Does cultural transmission of displays promote hybridization in bowerbirds ?

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ABSTRACT Species with highly complex and distinct displays are expected to have strong reproductive isolation and are unlikely candidates to produce hybrids[1]. Bowerbirds have among the most complex sexual displays, yet contrary to expectations, there have been anecdotal reports of ongoing hybridization between great (*Chlamydera nuchalis*) and spotted bowerbirds (*Chlamydera maculata*), which have distinctive phenotypes[2]. Here we report finding a population with a high frequency of hybridization between these species and provide evidence of hybridization from plumage, morphology, mtDNA and behavior. We suggest that reproductive isolation may be particularly susceptible to break-down under conditions where males can learn display from individuals other than their parent. Evidence showing that individuals of each species attend heterospecific bowers and receive courtship, and that some hybrids and birds with parental-species phenotypes use displays of both species supports the hypothesis that bowerbird displays are learned[3]. It also suggests that cross-species cultural exchange occurs and may account for the occurrence of hybrids even between species with complex and highly differentiated display. The high level of hybridization detected does not support a reinforcement model of display divergence in bowerbirds[4].

METHODS

STUDY SITES

- SYMPATRY: ~120 km long (N-S) by 40 km wide area in NW Queensland, AUS. *C. nuchalis* phenotype is more common in the north and *C. maculata* in the south.
- ALLOPATRY: 4 locations for *C. maculata* in central and western QLD and 1 location for *C. nuchalis* in NE QLD.

DATA COLLECTED

- MORPHOMETRY: Weight, wing length, tarsus length, bill length (Table 1).
- PLUMAGE: For each bird, we combined the scores of 5 species-diagnostic plumage areas[5] (Table 1).
- MOLECULAR: mtDNA (cytB) sequence.
- DISPLAY: Automated video cameras recorded behavioral display at multiple bowers per location for up to 1 month[6]. We also collected data on bower displays.

ANALYSES

- We performed a principal components analysis on morphological and plumage characters. We plotted the first two components for captured birds of each parent-species in allopatry and birds of the sympatric population (Figure 1). We classified individuals as hybrid based on; (1) phenotype that was intermediate to parent-species, or (2) phenotype-mtDNA genotype mismatch.
- Birds on video (not captured) were classified based on visual assessment of plumage and size. These birds were used only for analysis of display transfer.
- We scored displays of birds in sympatry for elements unique to parent-species in allopatry, (14 *C. maculata* elements, 8 *C. nuchalis* elements)(Table 2). Display types scored include "dancing", display distance, bower materials and size.

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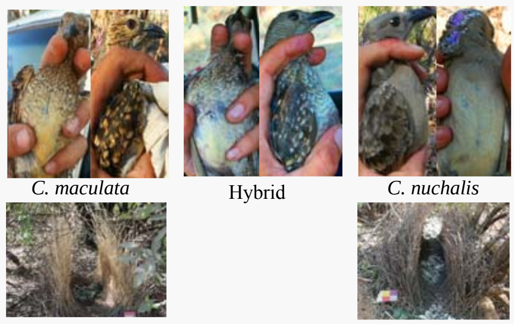

MORPHOLOGY AND PLUMAGE DATA					
Parent species	**Weight (g)**	**Wing(mm)**	**Tarsus(mm)**	**Bill (mm)**	**Plumag**
C.maculata (n=13)	138 (5.8)	152 (6.4)	41.3 (6.9)	16.6 (0.58)	6-7
C. nuchalis (n=17)	190 (8.8)	168 (3.7)	46.7 (0.99)	18.8 (0.77)	27-30

Table 1. Means (SD) of phenotypic characters used in PCA. Range is given for plumage scores. Independent t-tests show highly significant differences between species in all trait values ($p<.00001$).

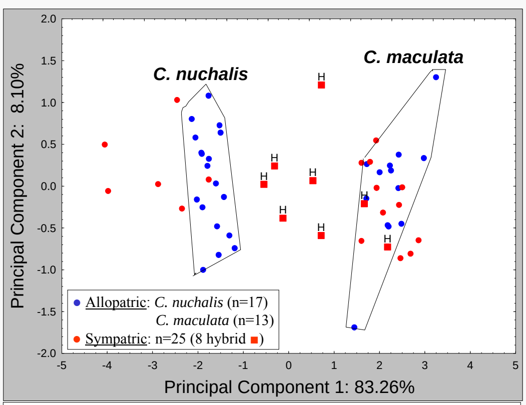

Figure 1. Principle components plot for allopatric and sympatric individuals based on plumage and morphological traits. Areas enclosed in polygons include all birds from allopatric populations, for each parent-species. Eight hybrids include six birds with phenotype intermediate to parent-species (between -1 and 1 on X-axis) and two with phenotype - mtDNA mismatch.

DISPLAYS				
Location	**Bird type**	**Display elements used**		
		Only Spotted	**Only Great**	**Both**
Sympatry	Spotted	12 (4)	0(0)	2(2)
	Great	0(0)	3(0)	0(0)
	Hybrid	5(1)	1(1)	2(1)
Allopatry	Spotted	24(12)	0(0)	0(0)
	Great	0(0)	7(2)	0(0)

Table 2. Number of birds of each type that performed only spotted display elements, only great display elements or elements of both species. Number in parentheses represents captured birds that were identified using plumage, morphology, and mtDNA. There were three hybrid bower-owners; red indicates *C. nuchalis* mtDNA and green indicates *C. maculata* mtDNA.

References

1. Coyne, JA and HA Orr. 2004. Sinauer Associates
2. Frith, CB and Frith, DW. 1995. Memoirs of Qld Museum. 38, 471-476.
3. Madden, JR. 2008. *Anim. Cog.* 11: 1-12
4. Endler et al. 2005. *Evolution.* 59(8):1795–1818
5. Moore, WS and DB Buchanan. 1985. Evolution. 39:135-151
6. Borgia, G. 1995. *An. Behav.* 49: 1291-1301

RESULTS

HYBRIDIZATION

- 8 confirmed hybrids out of 25 birds captured in sympatry (see Fig. 1).
- Bidirectional hybridization (2 hybrids have mtDNA typical of *C. maculata*; other 6 have *C. nuchalis* mtDNA).

CULTURAL TRANSFER

- 2 putative *C. maculata* bower-owners (classified by phenotype and mtDNA) performed displays of both species.
- One hybrid bower-owner in the northern region, where *C. nuchalis* is more common, used only *C. nuchalis* displays. In the southern region, where *C. maculata* is more common, 1 hybrid bower-owner used only *C. maculata* displays and one other bower owning hybrid used displays of both species. All hybrid bower-owners were classified by phenotype and mtDNA

HETEROSPECIFIC COURTSHIP

- Putative *C. nuchalis* females (not-captured) observed receiving courtship from a *C. maculata* male (1 obs.) and a hybrid male (3 obs.). Males were classified by phenotype and mtDNA.

DATA SUMMARY

- This is the first confirmed hybrid zone between any pair of bowerbird species.
- Bi-directional hybridization shows females of both species mate with heterospecifics
- Some putative *C. maculata* males used *C. nuchalis*-type display elements which suggests that interspecific cultural transfer of male display has occurred.
- Hybrid bower-owners use displays of locally common parent-species suggesting that display acquisition is strongly influenced by which display model males are more likely to encounter.
- Heterospecific courtship suggests that hybridization is the result of female choice, and not forced copulation. Females may hybridize with males that have learned to produce heterospecific displays.
- High frequency of hybridization suggests that display divergence between these species is not the result of reinforcement.