

Complex male display and female choice in the spotted bowerbird: specialized functions for different bower decorations

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Abstract. Male bowerbirds build and decorate bowers to attract females as copulation partners. Spotted bowerbirds, *Chlamydera maculata*, are atypical in having widely spaced display sites, bowers that are greatly diverged from those of closely related species, and extremely intense, aggressive displays. Results from the continuous monitoring of bowers show that (1) a few males account for the majority of matings, (2) the two most common decoration types, bones and glass, explain a large proportion of the variation in male mating success and (3) large inter-bower distances relate to low levels of decoration stealing and bower destruction. Components of male mating success, male ability to attract female visitors to the bower, and male courtship success correlate respectively with counts of bones and glass. Bones are spread widely around the bower and glass is placed close to it supporting the hypothesis that bones act to attract females towards the bower and glass functions later to stimulate females in the bower. This temporal sequencing of courtship functions represents a novel explanation for the evolution of complex male display traits.

Mate selection in species with elaborate male display traits is a topic of much interest in evolutionary and behavioural biology (Fisher 1930; see Bradbury & Andersson 1987). In such species, males commonly make no material contribution to females or their offspring and females often show preference for a limited set of males (e.g. Andersson 1989; Höglund & Lundberg 1987; Pruett-Jones & Pruett-Jones 1990; and references in Bradbury & Gibson 1983; Wiley 1991).

There are now numerous hypotheses explaining how extreme displays evolve. 'Good genes' models propose that extreme sexual displays function as indicators of male quality to choosing females (e.g. Trivers 1972; Zahavi 1975; Borgia 1979; Andersson 1982, 1986; Hamilton & Zuk 1982). Alternatively, the runaway model (Fisher 1930; see also Lande 1981; Kirkpatrick 1982, 1986) posits that female preferences produce greatly elaborated male display traits without providing enhanced vigour to offspring. Other models include: passive choice (Andersson 1982; Parker 1983), intra-sexual signalling (Halliday 1978; LeCroy et al. 1980), proximate benefits (e.g. protection to females provided by well-constructed bowers; Borgia et al. 1985) and innate preferences (Burley 1985; Kirkpatrick 1987; Ryan et al. 1990).

Recent empirical studies have shown that elaborated traits in polygynous species are often complex sets of traits (Borgia 1985a; Borgia et al. 1987; Andersson 1989; McDonald 1989; Prum 1990; Zuk et al. 1990; Gibson et al. 1991; Møller & Pomiankowski 1993). The function of these traits and reasons for their complexity is just beginning to be explored.

Bowerbirds have among the most complex set of display traits of any organism. Bowerbird bowers are built of sticks on the ground in association with decorated display courts. Bowes and display courts provide a stage for male behavioural display that includes plumage, acoustical and dancing elements directed at females during courtship. Comparisons of different species led Gilliard (1956, 1963) to suggest that bowers and decorations serve as a replacement for elaborate plumage characters, but recent tests of this hypothesis have led to ambiguous results (Kusmiński et al. 1993).

Female satin bowerbirds, *Ptilonorhynchus violaceus*, prefer males with well-built and well-decorated bowers (Borgia 1985a; Borgia & Mueller 1992), indicating that bowers and decorations play an important role in mate attraction. For satin bowerbirds, bower destruction affects bower quality (Borgia 1985b) and decoration