Degree of male ornamentation affects female preference for conspecific versus heterospecific males

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Several studies have shown female preference for conspecific males with the attached artificial ornaments of more elaborate heterospecifics. However, preference for heterospecifics under natural conditions is relatively rare. We tested what factors affect behavioural mechanisms of species isolation using three species of estrildid finch (genus *Uraeginthus*) that occur in both sympatry and allopatry. These finches differ in degree of sexual dimorphism; male ornamentation; behavioural and morphological similarity; and phylogenetic distance. Paired mate-choice trials were used in which females were presented with a conspecific and heterospecific male to test which of the above between-species differences best predicted the degree of premating isolation. The three species differed in the degree of species-specific mate preference shown. Females from the brighter two species discriminated against dull males, independently of sympatry–allopatry, similarity and phylogenetic distance. Females from the dull species reacted to conspecific males and brighter heterospecific males equally strongly, independently of similarity and phylogenetic distance. In contrast to previous studies, an equal preference for heterospecific and conspecific males was found under natural conditions. It is suggested that differences between closely related species in male ornamentation affect the likelihood that premating isolation will occur due to the fact that sexual selection tends to drive preferences for exaggerated ornamentation.

Keywords: sexual dimorphism; reinforcement; female preference; estrildid finch

1. INTRODUCTION

Individuals of most species typically prefer to mate with conspecifics over heterospecifics (e.g. Ratcliffe & Grant 1983). However, under certain circumstances heterospecific individuals may be preferred as mates (e.g. Ryan & Wagner 1987; McClintock & Uetz 1996). Also, hybrid zones do occur (e.g. Gill & Murray 1972; Grant & Grant 1992; references in Arnold & Hodges 1995), indicating that there has been either an inability to recognize conspecifics (Grant & Grant 1997) or the lack of a strong preference for conspecifics (Gill & Murray 1972). There are several factors that may influence the degree of species-specific mating preference shown: species distribution (Dobzhansky 1940); sexual selection (Ryan & Rand 1993); similarity of secondary sexual characteristics (Grant *et al.* 2000); and phylogenetic distance (de Kort & ten Cate 2001). How these forces interact, and their relative importance in particular species has yet to be investigated.

First, let us consider species distribution. Theory indicates that, in sympatry, premating reproductive isolation will occur (Dobzhansky 1940; Rice & Salt 1990) as a response to the costs of hybrids (but see Arnold & Hodges 1995). This may be achieved by changes in existing mate-preference criteria (Ratcliffe & Grant 1983; Baker & Baker 1990; Gerhardt 1994; Marquez & Bosch 1997). Alternatively, ecological-character displacement in sympatric populations can lead to greater premating isolation as a

correlated response (Rice & Salt 1990; Howard 1993). These two theories have been collectively called 'reinforcement' (Noor 1997), i.e. reinforcement of premating barriers to mating. Although the above idea is intuitively logical, theoretical investigations have yielded contradictory results (cf. Butlin 1987, 1995). The conditions under which reinforcement maintains or induces species isolation appear to be rather restrictive (Servedio & Kirkpatrick 1997; Kirkpatrick 2000; Servedio 2000). Migration levels between populations (Servedio & Kirkpatrick 1997) and mate-choice mechanism (Servedio 2000) both affect the likelihood of premating isolation developing. However, several empirical studies have shown that, in sympatric populations, females discriminate more strongly against heterospecific males than females in allopatry (Lynch & Baker 1990; Noor 1997, 1999; Marquez & Bosch 1997), and that male characteristics have diverged in sympatric populations (Sætre *et al.* 1997; Rundle & Schluter 1998). At present, reinforcement enjoys wide support, even though the details and extent of the process, and the role it has in speciation, are not understood (Noor 1999; Kirkpatrick 2000; Servedio 2000). Thus, reinforcement is likely to be a strong influence on whether species show strong species-specific mating preferences.

The second important factor affecting species-specific mating preferences is the role of sexual selection, specifically female preference for exaggerated male secondary sexual characteristics (Ryan & Rand 1993). Females tend to show directional preferences for more elaborate males (references in Anderson 1994). One theory is that females may mate with heterospecifics, because they resemble

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high-quality conspecifics (Pfennig 1998, 2000). Females can assign priority to mate-quality recognition and risk heterospecific mating, or species recognition and risk mating with low-quality males (Pfennig 1998). Which of these is given priority may depend on the likelihood of encountering heterospecifics and the cost of mistakes, i.e. hybrid fitness (e.g. Noor 1995). However, hybrid fitness will not always be low (see review in Arnold & Hodges 1995), so mate quality may be given priority even in sympatry.

In the examples that Pfennig (1998) discusses, there are overlaps between the sexual signals of the different species, e.g. call characteristics in anurans (Gerhardt 1994; Marquez & Bosch 1997; Pfennig 2000). This could make species recognition more difficult. However, even in cases in which there are categorical differences between species, preferences for characteristics found in heterospecifics have been found (McClintock & Uetz 1996; Basolo 1998; Jones & Hunter 1998). Least auklets (*Aethia pusilla*) are crestless, but respond more strongly to conspecific models with crests that are similar to two related species (Jones & Hunter 1998). Basolo (1990, 1998) showed that females of two non-sworded fish (*Xiphophorus maculatus* and *Priapella olmecae*) preferred conspecific males with an attached sword, found in a closely related, sworded species (*Xiphophorus helleri*). In the above cases, the preferences are probably due to a sensory bias for a particular ornament (Ryan & Rand 1993). Thus, female preference for ornamentation may affect the evolution of discriminatory mating preferences. This is called the 'ornamentation' hypothesis.

Similarities in behaviour and morphology may make some species more likely to respond to each other (Pfennig 1998, 2000; Grant *et al*. 2000). Pairs of species that are similar in appearance and behaviour are more likely to show heterospecific mate preferences than species whose behaviour and appearance are different (Gill & Murray 1972; Grant *et al*. 2000). This may be due to the difficulty of discrimination (Grant *et al*. 2000) or the conflict between quality and species recognition (Pfennig 1998). This is called the 'similarity' hypothesis.

Phylogenetic distance may also play a part over and above behavioural and morphological similarity. In general, similarity between species signals is measured by the experimenter in an objective way. However, objective similarity may not be as important as the possession of some specific signal characteristic. These specific signal characteristics are more likely to be found in closely related species (de Kort & ten Cate 2001), and so this is included as another potential factor that influences response to heterospecific individuals. This will be called the 'phylogeny' hypothesis.

These hypotheses are not mutually exclusive. Differences in tendencies to respond sexually to heterospecifics may be explained by one or more of the four hypotheses outlined already (reinforcement, ornamentation, similarity and phylogeny).

We tested which of the above factors influences mate choice in three species of closely related estrildid finch that differ in their degree of sexual dimorphism, phylogeny and behavioural–morphological similarity, and occur in both sympatric and allopatric populations.

(a) *Study species*

The study species are from the genus *Uraeginthus* found across sub-Saharan Africa. The blue breast (BB, *Uraeginthus angolensis*) is found across Southern Africa and the red-cheeked cordon bleu (RC, *Uraeginthus bengalus*) across Central Africa, with a small area of overlap. The blue-capped cordon bleu (BC, *Uraeginthus cyanocephalus*) is found from southern Somalia to central Tanzania; its range is encompassed within that of the RC and there is a small area of sympatry with the BB (Goodwin 1982). There are no known hybrids, but little work has been done in the sympatric zone (Goodwin 1982).

All three species have a brown–grey back, blue face–breast and pale pink–buff belly. The BB males and females are almost indistinguishable unless in the hand, when the male appears a slightly deeper blue. The RC male is distinguished from the BB male by the presence of a red cheek patch. The female RC lacks the cheek patch of the male and is a slightly paler blue. Female BBs and RCs are very difficult to distinguish, but the female RC has a slightly pinker beak. The BC male has a bright blue head and a red beak. The blue on the head is less extensive in female BCs and they are much paler blue than the males. Thus, the BC and RC are sexually dimorphic in both colour and morphology (see § 2). There is no dimorphism in any of the morphological characteristics measured in the BB (see § 2). There is almost some ultraviolet (UV) reflectance from the plumage and beak of all three species (measured with an Ocean Optic 2000 spectrophotometer, Ocean Optics Inc., The Netherlands), but no cryptic dichromatism (S.A.C., unpublished data).

The song and sexual display of all three species (both males and females sing) is very similar, although the song of the BC is higher in frequency (Goodwin 1982; S.A.C., unpublished data). Songs are individually distinct, and variable between individuals within a species (Goodwin 1982). Therefore, identification of species by song (except for the BC) is not straightforward, at least by human listeners. The BB and RC are morphologically and behaviourally more similar to each other than either is to the BC (Goodwin 1982; S.A.C., unpublished data) and they share a more similar colour pattern.

The phylogeny of the genus has recently been resolved (100% boostrap support), based on 1600 base pairs of mitochondrial DNA. The BC and the RC cordon bleu are more closely related to each other (2% divergence) than to the BB (4% divergence from both other species) which is basal to the other two species (M. D. Sorenson and R. B. Payne, unpublished data).

Female preference for a conspecific versus each of the two heterospecifics was tested in standard mate-choice trials (e.g. Collins *et al*. 1994; de Kogel & Prijs 1996; Witte & Curio 1999). We did not measure preference for two heterospecific males as it was wished to measure preference for heterospecific relative to conspecific males. In addition, we avoided presenting the females with two non-preferred individuals. The predictions of each of the four hypotheses for the outcome of the trials are given in table 1*a–d*.

2. MATERIAL AND METHODS

All three *Uraeginthus* feed on grass seeds and insect larvae in mixed-species flocks. They do not defend territories but defend

Table 1. Predictions of all four hypotheses.
(We make the assumption that there is a general tendency to prefer conspecifics in all four hypotheses. BB, blue breast; BC, blue-capped; RC, red-capped.)

| | stimuli set | | |
female species	BB–RC	BB–BC	BC–RC
(a) predictions of reinforcement hypothesis			
BB	no preference	no preference	—
RC	no preference	—	no preference
BC	—	no preference	prefer own species—strong
(b) predictions of ornamentation hypothesis			
BB	no preference or prefer RC	no preference or prefer BC	—
RC	prefer own species—weak	—	prefer own species—weak
BC	—	prefer own species—strong	prefer own species—weak
(c) predictions of similarity hypothesis			
BB	prefer own species—weak	prefer own species—strong	prefer own species—strong–medium
RC	prefer own species—weak	—	prefer own species—strong–medium
BC	—	prefer own species—strong	—
(d) predictions of phylogeny hypothesis			
BB	prefer own species	prefer own species	—
RC	prefer own species—strong	prefer own species—strong	prefer own species—weak
BC	—	—	prefer own species—weak

an area around the nest. They are opportunistic breeders (Goodwin 1982) and are thus easy to maintain in breeding condition.

(a) Sexual dimorphism

Morphological characteristics of the three species were measured for our captive populations. Measurements were conducted in accordance with British Trust for Ornithology standards.

RC males ($n = 11$) have longer tails ($t = 2.9$, $p = 0.008$, d.f. = 22) and wings ($t = 2.7$, $p = 0.01$, d.f. = 22) than females ($n = 13$).

BC males ($n = 9$) have longer tails ($t = 4.5$, $p < 0.001$, d.f. = 18), are heavier ($t = 2.4$, $p = 0.03$, d.f. = 18) and have deeper ($t = 2.4$, $p = 0.03$, d.f. = 18) and wider ($t = 2.3$, $p = 0.03$, d.f. = 18) beaks than females ($n = 11$).

BB males ($n = 8$) do not differ from females ($n = 9$).

(b) Animals and housing conditions

Subjects were housed in cages (60 cm × 40 cm × 40 cm) containing eight individuals of one sex. Species were in visual but not acoustic isolation. All subjects were wild caught, therefore their breeding history is unknown. They were bought from reputable bird suppliers (San Bob Aviaries, Wigan, UK; Pegasus Birds, Essex, UK). The BBs and RCs were from South Africa and West Africa, respectively (exact location unknown). The BC is always sympatric with the RC but these individuals were from Kenya where they are allopatric to the BB (exact location unknown). Therefore, our populations of RCs and BBs are allopatric to each other, and the BC population is allopatric to the BB and sympatric with the RC.

Food and water were provided *ad libitum* and mealworms (*Tenebrio molitor*) and garden cress (*Lepidium sativum*) were provided regularly. The birds were maintained on a 14 L : 10 D cycle using tropical daylight tubes (includes UV frequencies). These lights were used in both the observation and the housing rooms. Temperature was maintained at 28 ± 5 °C.

(c) Experimental treatment

There were three stimuli sets of males used in the choice trials. Each set consisted of four pairs of males of two species as follows:

(i) *U. angolensis–U. bengalus*;
(ii) *U. angolensis–U. cyanocephalus*; and
(iii) *U. bengalus–U. cyanocephalus*.

It was planned to present all females with two stimuli sets, but some females became unwell during the experiment (cause unknown) and were removed. Therefore, although each female saw all four pairs of males from one stimuli set, different individuals were presented with each of the two sets as follows:

(i) *U. angolensis* females—sets 1 ($n = 7$) and 2 ($n = 6$): eight different females in total;
(ii) *U. bengalus* females—sets 1 ($n = 8$) and 3 ($n = 8$): 12 different females in total; and
(iii) *U. cyanocephalus* females—sets 2 ($n = 7$) and 3 ($n = 8$): 11 different females in total.

(d) Experimental procedure

Mate-choice trials were conducted in a pair-wise choice chamber. This consisted of a large central chamber (80 cm × 40 cm × 40 cm) with a mesh-covered front and sides. Food and water were provided in the centre of the cage. At either end of the choice chamber two movable mesh-fronted wooden stimulus cages were positioned. Each cage contained two perches. Lighting was enhanced by installing an extra strip light (tropical daylight) directly above the choice chamber.

Before the trials began, the experimental females from one species were placed as a group for 24 h in the choice chamber, in order to familiarize them with the apparatus. They were returned to their cage in the housing room for at least 24 h

before the start of the study. Males were placed in the stimuli cage and females in the choice chamber for 20 min before a trial to acclimatize them to the cage. An opaque barrier was placed between the males and female during the acclimatization period.

In each trial, a female was placed in the central chamber and two males (one a conspecific, one a heterospecific) in the stimuli cages. Each male was provided with five pieces of coconut fibre of standard size (8 cm), with which to display (males display by singing, whilst bouncing and holding a piece of straw in the beak). After acclimatization the barriers were removed for 40 min. The stimuli cages were exchanged after 20 min to control for side preferences.

Observations were made from behind a curtain using two stopwatches and a check sheet. The following behaviours were recorded:

(i) time spent by the female on the perch in front of the conspecific male and facing towards him (T_c);
(ii) time spent by the female on the perch in front of the heterospecific male and facing towards him (T_h);
(iii) the total time each male spent displaying; and
(iv) the number of solicitation displays by the female.

For each female the following averages (across the four trials) within each stimuli set were calculated using the measures taken above:

(i) percentage of time spent by conspecific mate

$$P_c = \frac{100 T_c}{T_c + T_h};$$

(ii) total amount of time spent choosing (measure of interest in choosing)

$$T_t = T_c + T_h;$$

(iii) number of solicitations to conspecific mate S_c; and
(iv) number of solicitations to heterospecific male S_h.

Each of the four pairs of males was presented to subject females of two species. Four trials were conducted per day in the active period of the finches (09.00–14.00). No individual was used more than once per day. Trials were balanced within species with respect to order, time of day and condition.

(e) Measurement of male display

In order to test for differences in male display duration between the three species males of all three species were presented to a conspecific female, and display duration over a 40 min period was measured. Display rate in the experimental trials is not a suitable measure, due to the fact that male display may depend on female preference (zebra finches: Collins *et al.* 1994), and could be a measure of male preference (zebra finches and Bengalese finches: ten Cate & Mug 1984).

(f) Analysis

Normality was tested using a Shapiro–Wilk's test. The number of solicitations and the number of male displays to conspecific females were not normally distributed.

A one-way ANOVA was performed with 'chooser species' as a factor in order to test for general differences during the choice trials between females of different species. Differences in male display rate of the three species were tested using a Kruskal–Wallis test with male species as the independent variable.
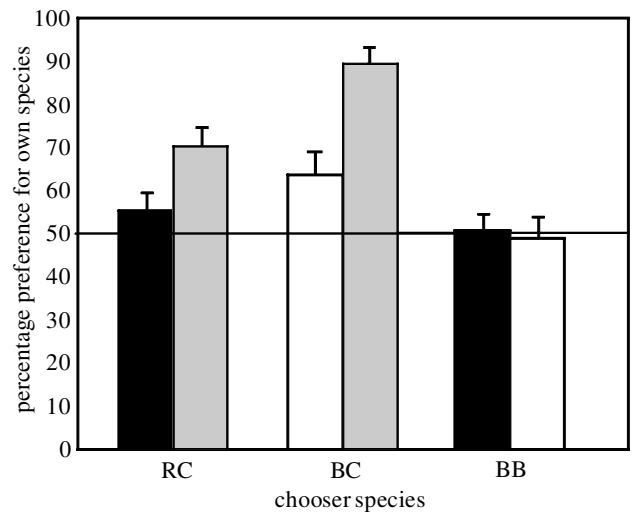
Figure 1. Mean ± s.e. percentage preference for own species when paired with each of the other two heterospecifics. Black, heterospecific BC; white, heterospecific RC; hatching, heterospecific BB.

Within each chooser species, the percentage preference for own species (P_c) in the two stimuli set conditions (i.e. paired with one or the other heterospecific male) was compared using an independent sample *t*-test. (Due to the fact some females were not exposed to both stimuli sets, we could not use a paired *t*-test).

A one-sample *t*-test against a mean of 50% was used to test whether females of a particular species showed a preference for their own species within each of the two stimuli sets to which she was exposed (dependent variable, P_c). For each chooser species, a Wilcoxon test was used with comparable solicitations to conspecific (S_c) versus heterospecific (S_h) males for both stimuli sets.

All tests were conducted on Spss v. 9.0.

3. RESULTS

(a) Overall results

There was a significant difference between P_c ($F_{2,41}$ = 12.5, $p < 0.001$: see figure 1) and T_t ($F_{2,41}$ = 9.9, $p < 0.001$) depending on choosing species (BB = 290 ± 53 s; RC = 528 ± 44 s; BC = 302 ± 31 s).

There were no differences in the total number of solicitations given by the three species (Kruskal–Wallis, not significant). Overall there was no significant difference in the S_c and S_h (Wilcoxon, $n = 44$: mean $S_c = 0.32$, mean $S_h = 0.26$). There was no significant difference in the amount of male display between the three species in a conspecific situation (Kruskal–Wallis; $p > 0.5$).

(b) Specific responses

(i) BB females

There was no difference in P_c, between the two stimulus sets. In both stimuli sets, P_c was not significantly different from 50% (figure 1: BC mean ± s.e. = 51 ± 4.0%, with RC mean ± s.e. = 49 ± 5.1%).

T_t was greater when conspecific males were paired with a RC male ($t = 3.7$, d.f. = 6.5, $p = 0.009$). There were no differences in S_c and S_h.

Table 2. Results of the experiments.

	stimuli set		
female species	BB–RC	BB–BC	BC–RC
BB	no preference	no preference	—
RC	prefer own species—70% (moderate)	—	no preference
BC	—	prefer own species—90% (strong)	prefer own species—64% (weak)

(ii) *RC females*

There was a significant difference in P_c depending on the stimulus set ($t = 2.32$, $p = 0.04$, d.f. = 14; see figure 1). P_c was significantly different from 50% when paired with the BB (one-sample t-test, $t = 4.2$, d.f. = 7, $p = 0.004$, mean ± s.e. = 70 ± 4.8%), but not when paired with the BC (mean preference = 55 ± 4.2%).

There was no difference in T_t between the two stimuli sets. There were fewer solicitations to BB than towards conspecific males (Wilcoxon: $z = 2.3$, $p = 0.02$, $n = 8$). There was no significant difference between solicitations to BC and conspecific males.

(iii) *BC females*

We found a significant difference in P_c by stimuli set ($t = 4.5$, $p = 0.001$, d.f. = 13; see figure 1). In both cases, P_c was significantly above 50% (BB: mean ± s.e. = 90 ± 2.6%, $t = 14.9$, $p < 0.001$, d.f. = 7; RC: mean ± s.e. = 64 ± 5.3%; $t = 2.55$, $p = 0.04$, d.f. = 6).

There was no difference in T_t between the two stimuli sets. There were no differences in S_c and S_h within a stimulus set.

4. DISCUSSION

We found that BB females showed no preference for males of their own species over those of heterospecific males. BC females preferred their own species under all conditions, but the preference was especially strong when the heterospecific was a BB male. RC females preferred their own species when paired with a BB male, but not when given a choice between a conspecific and a BC male (see table 2). Each of the hypotheses outlined in § 1 gave a different set of predictions. Table 1a–d shows the predicted outcome by, respectively, the reinforcement, ornamentation, similarity and phylogeny hypotheses. The predictions can be compared with the actual results in table 2.

As can be seen from table 1a, the reinforcement hypothesis was not supported by our results, except for BB females. The ornamentation hypothesis was supported by the results (table 1b). BC females had a weaker preference for conspecifics when paired with the more ornamented RC males than the dull BB males. Female RCs showed a strong preference for their own species when paired with the dull BB males, but showed no difference in preference for their own species compared with BC males. We had predicted a weak preference for conspecific males, and in this respect they differ from the BC females who preferred conspecifics to RC males. There are two explanations.

First, our RC females were from an allopatric population, and thus reinforcement cannot have occurred, as it may have done in the BC females. Second, perhaps the BC males are more intrinsically attractive than RC males. Female BBs reacted as strongly to ornamented male heterospecifics as they did to conspecifics. Both heterospecifics appeared to be equally attractive.

There was no support for the similarity hypothesis (table 1c). The phylogeny hypothesis (table 1d) was not supported by the results from the RCs and BBs. Only the results from the BCs supported the phylogeny hypothesis (de Kort & ten Cate 2001).

In all previous experiments in which preference for heterospecific signals or individuals has been tested, either artificial stimuli have been used (e.g. Basolo 1990, 1998; Ryan et al. 1990) or heterospecifics have been separated by a barrier (Ryan & Wagner 1987; McClintock & Uetz 1996). When contact occurs heterospecifics do not mate, because other cues to species identity allow discrimination (e.g. Ryan & Wagner 1987; McClintock & Uetz 1996). In our study, sexual response to heterospecifics is found in the presence of a conspecific in a situation allowing full contact. The response is unlikely to be due to the difficulty of species recognition versus quality recognition (Pfennig 1998) as there are categorical differences between the males of the three species. It is possible that there is a sensory bias (Ryan & Rand 1993) in this genus for red to be more attractive—both the RCs and BCs have red ornaments (cheek and beak, respectively). The BB female preference could be due to the presence of red in the other two species. However, the possession of a red ornament alone is not enough to elicit a sexual response. None of the three species showed any response to the common waxbill (*Estrilda astrid*), a more distantly related estrildid finch with red ear patches (S.T.L. and S.A.C., unpublished data). A related hypothesis is that the female BB may retain an ancestral preference. There are several closely related ornamented species (e.g. *Granatina* spp.), so it is possible that ornamentation was lost in the BB (see references in Wiens 2001), but that the female preference for ornamented males has not yet been lost.

A final possibility for our results is indicated by the 'chase-away' hypothesis of Holland & Rice (Rice & Holland 1997; Holland & Rice 1998) who suggest that male ornaments evolve to exploit pre-existing biases in females, and that this causes females to mate suboptimally, in turn giving rise to the evolution of resistance (to being stimulated by male ornaments) in females. Holland & Rice predict that, in closely related species, females from the species with ornamented males will in

fact show less interest in males with larger ornaments than individuals from species whose males are not ornamented due to the evolution of resistance in the former species. This idea has support from the results of Morris *et al.* (1996), McClintock & Uetz (1996) and Basolo (1998). It is possible that BC and RC females are resistant to 'male advertising', whereas BB females are not. In order to confirm this hypothesis we would need to show, for example, that males with larger, or redder, cheek patches elicited increased attention from BB females but not from RC females. The above hypotheses are now being investigated.

There are no differences in the duration of male display between the three species when presented with conspecific females. Therefore, it can be assumed that the results are not caused by differences in species' activity levels (ten Cate & Mug 1984).

Overall, the hypothesis that a response towards con- and heterospecific males is influenced by the level of ornamentation (whether red specifically, or ornamentation generally) with some effect of reinforcement, best explain our results. No effect of behavioural–morphological similarity was found and the reinforcement hypothesis alone was also not supported. We do not know whether hybrids between any two of the three species are at a disadvantage; therefore, it is possible that reinforcement is unlikely to occur in this species group (Servedio & Kirkpatrick 1997; Kirkpatrick 2000). However, the BC occupies drier habitat than the other two species and feeds on harder seeds (Goodwin 1982), and thus has a more robust beak. Feeding efficiency and thus fitness may be compromised in BC and RC or BB hybrids.

In conclusion, when females of closely related species that have many of the same secondary sexual characteristics choose between con- and heterospecific males they have a bias towards the more ornamented males that interferes with their preference for their own species. This bias is only partially extinguished in sympatry (BC females still respond more to RC than BB males). When secondary contact occurs and previously allopatric populations re-encounter each other we may expect that species with less-ornamented males are more likely to show a reaction towards heterospecific males. Therefore, hybridization will be asymmetrical. Of course male preferences will also influence the possibility of hybridization, but we found that BC and RC males show relatively weak preference for conspecific females (means 65 and 56%, respectively; S.T.L. and S.A.C., unpublished data).

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