



Illusions vary because of the types of decorations at bowers, not male skill at arranging them, in great bowerbirds



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Many animals use extended phenotypes to attract mates, but the availability of suitable resources in the environment can affect the size and form of these signals, with unknown consequences for honest signalling. In some populations of the great bowerbird, *Ptilonorhynchus nuchalis*, males arrange decorations by size, with smaller decorations placed closer to the bower entrance than larger decorations. This may create a more even background pattern from the female's viewpoint within the bower than if decorations were arranged randomly. Males show consistent, individual variation in the size–distance gradient, which could reflect variation among males in the cognitive skills needed to arrange decorations. We examined whether individual consistency in gradient characteristics is related to a male's skill at decoration arrangement or the types of decorations at bowers. We paired 18 males and switched bower decorations between pairs. We measured gradient characteristics before switching and 4 and 8 days after switching. Gradient characteristics after switching were related to those of the bower from which decorations were received, not to those of the male's own bower before switching. Gradient characteristics were also related to the types of decorations received, including bones and snail shells. These results suggest that variation among males in the size–distance gradient is explained by differences in the availability of decorations at bowers, not the cognitive skills required to arrange decorations. Although variation in gradient characteristics could indicate the male's ability to locate and transport particular decorations, it could also reflect local availability of objects, with no relationship to male quality.

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Many animals use nonbodily ornaments to attract mates, and recent studies have noted that these extended phenotypes may be uniquely suited to reveal honest information about male quality (Schaedelin & Taborsky, 2009). To locate and transport the objects that compose extended phenotypes, males may need to be in good condition (Backwell, Jennions, Christy, & Schober, 1995; Doerr, 2012; Soler, Martín-Vivaldi, Marín, & Møller, 1999), and in order to construct the most attractive signals, they may need to have advanced cognitive skills (Keagy, Savard, & Borgia, 2011; Kelley & Endler, 2012a). However, extended phenotypes also have drawbacks in terms of honest signalling. By definition, extended phenotypes are composed of objects that must be acquired from the environment, so the size and form of these signals is highly dependent on environmental conditions. If the resources that compose these signals are too scarce in the environment, males

may be unable to construct complete signals, but if the resources are too common, males may need to invest little time or energy in acquiring them (Borgia, Kaatz, & Condit, 1987; Hunter & Dwyer, 1997; Madden & Balmford, 2004); both situations could reduce the indicator value of the signals (Leighton, 2014; Schaedelin & Taborsky, 2009). Similarly, if the availability of suitable objects varies along an environmental gradient, then intrapopulation variation in signal form may reflect local environmental characteristics rather than male characteristics. To date, however, the effects of environmental variability on the honesty of extended phenotypes are poorly understood.

Bowerbirds build and decorate stick structures, called bowers, to attract females. The bower of the great bowerbird, *Ptilonorhynchus nuchalis*, can be more than 1 m in length and decorated with over 1000 decorations (Frith & Frith, 2004). Males of this species arrange grey and white decorations on the courts of the bower, and these decorations appear to serve as a background against which more colourful green and red decorations are displayed (Endler & Day, 2006; Endler, Westcott, Madden, & Robson, 2005; Katsuno, Eguchi, & Noske, 2013). In some populations of this species, the

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grey and white decorations are arranged by size, with smaller decorations placed closer to the bower entrance than larger decorations (Endler, Endler, & Doerr, 2010). Since the female usually sits within the bower and looks out over the court during display, this arrangement of decorations by size may create a more even background pattern from the female's viewpoint than if decorations were arranged randomly. This size–distance gradient may even function as an optical illusion that affects the female's perception of the male's size or that holds her attention for a longer period (Kelley & Endler, 2012a). Previous studies have reported that males vary in the degree to which they arrange decorations by size. When the size–distance gradient was experimentally altered, males recreated their gradients in a few days, with a strong correlation between pre- and postmanipulation values (Endler et al., 2010; Kelley & Endler, 2012b). Thus, variation among males in the size–distance gradient may be an honest signal of a male's skill at arranging decorations, and this may reflect his cognitive ability or overall quality as a mate. A recent study found that male mating success was significantly related to gradient characteristics, which supports the possibility that females use the size–distance gradient to assess male quality (Kelley & Endler, 2012a).

However, there is also considerable within-population variation in the numbers and types of decorations at bowers of this species (Doerr, 2012; Endler & Day, 2006; Endler et al., 2005; Katsuno et al., 2013). If different types of decorations have different shapes and sizes, then this could place limits on the type of size–distance gradient that can ultimately be produced. For example, some bowers of the great bowerbird contain large numbers of snail shells, which are round and relatively uniform in size. Males with many snail shells may produce shallow or no size–distance gradients because the objects at their bowers are all about the same size (Katsuno et al., 2013). In contrast, bowers that contain large numbers of bones, which show variation in shape and size within and between bones (Solomon, Minnegal, & Dwyer, 1986), may have steeper size–distance gradients than bowers with mostly shells. While it is clear from previous studies that males arrange grey and white decorations by size (Endler et al., 2010; Kelley & Endler, 2012b), intrapopulation variation in gradient characteristics may be due to differences in the types of decorations at bowers rather than differences in male quality. Since previous studies have only rearranged the decorations already present at the bower, the extent to which variation in the size–distance gradient is related to male quality or to the types of decorations at bowers is unknown.

We conducted an experiment to determine whether individual consistency in the size/distance gradient is related to male quality or to the types of decorations at bowers of the great bowerbird. At our field site, gradient characteristics, such as the steepness and evenness of the gradient, differ between bowers along the Burdekin River and bowers along Six Mile Creek (Endler et al., 2010). Bowers along the Burdekin River also contain more bones, while bowers along Six Mile Creek contain more snail shells and man-made decorations. For the current study, we switched all grey and white decorations between nine bowers from the Burdekin River and nine bowers from Six Mile Creek. We measured the size–distance gradient immediately before decorations were switched and 4 and 8 days after switching. If variation among males in gradient characteristics is primarily explained by differences in male quality or cognition, then males should be able to create similar size–distance gradients when given a new set of decorations. This should result in a positive association between the size–distance gradient at a male's bower before decoration switching and at 4 and 8 days after switching. In contrast, if gradient characteristics are largely a consequence of the types of decorations at bowers, then this should result in a positive association between the size–distance gradient that a male achieved at

4 and 8 days after switching and the size–distance gradient of the bower from which he received the decorations.

METHODS

Study Site

This study was conducted at Dreghorn Station, a cattle ranch with a habitat of open eucalyptus woodland in Queensland, Australia (Doerr, 2009b). Bowers were located along the Burdekin River, which has water year-round, and along Six Mile Creek, which is usually dry. Bowers along the Burdekin River had more bones than bowers along Six Mile Creek (mean \pm SE: river: 78 ± 21 ; creek: 29 ± 11 ; *t* test: $t_{16} = 2.379$, $P = 0.030$), while bowers along Six Mile Creek had more snail shells and man-made decorations (snail shells: creek: 159 ± 80 ; river: 3 ± 1 ; Mann–Whitney *U* test: $U = 11.0$, $N_1 = 9$, $N_2 = 9$, $P = 0.009$; man-made: creek: 115 ± 62 ; river: 7 ± 4 , $U = 12.5$, $N_1 = 9$, $N_2 = 9$, $P = 0.013$).

Bowers and Bower Pairings

We switched decorations between 18 bowers by pairing nine bowers from Six Mile Creek with nine from the Burdekin River and switching decorations between each pair. When pairing bowers, we first divided the study site into three sectors along Six Mile Creek and three sectors along the Burdekin River, based on each sector's accessibility to the road and a clustering of three bowers within each sector. Then we randomly paired one sector from the creek with one from the river and randomly paired bowers between the two sectors. We chose this approach because travel distances between the creek and river are large (maximum linear distance: 8 km) and must be covered at least in part on foot. Thus, this approach allowed us to switch decorations between bowers more rapidly than if we had paired bowers anywhere on the site. We switched decorations between two sectors per day (i.e. three bowers along the creek and three bowers along the river) during 14–16 October 2012, and we returned decorations to their original owners after 8 days (22–24 October 2012).

We also monitored gradient characteristics at nine additional bowers: four completely undisturbed bowers at which we never touched the decorations and five bowers at which we removed decorations and then immediately returned them two times, once to correspond with the switching of decorations between experimental bowers, and once to correspond with the return of decorations to experimental bowers. The purpose of these additional bowers was to illustrate that males show consistency in gradient quality over time, as observed in previous studies (Endler et al., 2010; Kelley & Endler, 2012b).

This study was conducted with permission from Queensland Environmental Protection Agency (WISP01994004) and the Deakin University Ethics Committee (A22-2010). Note that we have given male bowerbirds new sets of bower decorations in previous studies with no adverse effects on survivorship or site fidelity (Doerr, 2010a, 2010b). The males in the current study accepted the new decorations and rearranged them, with no cases of bower abandonment.

Decoration Switching

At each of the 18 experimental bowers, we removed all grey and white decorations from the two courts and from the inside of the bower (i.e. the 'avenue'), counted them, placed them in plastic bags labelled with the bower name and location (e.g. north or south court, avenue), and moved them to the other bower. We did not move coloured decorations, such as green glass, green leaves or red

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