicates no bias; however, this is not a reasonable test because mating success rates in bowerbirds are highly skewed (2, 3) and represent a fraction of all behaviors that may trigger cameras. Also, their near-significant result for courtships ( $P = 0.06$ ) does not strongly support the suggested lack of association. Alternatively, male courtship success—the proportion of displays that lead to copulations—is a more reliable measure of male attractiveness in bowerbirds when cameras are fully operational and females are either individually marked (4) or unmarked (5). It more directly measures male display performance (4) (relevant for testing the effect of an illusion) and thus should more effectively correct for camera malfunctions. We found no correlation between the mating rate measured by Kelley and Endler (*I*) and courtship success ( $r^2 = 0.07$ ,  $df = 1,6$ ,  $P =$

0.49), which suggests that their use of mating rate may be flawed. There was no significant relationship between male courtship success with  $Wslope$  ( $r^2 = 0.09$ ,  $df = 1,6$ ,  $P = 0.55$ ),  $Dslope$  ( $r^2 = 0.15$ ,  $df = 1,6$ ,  $P = 0.82$ ),  $\Phi_W$  ( $r^2 = 0.16$ ,  $df = 1,6$ ,  $P = 0.18$ ), or  $\Phi_D$  ( $r^2 = 0.16$ ,  $df = 1$ ,  $P = 0.91$ ), which does not support their prediction that display object gradients measured directly or as standard deviation of visual angles affects male attractiveness (Fig. 2).

Kelley and Endler excluded 9 of 17 bowers from their analysis in cases where they determined that females had insufficient time for “gazing at the scene on the court” [supporting online material for (*I*)]. Females who observed males for less than 55% of the time did not mate, and they indicate that they used this measure of female behavior to exclude males from their sample. However, three females who did not mate spent more than 55% of the time gazing at the scene in the bowers of excluded males [figure S3 and table S2 of (*I*)]. By their criteria, these males should have been included in the analysis. Also, several of the reasons the authors give for a display object gradient to correlate with male mating rate do not require females to look at males for any particular percentage of time, so excluding such a large number of males for whom they have information on display object gradients is inappropriate.

Kelley and Endler (*I*) do not consider any other hypothesis that might explain decoration gradients on great bowerbird bowers. An obvious alternative is that males avoid placing large objects on display courts near the bower so as not to hamper their own movements during courtship displays to females; this is consistent with the step-like pattern of size change seen in decorations of other species (5).

Finally, bowerbird display is complex and consists of multiple interrelated traits. Anderson

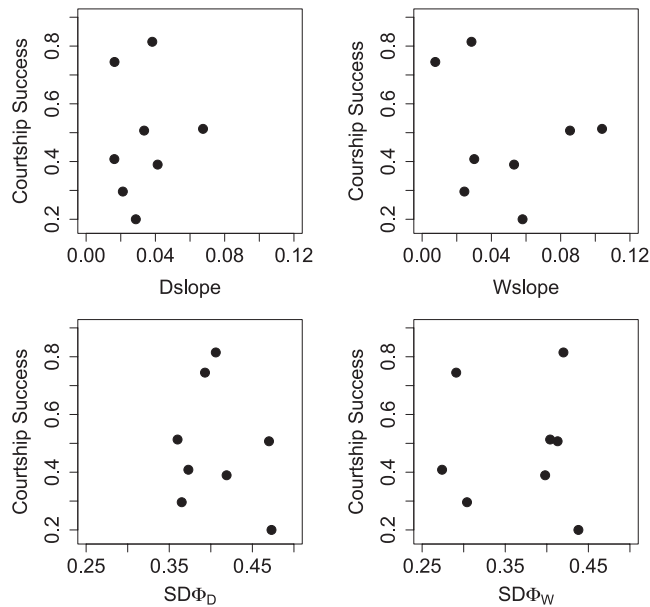


**Fig. 1.** Relationship between mating rate and display object gradients ( $Dslope$  and  $Wslope$ ) or the standard deviation of the visual angles ( $\Phi_W$  and  $\Phi_D$ ). Significant regression for  $Dslope$  is indicated with a solid regression line, with dotted lines denoting 95% confidence intervals.

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**Fig. 2.** Relationship between courtship success and display object gradients (Dslope and Wslope) or the standard deviation of the visual angles ( $\Phi_W$  and  $\Phi_D$ ). None of the relationships are significant.



(6) noted that Kelley and Endler (1) failed to consider bower symmetry, which is known to explain male mating success in other bowerbirds, as possibly accounting for variation in mating

success in their study. He is correct, but he understates the problem. Mating success is affected by multiple male display traits in bowerbird species, including number of decorations

(2, 4, 5, 7), bower quality (2, 3), bower stick diameter (2), bower size (8), vocal display quality (9, 10), and intensity of male courtship display (4, 9). These display elements are commonly significantly correlated (2, 3, 11) and shared across species, which suggests that any effect of gradients on great bowerbird mating success should have been considered in relation to these other variables.

These considerations cause us to question whether male great bowerbirds construct illusions that affect male mating success.

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20 February 2012; accepted 7 June 2012  
10.1126/science.1220775