

SEXUAL SELECTION DRIVES RAPID DIVERGENCE IN BOWERBIRD DISPLAY TRAITS

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Abstract.—Sexual selection driving display trait divergence has been suggested as a cause of rapid speciation, but there is limited supporting evidence for this from natural populations. Where speciation by sexual selection has occurred in newly diverged populations, we expect that there will be significant differences in female preferences and corresponding male display traits in the absence of substantial genetic and other morphological differentiation. Two allopatric populations of the Vogelkop bowerbird, *Amblyornis inornatus*, show large, qualitative differences in a suite of display traits including bower structure and decorations. We experimentally demonstrate distinct male decoration color preferences within each population, provide direct evidence of female preferences for divergent decoration and bower traits in the population with more elaborate display, and show that there is minimal genetic differentiation between these populations. These results support the speciation by sexual selection hypothesis and are most consistent with the hypothesis that changes in male display have been driven by divergent female choice.

Key words.—*Amblyornis inornatus*, bowerbirds, premating isolation, sexual selection, speciation.

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Over a century after Darwin (1859) first considered the significance of speciation, its causes are still hotly debated (see Otte and Endler 1989; Coyne and Orr 1998). Speciation models differ in the amount of genetic differentiation required for reproductive isolation. The allopatric speciation model suggests that pre- and postmating isolation evolve as by-products of large-scale genetic differentiation while populations are geographically isolated (Mayr 1942). The reinforcement model suggests that populations first diverge in allopatry and then the reduced fitness of hybrids during secondary contact selects for premating isolation (Dobzhansky 1937). Both of these models generally require substantial amounts of genetic change for reproductive isolation to arise.

The speciation by sexual selection (SSS) hypothesis argues that divergent female preferences may cause strong premating isolation with very little genomewide or other morphological differentiation after reproductive isolation (Lande 1981; West-Eberhard 1983; Schluter and Price 1994; Turner and Burrows 1995). Thus, the SSS hypothesis differs from other models because reproductive isolation can result from relatively few genetic changes associated with female preferences and male display traits.

Spieth (1966) proposed that the major species differences in male display traits among Hawaiian *Drosophila* were products of divergent sexual selection. Subsequent studies indicate that sibling species are genetically similar and reproductively isolated by minor changes in male courtship and morphological display traits (see Kaneshiro 1988), supporting the SSS hypothesis. Similar premating isolation has been experimentally shown between closely related African and cosmopolitan populations of *D. melanogaster* (Wu et al. 1995). However, Boake et al. (1997) have argued that the SSS hypothesis may not apply in the Hawaiian *Drosophila* because in the sibling species pair they tested, females do not use sexually selected traits in species recognition. Thus, the degree to which sexual selection has contributed to the rapid speciation in *Drosophila* remains controversial (Boake et al. 1997).

The explosive diversification of cichlids in African rift lakes has also been attributed to SSS (McKaye 1991; Galis and Metz 1998). Closely related cichlid species often show low genetic divergence, but substantial changes in male reproductive coloration that is used in mate choice and species recognition (Meyer 1993; Seehausen and van Alphen 1998). This suggests that divergent sexual selection has driven the rapid speciation in African cichlids.

Claims supporting the SSS model in birds come from four recent comparative studies (Barracough et al. 1995; Mitra et al. 1996; Prum 1997; Møller and Cuervo 1998) that relate speciation rate with likely correlates of intensity of sexual selection. However, because divergence of male display could have occurred after the completion of speciation, the SSS hypothesis remains only one of several possible alternatives (Coyne and Orr 1989; Schluter and Price 1993).

A more direct test of the SSS hypothesis is to demonstrate large differences in male display traits and related female preferences in recently diverged taxa that show little or no genetic differentiation (see Kaneshiro 1988; Meyer 1993). We use this test of the SSS hypothesis in a comparison of two populations of the Vogelkop bowerbird (*Amblyornis inornatus*) that show large differences in male displays, but are otherwise morphologically identical (Diamond 1985, 1986; Beehler et al. 1986). We demonstrate distinct male preferences for bower decorations and female choice for those preferences. Information on the genetic distance between these Vogelkop populations suggests that there is little genetic differentiation and that their divergence is recent. Thus, these results provide the first direct evidence for the SSS hypothesis in birds.

MATERIALS AND METHODS

Study System

Bowerbirds are known for their elaborate bowers and decorated display courts that evolved as a result of female preferences (Borgia 1985, 1995a,b; Borgia et al. 1987). Allopatric

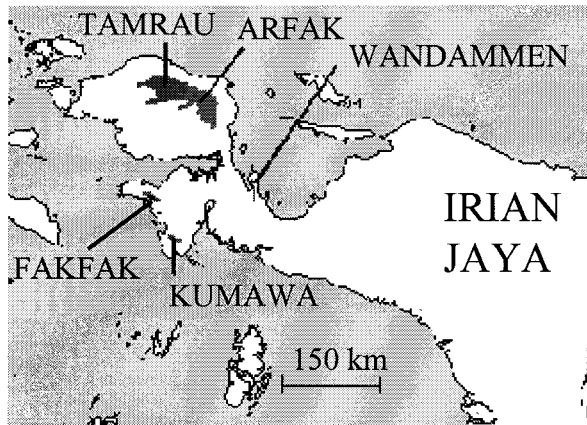


FIG. 1. Map of Vogelkop bowerbird populations in Irian Jaya, Indonesia.

populations of the Vogelkop bowerbird show large qualitative differences in a suite of display traits including bower structure and decorations (Beehler et al. 1986; Diamond 1986, 1988). Adult males of the Arfak, Tamrau, and Wandammen Mountains (Fig. 1) build hutlike bowers that are the largest and most elaborate among bowerbirds (Ripley 1942; Gilliard 1969; Diamond 1986). These bowers are copiously decorated with colorful objects collected from the surrounding habitat (Fig. 2A, Table 1). In contrast, Vogelkop populations in the Kumawa and Fakfak Mountain ranges (150 km south of the hut-builders; Fig. 1), build maypole bowers (bowers supported by a sapling) that lack the hut cover and

TABLE 1. Comparison of display traits between the hut-building (Arfak Mountains) and non-hut-building (Fakfak Mountains) populations of the Vogelkop bowerbird. We observed 10 major differences in bower display between these populations and tested for these differences using a Mann-Whitney *U*-test for quantitative traits (e.g., slope and court area) and Fisher's exact test for qualitative traits (** $P < 0.01$, * $P < 0.05$). Means are expressed as $\bar{X} \pm SD$. Slope was quantified by measuring the amount of vertical change of the area around the bower, starting from the edge of the court until 1 m beyond it.

Display	Arfak	Fakfak
Bower:		
Structure**	hut	open tower
Location*	slope (0.36 \pm 0.23)	flat ridge (0.13 \pm 0.09)
Court:	oval	circular
Size*	(2.81 \pm 1.09 m ²)	(1.71 \pm 0.38 m ²)
Material**	green moss	black moss
Decorations:		
Colorful**	yes	no
Fruits**	yes	no
Flowers**	yes	no
<i>Pandanus</i> **	no	yes ¹
Placement of decorations:		
On court**	yes	no
Off court**	yes	no

¹ See Figure 2b.

decorate them with drab-colored decorations exclusively (Fig. 2B, Table 1; Diamond 1986, 1988). Although bower structure and decoration-use are dramatically different, identical morphology has been used to classify these populations

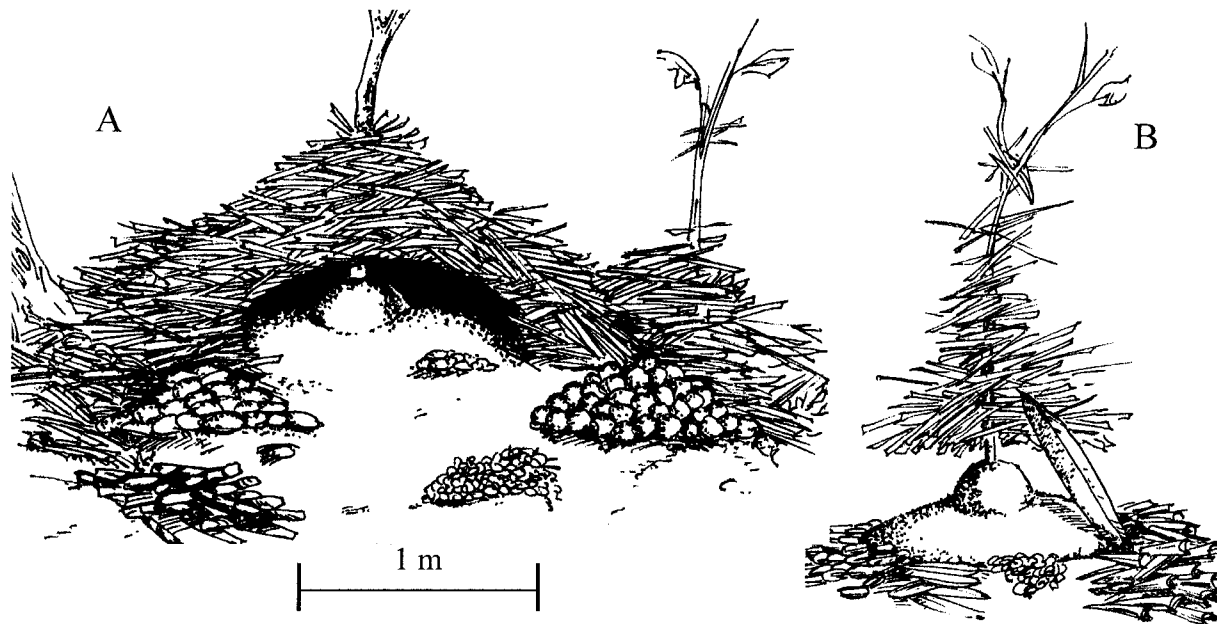


FIG. 2. The bower structure and decorations of two divergent populations of the Vogelkop bowerbird. (A) A hut bower built on a mountain slope by a male from the Arfak Mountains. Bowers are built from sticks tightly woven around a sapling (maypole) and can be over 2 m wide and 1 m tall. Decorations such as insect parts, fungi, seedpods, and colorful fruits and flowers are arranged neatly in piles by color and type. (B) An open bower built on a flat ridge by a male from the Fakfak Mountains. Bowers are built from sticks loosely interwoven around a central maypole and can be over 2 m tall. Males exclusively use drab-colored decorations such as bamboo bark, rocks, and snail shells placed on the periphery of the circular court. Males also typically prop dried palm (*Pandanus* sp.) leaves against the maypole tower.

as a single species (Diamond 1985; but see Beehler et al. 1986).

Study Site

Vogelkop bowerbirds are found in the extreme north-western mountain ranges of Irian Jaya, Indonesia (Gilliard 1969; Diamond 1986). The study site in the Arfak Mountains was located 2 km from the village of Testega (01°23'S, 133°36'E) in rain forest at elevations between 1620 m and 1860 m (Fig. 1). The study site in the Fakfak Mountains was located 10 km north of the coastal village of Worserat (03°10'S, 132°50'E) in rain forest at elevations of 1050 m to 1300 m (Fig. 1).

Experimental Tests of Decoration Preferences

In species that collect bower decorations, experimental tests are needed to accurately assess male decoration preferences (see Diamond 1986, 1988; Borgia et al. 1987). A simple assessment of decorations on bowers would not reveal if some decorations were missing because they were unavailable in the habitat or if they had some chemical or other deterrent that made them unattractive. Color and shape preferences for decorations used by bower holders from the Arfak and Fakfak populations were tested using square and triangle plastic color tiles from November 6 to December 1, 1994 in Arfak and November 1–13, 1994 in Fakfak. Tiles were arranged and spaced equally along four rows, forming a square 60 cm off males' courts. In separate trials, males were exposed to either 21 different-colored square or 16 different-colored triangle tiles. Trials lasted for 4 h and observers noted when and which individual tiles were used. Of the 12 total Arfak males we tested, 11 were tested with the triangle tiles and seven were tested with the square tiles (six of the 12 males were tested once with the triangle, and, at a different trial, with the square tiles; treatments were given in random order). For two males results were excluded in tests requiring the exact time tiles were harvested because this information was incomplete. Five Fakfak males were tested with the square tiles only.

For Arfak males, Monte Carlo simulations involving 50,000 iterations for each treatment (Manly 1991) were used to determine the probability that the observed consistent use of specific colors was due to chance. Similar analyses could not be done for the Fakfak population because bower holders generally failed to use the color tiles. To determine male decoration color preferences, we calculated the mean of the time elapsed from the bower owner's arrival until the tile was harvested (mean time taken) for each color across the Arfak and the Fakfak males. Tiles not used by bower owners were given a value of 240 min, because each trial lasted for 4 h. Colors harvested early in the trial (low mean time taken) are considered to be more preferred than colors that were harvested later in the trial (high mean time taken). Using population as a grouping variable, we then used a Mann-Whitney *U*-test to determine if the Arfak and Fakfak males differed in their color preferences. To test for population differences in overall attraction to decoration color, we used Fisher's exact test for each color to determine if the inter-

action between population (Arfak or Fakfak) and tile use (yes or no) is significantly different from zero.

Test of Female Preferences for Divergent Traits

The SSS hypothesis predicts that females will prefer the display traits of males from their own population. To test this prediction in Vogelkop bowerbirds, 16 bowers in the hut-building Arfak population were monitored continuously with automatic video cameras from October 18 to December 4, 1994 (for a detailed description of camera set-up, see Borgia 1995a). Each male's mating success was determined by an analysis of videotapes from monitored bowers. Because females initiate all courtships and can choose freely among males (Borgia 1985) and male-male interactions mostly have an indirect effect on mating success by altering the quality of male display (Borgia 1995b), we use male mating success as a measure of female preferences. Bower holders arranged decorations by color and type in discrete piles (Fig. 2A), and so the area that the decorations covered on the court was the most consistently measurable indicator of number of decorations (natural decorations often fell apart when counted and individual berries often fell off clusters when brought to the bower). Bower dimensions (height, width, circumference) were measured, and from these the volume of a cone approximating the shape of the bower was calculated. Univariate linear regression was used to determine the effects of bower volume ($n = 15$), amount of blue ($n = 16$) and amount of red ($n = 15$) decorations on male mating success. We chose blue and red decorations because all the Arfak males tested with color tiles strongly preferred these colors, suggesting their importance in mate choice. The assumptions of the univariate regression model were met by \log_{10} transformation of the dependent variable (number of matings). Further, we used multiple regression analysis to determine the simultaneous effects of the multifaceted display components on male mating success. For this analysis, we used the two display components (bower size and area of blue decoration) that were found to be significant in the univariate regression tests. Multiple regression assumptions of homogeneity and normality of residuals were met without data transformation. All tests of significance were two-tailed. We originally planned to measure male mating success in the Fakfak population as well, but the Indonesian government closed Irian Jaya to scientific study before this could be done.

Genetic distances were calculated under the HKY85 model (Hasegawa et al. 1985) using PAUP 3.1.1 (Swofford 1993). Mitochondrial cytochrome *b* sequence data was taken from Kusmiński et al. (1997), and unpublished data (for *Chlamydera gutatta*; J. Bollback, pers. comm. 1998). Genetic distances were calculated for all known bowerbird species with geographically isolated population for which phylogenetic relationships are known (*A. macgregoriae*, *C. gutatta*, and *Ptilonorhynchus violaceus*). Genetic distances were calculated for the three most recently diverged sister species pairs (*C. nuchalis* and *C. cerviniventris*, *C. maculata* and *C. gutatta*, *A. inornatus* and *Archboldia papuensis*; see Kusmiński et al. 1997). Average genetic distances are expressed as $\bar{X} \pm SD$.

RESULTS AND DISCUSSION

Decoration Preferences

Differences in decoration use between the Arfak and Fakfak populations (Fig. 2, Table 1) may be due to distinct decoration type and color preferences or differences in current decoration availability in the habitat. Comparisons of square and triangle tile treatments at the Arfak study site show a strong effect of male preference for color, but not for shape (Friedman's ANOVA: $\chi^2 = 90.817$, $n = 4$, $P < 0.001$; coefficient of concordance = 0.770), indicating that color critically affects decoration use, but that shape does not. Moreover, the percentage of decorations used during the square and triangle treatments did not differ significantly (ANOVA: $F_{1,10} = 0.386$, $df = 1$, $P = 0.55$). The strong concordance between the square and triangle treatments allowed us to combine these results (Fig. 3).

Arfak males readily responded to the colored tiles, collecting 86% of the total number of color tiles they would use in the trial during the first hour of observation. In contrast, Fakfak males showed very low levels of tile use during our 4-h observations, and tiles that were left on Fakfak display courts for 24 h showed no change from the initial response. In all trials, Fakfak bower owners visited their bowers and inspected the experimental tiles, indicating that males were in the vicinity of their bowers and aware of the tiles' presence.

In the hut-building Arfak population, blue and red tiles were consistently among the first four tiles taken by bower owners (Monte Carlo simulations: triangle tiles, $P = 0.015$; square tiles, $P = 0.007$), indicating strong preferences for blue and red decorations (Fig. 3A). Brown and other drab-colored tiles, on the other hand, were least preferred (Fig. 3A). In contrast, males of the non-hut-building Fakfak population exhibited little interest in harvesting the color tiles, thus showing different decoration color preferences (Fig. 3). Consistent with this observation, colorful fruits, berries, and flowers commonly used as decorations by the Arfak males were also present in nearly equal abundance (pers. obs.) but were not used at the Fakfak study site. Thus, the tendency of the non-hut-builders to ignore decorations that were used consistently by the hut-builders indicates that the absence of colorful decorations among the Fakfak bowers is not caused by decoration availability. Our results parallel an earlier study in which six colors of poker chips showed a similar pattern of differences between hut-building (Wandammen Mountain) and non-hut-building (Kumawa Mountain) Vogelkop populations at locations geographically distinct from ours (see Fig. 1; Diamond 1988).

Sexual Selection and Speciation

Univariate regression analyses indicate that area of blue decorations ($F_{1,14} = 10.20$, $r^2 = 0.42$, $P = 0.004$) and bower volume ($F_{1,13} = 4.87$, $r^2 = 0.27$, $P = 0.02$) each explained a significant portion of the variance in male mating success in the Arfak population (Fig. 4). Area of blue decorations ($\beta_1 = 0.52$, $n = 16$, $P = 0.02$) and bower volume ($\beta_2 = 0.44$, $n = 15$, $P = 0.04$) produced a highly significant multiple regression model ($F_{2,14} = 7.53$, $r^2 = 0.564$, $P < 0.01$). Therefore, our results suggest that females from the Arfak popu-

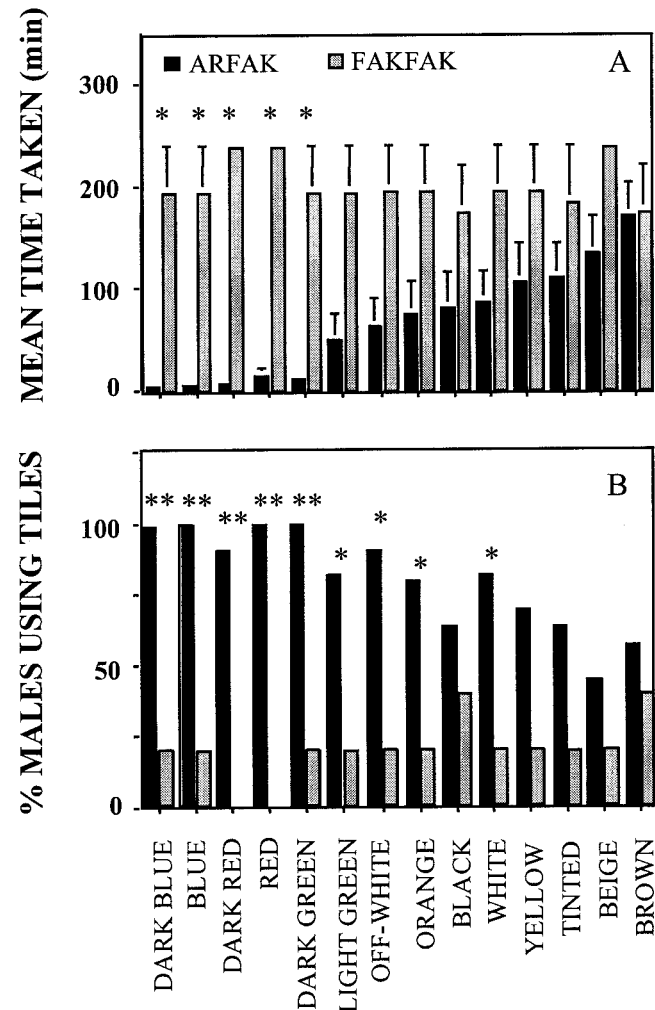


FIG. 3. Histograms showing decoration color preferences for the Arfak and Fakfak populations of the Vogelkop bowerbird. (A) Decoration color preferences as shown by mean (± 1 SE) time taken (time between bower owner's arrival and first use of tile) for the Fakfak and Arfak males (Mann-Whitney U -test; $**P < 0.01$, $*P < 0.05$). Because color was the main criterion used by the Arfak birds in choosing decorations (see text), triangle and square tile treatments were combined into a single experiment with the 15 common tiles from both treatments grouped by their respective colors. (B) Overall attraction to color decorations as shown by percentage of males from each population that used the color tile within 240 min (for each color: $df = 1$, $**P < 0.01$, $*P < 0.05$).

lation consistently used two distinct components of male display in mate choice: (1) decoration colors absent in the bowers of Fakfak males were important in mate choice at the hut-building Arfak population; and (2) bower volume was greater at Arfak than at Fakfak (t -test: $t = 2.68$, $df = 18$, $P = 0.02$), with none of the Fakfak males having a bower volume within the 95% confidence interval of the males who received copulations at Arfak. These differences suggest that Fakfak bower display would be ineffective in attracting Arfak females.

Although red decorations were preferred strongly by Arfak males, we did not find a significant effect of area of red decorations on male mating success ($F_{1,14} = 2.33$, $r^2 = 0.14$, $P = 0.15$). This may be explained by differences in the dis-

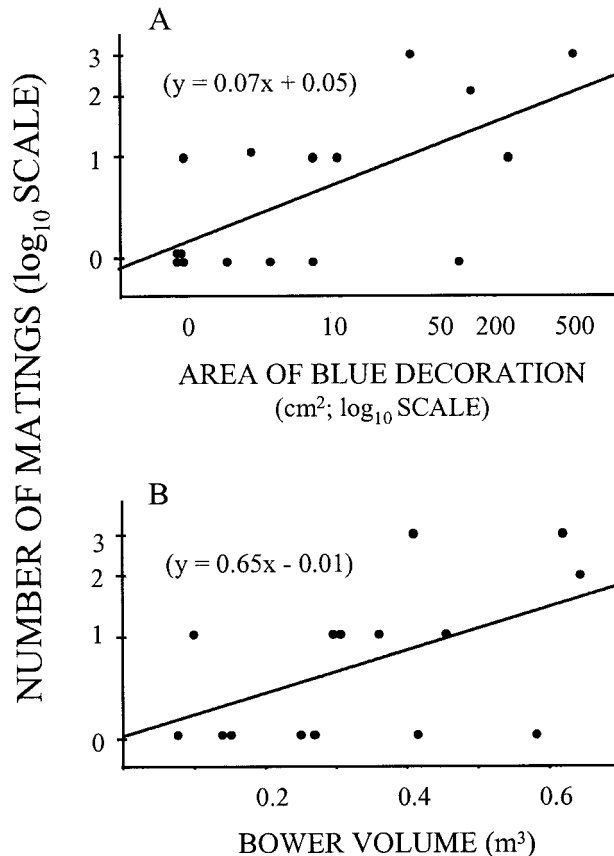


FIG. 4. Regression of male mating success on (A) the area of blue decorations; and (B) bower volume for males of the hut-building Arfak population.

tribution of blue and red objects on the bower. Amount of blue decorations was highly variable ($CV = 227.79\%$) among males, whereas amount of red decorations was not ($CV = 79.26\%$). Red decorations were much more common in the surrounding habitat than blue (pers. obs.) and this may have led to the lower overall variation in red on bowers. Because of this lower variation in amount of red decorations, such objects, if attractive to females, are less likely to show a positive association with mating success. All males who received matings had red decorations, so females may use the presence of red decorations as a minimum requirement for consideration as a mate.

Under the SSS model, divergence in male display and female preference should not be associated with substantial genetic differentiation at the time of speciation. Comparison of 924 mtDNA sequence from the Arfak and Fakfak populations indicates a genetic distance of 0.005. This value is similar to the average interpopulation genetic distance (0.004 ± 0.002) within three different bowerbird species (*A. macgregoriae*, *P. violaceus*, and *C. gutatta*) that show comparable geographic separation, but do not differ in bower form and decoration preferences. Moreover, the genetic distance of the Arfak and Fakfak populations is only 16% of the average genetic distance (0.035 ± 0.003) between three pairs of bowerbird sister species (*C. nuchalis* and *C. cerviniventris*, *C. maculata* and *C. gutatta*, *A. inornatus* and *Archboldia pa-*

puensis; see Kusmierski et al. 1997). These comparisons indicate a very low level of genetic differentiation between the Arfak and Fakfak populations despite the large changes in male display (Fig. 2, Table 1) and female preferences and provide strong support for the SSS hypothesis. Other likely causes of speciation (e.g., differentiation as a result of pleiotropic change or reinforcement) are not consistent with the observed divergence in male display traits coupled with the low level of genetic differentiation.

Changes in male display by sexual selection could have resulted from (1) replacement of existing female preferences with new preferences; (2) a shift in male display to exploit preexisting female preferences (e.g., sensory exploitation; Ryan 1990); or (3) selection for less choosy females in founding populations that led to the arbitrary loss of male display elements (e.g., Kaneshiro 1988). We favor the hypothesis that nonarbitrary changes in female preferences account for the differences in male display between the Arfak and Fakfak populations of the Vogelkop bowerbird. This view is developed from recent interspecific studies of display-trait evolution in bowerbirds. These comparisons show coordinated changes between environmental conditions and male display (G. Borgia, unpubl. data), a pattern inconsistent with the prediction of arbitrary trait evolution from the Kaneshiro (1988) and early versions of the preexisting preference (e.g., Burley 1986) hypotheses. More recent versions of the preexisting preference hypothesis (including sensory exploitation; Ryan 1990; Ryan et al. 1990) suggest that this mechanism can produce a correlation between display trait and ecological conditions through pleiotropy, but this has yet to be demonstrated. Further, bowerbirds show high lability in male display that is consistently related to female trait preferences even between sister taxa (Borgia 1985, 1995a; Borgia and Mueller 1992; Kusmierski et al. 1997; Borgia and Presgraves 1998; G. Borgia, unpubl. data). This close association between male traits and female preferences suggests that display trait divergence in bowerbirds more likely results from rapidly evolving female preferences than a situation where males of only some taxa successfully exploit relatively few, indirectly selected, preexisting female preferences. Without observations on female choice in the Fakfak population, however, we cannot rule out the preexisting preference hypothesis.

An alternative to the SSS hypothesis is the possibility that high levels of predation may have driven the loss of conspicuous display in Fakfak males, as seen in divergent guppy (*Poecilia reticulata*) populations in Trinidad (Houde and Endler 1990). Fakfak bowers were monitored continuously from October 30 to November 15, 1994 with automatic cameras. We did not observe any predation attempts during this period, but we only monitored three bowers for a limited time. However, in a more detailed study of the MacGregors bowerbird (15 bowers monitored for a total of 11,760 h) that is similar to the Fakfak birds in bower and decoration behavior, there was no evidence of an important predation effect shaping male display (Borgia 1995b; G. Borgia unpubl. data).

The presence of preferences in Arfak females for large bowers and blue decorations and the absence of these traits in Fakfak displays suggest that the highly divergent bower displays of Fakfak males would be inadequate to attract Arfak

females. This result indicates that premating isolation may have evolved at least in one direction between these populations, suggesting the possibility that they are incipient species.

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