Male Great Bowerbirds arrange red wires at bowers by size, without forced perspective

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Abstract

Male Great Bowerbirds (*Ptilonorhynchus* [*Chlamydera*] *nuchalis*) build and decorate stick structures (bowers) to attract females. In some populations, they arrange grey and white decorations by size, with smaller decorations closer to the bower entrance. This size-distance gradient has been hypothesized to create a "forced perspective" illusion that females prefer. I assessed whether a common type of red decoration – red wire – was also arranged by size at 18 bowers in Townsville, Queensland. Males placed shorter wires closer to the bower structure, but most wires were outside of the females' field of view, precluding them perceiving forced perspective. Instead, males might keep shorter wires closer to the bower because they frequently use red wires during display, and shorter wires might be easier to handle during display movements. Longer wires farther away might aid in long-distance mate attraction.

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Introduction

Compared to morphological signals such as plumage patches, non-bodily, or external, ornaments give signallers broad scope to arrange signal components in space and time to best capture the viewer's attention (Schaedelin & Taborsky 2009). Bowerbirds (Ptilonorhynchidae) build and decorate stick structures, called bowers, to attract females (Frith & Frith 2004), and thus present a rare opportunity to study the strategic arrangement of non-bodily ornaments and their influence on female choice.

In the Great Bowerbird (*Ptilonorhynchus* [*Chlamydera*] *nuchalis*), bowers consist of a central avenue enclosed by two parallel walls of sticks, with a decorated court at either end of the avenue. During courtship, the female enters the avenue and watches the male displaying on one of the courts. In some populations of this species, males arrange grey and white decorations (e.g., stones, shells, and bones) by size on the courts, with smaller decorations closer to the avenue entrance (Endler *et al.* 2010). From the female's viewpoint within the avenue, this size-distance gradient might create a "forced perspective" illusion in which the grey and white decorations appear to be all about the same size (Endler *et al.* 2010). The illusion has been hypothesized to enhance the female's perception of the male and/or his display (Endler *et al.* 2010) and thus improve male mating success (Kelley & Endler 2012).

In addition to grey and white decorations, bowers of this species contain colourful decorations, mostly green and red, a few of which males present to females during display by holding them in the beak and/or tossing them (Endler *et al.* 2014). When not displaying, males usually keep colourful decorations outside of the female's field of view (Endler *et al.* 2014), where these decorations cannot help create the forced perspective illusion. Since size-distance gradients could also serve other functions, such as long-distance mate attraction achieved by larger decorations (Borgia & Keagy 2015), studies that assess the arrangement of colourful decorations could help assess alternative functions for size-distance gradients.

Here, I report the size-distance arrangement of red wire at bowers of the Great Bowerbird in Townsville, Queensland. I chose red wire because it is one of the most common red decorations at bowers of this suburban population (Doerr in preparation), it can be measured quickly and accurately in the field, and males frequently use red wire during display and steal this decoration type from the bowers of rival males (Doerr 2010a,b).

Methods

This study occurred in Townsville, Queensland, from 15 November – 16 December 2018 during the Great Bowerbird breeding season. The abundance of human-made decorations in this suburban environment (Frith *et al.* 1996) ensured males had access to red wires of a range of sizes (Fig. 1).

At 18 bowers, I measured the length and diameter of each red wire, as well as the shortest distance from the avenue centre to the nearest edge of each decoration. I also placed a pair of wooden dowels on each court, following the methods of Endler *et al*. (2010). The dowels delineated the field of view of a female within the bower structure gazing out at each court. This allowed me to count the number of red wires inside and outside of the female's field of view from within the avenue.

To control for differences in decoration properties (e.g., brightness, texture) among wires, I also ran an experiment where I cut red automotive wire (diameter 3 mm) into four lengths (7.5 cm, 15 cm, 22.5 cm, and 30 cm) and placed a set of eight wires (two per length) on the courts of 13 bowers. Three days later, using the methods above, I recorded how males had arranged the wires. Theft or loss of red wire occurred at five bowers, reducing the sample to nine bowers with at least one red wire per size. Thus, I also combined the data into just two size categories (short, long) to increase the sample. I included stolen wires in the analyses; excluding them did not change the results.

Statistical analysis

I used a Spearman rank correlation at each bower to assess the relationship between the size of red wires and distance from the avenue centre. Then, I summed the number of bowers at which this relationship was significant and used a sign test to identify a population-wide trend.

For the experiment, I used an ordered hetero-geneity (OH) test (Rice & Gaines 1994). OH tests allow a comparison of means when the order of the means is important, and they can improve power for small sample sizes. To run the test,

Figure 1. Male Great Bowerbird at bower in Townsville, Queensland, with a red wire in its bill. Additional red wires are propped up against the front of the bower wall.

I averaged the data within each size category for each bower. Then I used a Friedman test to assess differences in the rank mean distance by size, and a Spearman correlation to assess whether the ranks of the means were in the predicted direction (lower means for shorter wires). From these tests, I calculated the product: r_s*(1-$P_{Friedman}$), and used the table of critical values in Rice and Gaines (1994) to assess significance ($P < 0.05$, two-tailed).

Results

Bowers had a mean and standard error of 31.8 ± 3.6 red wires, with mean length of 15.0 ± 0.5 cm, mean diameter of 0.2 ± 0.01 cm, and mean distance from the avenue centre of 66.7 ± 4.5 cm.

At 15 of the 18 bowers, the length of red wires was significantly positively correlated with distance from the avenue centre (Fig. 2); a sign test confirmed a significant, population-wide association between wire length and distance (15/18, P = 0.0075). The diameter of red wires was positively correlated with distance from the avenue centre at only two bowers, perhaps because diameter showed little variation in the sample (70% had diameter = 0.2 cm; range, 0.1 to 0.8 cm). On average, 3.9 ± 0.9 wires were in the female's field of view, and 27.9 ± 3.3 wires (86.8 ± 2.9%) were outside of it.

For experimental red wires, wire length was positively associated with distance from the avenue centre (OH test, P < 0.002, k = 4); the mean distance from the avenue centre was 37.1 ± 2.1 for 7.5 mm wires, 42.2 ± 3.1 for 15 mm wires, 64.8 ± 15.3 for 22.5 mm wires, and 66.5 ± 9.2 for 30 mm wires. Likewise, when the data were collapsed into two size categories, shorter wires were closer to the bower (sign test, 11/11 plus 1 tie, P = 0.001; Fig. 3).

Discussion

In a suburban population of Great Bowerbirds, males arranged red wires by size, with shorter wires closer to the bower structure than longer wires. As in a previous study (Endler *et al.* 2014), most red wires were outside of the female's field of view, so the female could not see them from her location within the bower. Many red wires were also scattered widely around the bower (Doerr personal observation). Thus, the overall size-distance arrangement of red wire did not appear to create a forced perspective illusion, in contrast to the hypothesis for grey and white decorations (Endler *et al.* 2010).

Instead, red wires might be arranged by size to facilitate specific courtship movements. During courtship, males stand close to the bower entrance and incorporate nearby colourful decorations (Okida *et al.* 2010; Endler *et al.* 2014), including red wires, into an integrated display: they pick up a decoration, present it to the female while vocalizing and posturing, and toss the decoration

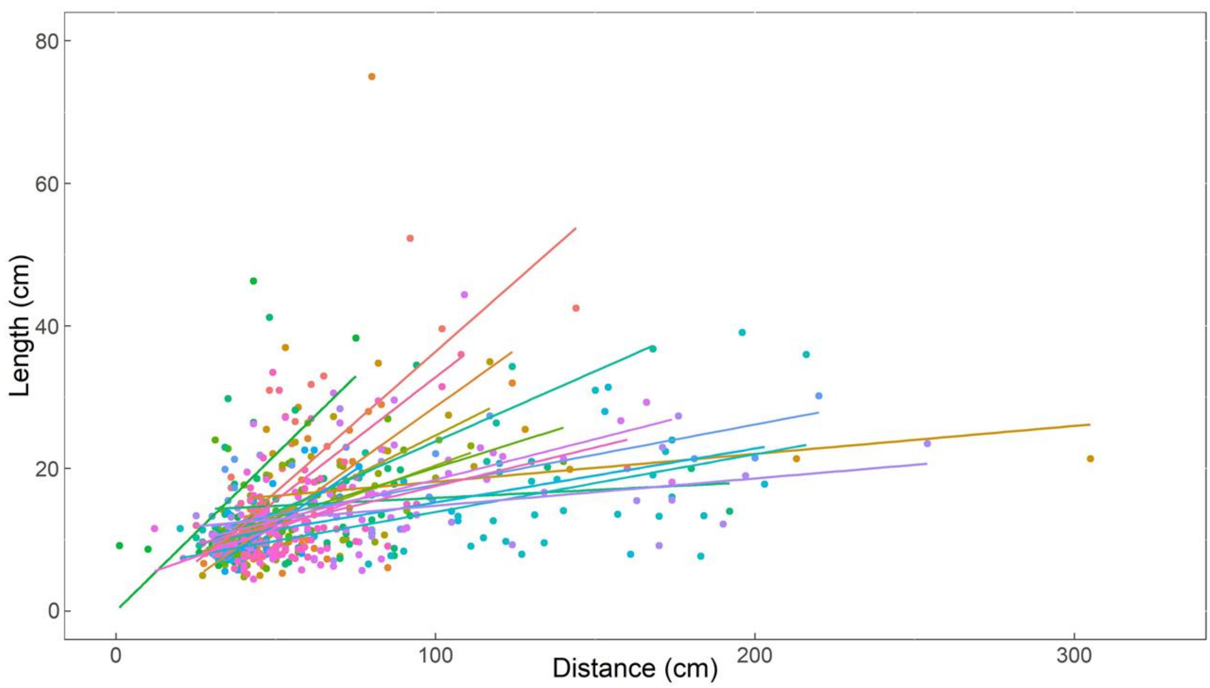

Figure 2. Length of red wires and distance from the avenue centre for 18 bowers.

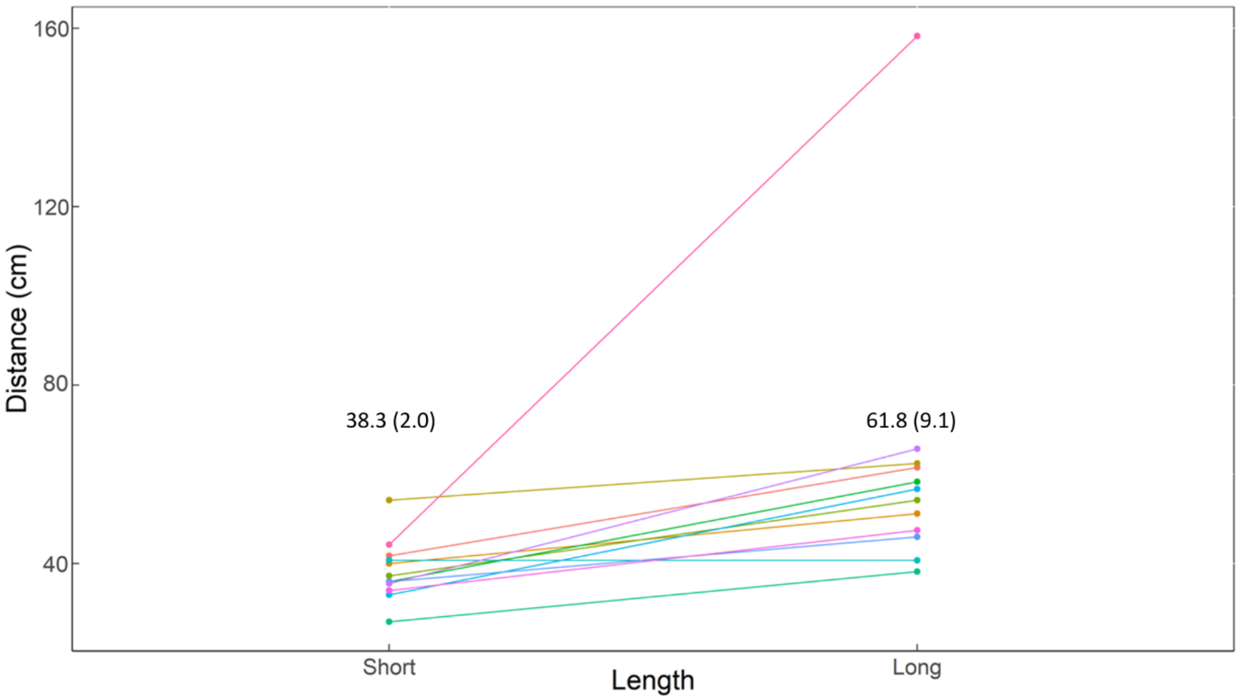

Figure 3. Mean distance from the avenue centre for short (7.5 cm, 15 cm) and long (22.5 cm, 30 cm) experimental red wires at 12 bowers. Overall sample mean (SE) is shown above each category.

across the avenue entrance (see Doerr (2018) for video examples). These actions may be easier to perform with shorter wires, especially if the height or distance of the tossed decoration is important. A previous study found that Townsville males had higher mating success when supplemented with relatively short red wires (11 cm in length) and red rings, and they tended to place these decorations close to the bower structure and use them in display (Doerr 2010b). Borgia and Keagy (2015) suggested that males place smaller decorations closer to the bower to avoid tripping over them during courtship. Males also prefer to steal shorter red wires (Doerr in preparation). Thus, decoration size may influence the ease of both mate attraction and male-male competition, with potential consequences for male mating success.

Longer wires may be placed farther away to visually attract females from a distance, as suggested for male Spotted Bowerbirds (*P. maculatus*), which place larger decorations (bones) more distant from the bower than smaller ones (Borgia 1995).

Although red wire is a humanmade decoration, red twigs are common at bowers in more natural habitat populations, and these could serve a similar function. The red decorations at Townsville bowers also include objects of a bulky or round shape, such as bottlecaps or fruit, which males appear to arrange differently than red wires (Endler & Day 2006). In addition, the western subspecies of the Great Bowerbird does not use red decorations, and its grey and green decorations are not arranged by size (Katsuno *et al.* 2013). To better understand how signallers source, arrange, and integrate non-bodily ornaments into display, further research on the properties and placement of decorations in relation to display behaviours and mating success are required across the Great Bowerbird's range.

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