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"A Taste for the Beautiful": Latent Aesthetic Mate Preferences for White Crests in Two Species of Australian Grassfinches

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ABSTRACT: Darwin first hypothesized that bright colors and elaborate ornamentation of male animals evolved in response to the "aesthetic" mate preferences of females. By this reasoning, potentially costly male secondary sexual traits may evolve not in response to selection for demonstration of vigor but, rather, in response to latent, nonfunctional preferences by females. Recent comparative evidence for this phenomenon is equivocal. Here we present experimental evidence that two avian species from a lineage devoid of crested species have mate preferences for opposite-sex conspecifics wearing artificial white crests. Other colors of crests that have been studied are not preferred. Preferences for white crests did not diminish over the longest experimental interval (12 wk). These results are additional powerful evidence for highly structured aesthetic mate preferences in estrildine finches. Sex differences in the expression of preferences, and the widespread occurrence of facial ornamentation in birds, suggest that the preference "structure" is influenced by the central nervous system. We hypothesize that aesthetic preferences are a potent force in the early evolution of sexually selected traits, and that "indicator" traits evolve secondarily from traits initially favored by aesthetic preferences.

Keywords: sexual selection, aesthetic mate preferences, estrildine finches.

Over the past decade, several authors have suggested that organisms possess latent mate preferences for traits that have yet to evolve (Burley 1985, 1986*b*, 1986*c;* Rowland 1989; Basolo 1990; Ryan and Keddy-Hector 1992). These preferences, which are thought to be caused by properties of neurophysiological/sensory systems (e.g., Endler 1993; Enquist and Arak 1993), provide structure to the evolution of species-specific and secondary sexual traits by constraining the evolution of unfavored (unattractive) traits and favoring nonfunctional attractive traits (Burley 1985). These ideas are in keeping with Darwin's conclusion that many secondary sexual traits are fundamentally not understandable through viability selection. Instead, Darwin (1874) ascribed the origin of such traits to unexplained "aesthetic" mate preferences possessed by female conspecifics.

Historical Perspective

From Darwin's time to the present, an interesting intellectual circle has been completed: Fisher (1930) argued that aesthetic mate preferences evolved from functional ones (see Andersson 1994 for recent variants on this idea); proponents of "good genes" models of sexual selection have hypothesized that differential expression of secondary sexual traits typically functions to indicate genetic or physiological quality of the bearers of the traits (e.g., Zahavi 1975; Hamilton and Zuk 1982; Kodric-Brown and Brown 1984), a view that discounts the role of aesthetic preferences. Most recently, authors have suggested nonfunctional hypotheses that mirror Darwin's. These include hypotheses invoking "sensory bias" and "sensory exploitation."

"Sensory bias" implies an underlying neurophysiological bias that has an "accidental" influence on mate preference. Burley (1985, p. 31) hypothesized that sensory bias was ubiquitous: "The sensory system of any species will . . . be preadapted to perceive some not-yet-evolved stimulus in a particular way." Over the last decade there has been a proliferation of approaches to the concept of sensory bias, including environmental influences on sensory structure (e.g., Endler 1992; Marchetti 1993) and psychological and psychophysical considerations (e.g., Guilford and Dawkins 1991; Arak and Enquist 1993). "Sensory exploitation" implies capitalization by one group on the sensory biases of another. Thus, males evolve secondary sexual traits that "exploit" the mate preferences of females (e.g., Ryan and Keddy-Hector 1992).

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Aesthetic versus Functional Preferences

Models in which latent mate preferences produced through various neurophysiological phenomena have the potential to drive the evolution of sexually selected traits can be parsimoniously classed together as "aesthetic" (Burley 1985, 1986*c*) in deference to Darwin's articulation of the idea that a vast array of secondary sexual traits evolved in response to a "taste for the beautiful" (Darwin 1874, p. 469), widespread among vertebrates and resulting from the organization of the "nerve cells of the brain" (Darwin 1874, p. 705). Aesthetic preferences, then, are emergent properties of the central nervous system and sensory systems that originated incidentally, not through active selection on mate preferences. They can be contrasted with "functional" mate preferences that have evolved through direct selection on mate preferences that enhance offspring numbers and/or viability.

While functional and aesthetic preferences are clear conceptual alternatives, we view them as complementary evolutionary agents. Aesthetic preferences may account for the early evolution of traits, while functional preferences may shape their subsequent amplification. Functional models, notably "good genes" models, typically fail to account for the origin of sexually selected traits. That is, for example, a random mutation conferring a red spot on the crown of a bird does not constitute an indicator trait; indicator status has to evolve subsequently. However, neither the red spot nor its indicator status can easily evolve in the absence of mate preferences or some other active agent. By contrast, aesthetic mate preferences can favor the establishment of novel traits arising through mutation, particularly if the reservoir of latent aesthetic preferences in a population is large. Thus, documentation of latent aesthetic preferences will greatly enhance our understanding of sexual selection and speciation processes.

Measuring Aesthetic Preferences

Contemporary evidence for latent aesthetic preferences comes from two research approaches. One line of evidence involves comparison of preferences of related species with differing secondary sexual traits. Basolo (1990), for example, studied poeciliid fishes of the genus *Xiphophorus,* in which an elongated caudal fin or "swordtail" is a common secondary sexual trait. She found that females of a species lacking swordtails (*X. maculatus*) preferred males with artificial tails and concluded that her results were evidence for "sensory bias." Meyer et al. (1994) criticized this interpretation on the basis of a molecular phylogeny that suggested the swordtail was present in the common ancestor of the genus. Similar ambiguity of evidence for other cases (e.g., Ryan et al. 1990; Shaw 1995) points out the chicken-versus-egg dilemma inherent in this approach: because phylogenetic analysis is subject to revision, and the origin and antiquity of extant traits cannot be determined with precision, comparisons involving closely related species may not provide unambiguous evidence for preexisting preferences.

An alternative approach is to demonstrate the occurrence of mate preferences for truly novel traits—those with no expression within a taxon. This approach has been taken by Burley and colleagues in a series of experiments on zebra finches (*Taeniopygia guttata*), a socially monogamous, sexually dichromatic species. In zebra finches, leg band color affects mating attractiveness of both sexes to conspecifics (Burley 1985, 1988*b*). These preferences are not predictable simply on the basis of existing species-specific and secondary sexual traits (Burley 1985). Mate preferences for novel traits are sufficiently strong to affect social (Burley 1986*c*) and genetic (Burley et al. 1996) parentage. Moreover, individuals whose attractiveness has been altered by color banding spontaneously develop mating tactics consistent with their attractiveness (Burley 1986*b,* 1988*a;* Burley et al. 1994, 1996). Thus, "mutant" attractive traits could readily increase in frequency in response to aesthetic mate preferences. Preferences for novel leg band colors have also been found in other estrildines (e.g., Burley 1986*a*) and in nonestrildine finches (Johnson et al. 1993).

Crests and Grassfinches

Here we report results of experiments performed to determine whether estrildine finches have latent mate preferences for novel ornaments in any other body region. We focused on the head because crests, or "elongated feathers originating from the avian forehead, crown, and/or nape," have evolved repeatedly among avian lineages (Armstrong 1947; Morris 1956; Gill 1990). Crests occur in at least 20 of the 30 orders of extant birds, and in all major groups of passerines (N. T. Burley, unpublished data).

Grassfinches, however, lack crests; indeed, there are no crested species in this group (Estrildidae [Goodwin 1982] or Estrildinae [Sibley and Ahlquist 1990]), which contains about 120 extant species (Goodwin 1982). The closest relatives are the viduines (fewer than 15 species, all uncrested) and the ploceine weavers (about 110 species). Among the weavers, crests occur rarely (*Malimbus malimbicus* has a well-defined crest; males of several *Euplectes* species have elongated nape feathers [Serle et al. 1977]). Based on DNA-DNA hybridization evidence, the estrildine and ploceine lineages diverged 20–25 million years ago (Sibley and Ahlquist 1990). Thus, if preferences for

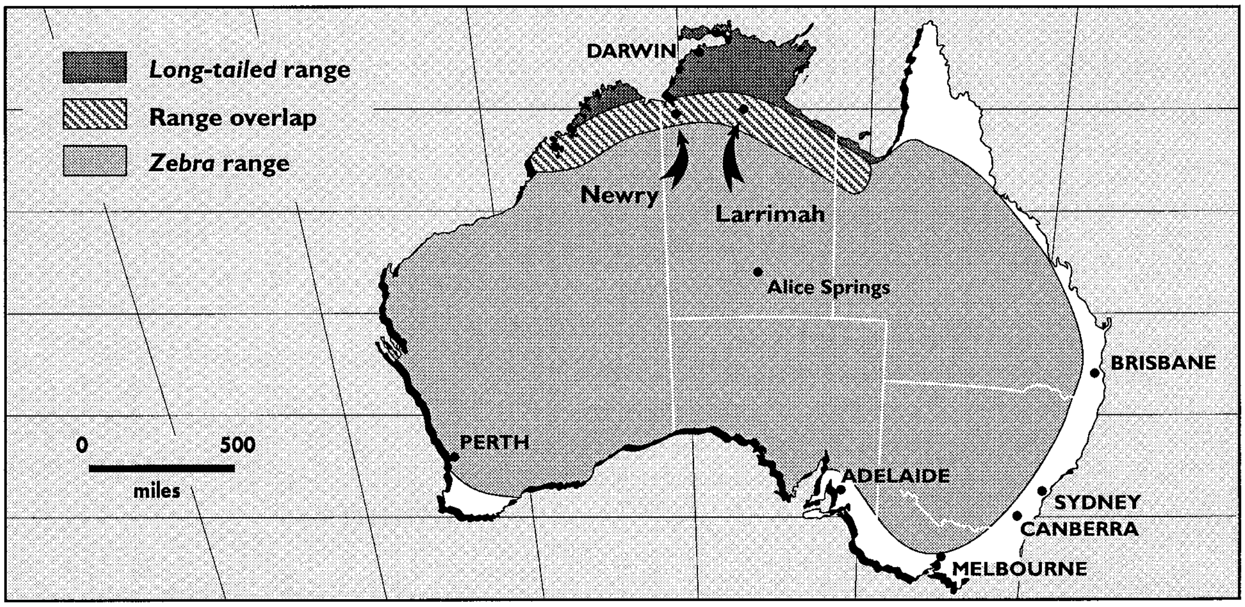

Figure 1: Distribution of zebra finches and long-tailed finches in Australia (after Pizzey 1980). Long-tailed finches employed in experiments 2 and 3 were first-generation, captive-reared offspring of birds captured at two sites in the Northern Territory: Newry, a cattle ranch, and Larrimah, a small town.

crests occur in extant grassfinches, they did not coevolve with crests; rather, the preferences are either "preexisting" or, if they evolved in some remote, crested ancestor, they have somehow survived vast spans of evolutionary time without expression.

We tested the preferences for crested, opposite-sex conspecifics of two grassfinch species: zebra finches (*Taeniopygia guttata castanotis*) and long-tailed finches (*Poephila acuticauda*). These species have typically been considered congeners or members of sister genera (Goodwin 1982), but more recent analysis (Christitis 1987) suggests they may be somewhat less closely related. Zebra finches range widely over the continent of Australia (fig. 1), but no regional variation in plumage patterns or soft-part coloration has been found (Keast 1958; N. T. Burley, unpublished data). Long-tailed finches live in a longitudinal belt across the Northern Territory and Western Australia. The zebra finch occurs, albeit uncommonly, throughout much of the breeding range of the long-tailed finch (fig. 1).

Long-tailed finches are often characterized as having two distinct subspecies, *hecki* and *acuticauda.* Birds of the *acuticauda* type have yellow-orange beak, whereas those of the *hecki* type have bright red beaks. In actuality, beak color shows continuous variation in the Northern Territory. Moreover, populations trapped at intervals 100 km apart show other distinctive characteristics (N. T. Burley and R. Symanski, unpublished data). In 1992, we captured birds at two locations in the Northern Territory (fig. 1) and exported them under permit to the United States. Birds from Larrimah have bright red beaks, small bibs and are sexually indistinguishable (Burley 1981*a*, 1986*a*). Birds from Newry have yellow-orange beaks, larger bibs, and are mildly sexually dimorphic in plumage traits. These differences persist among first and second laboratory-hatched generations; thus, major population differences are not the result of environmental variables such as diet. In captivity, birds will not readily form pair-bonds with individuals from the opposite population (N. T. Burley, unpublished data).

Three experiments measured heterosexual social preferences using a design previously established to measure mate choice (Burley 1986*a;* Burley et al. 1994, 1996). Birds were given choices of four opposite-sex social partners having randomly assigned experimental phenotypes (e.g., crests of various colors). The major goals of the experiments were to determine whether members of an uncrested lineage have preferences for or aversions to crests, and whether there are species and/or population differences in preference. An additional goal of the third experiment was to assess individual variation in preference for crests.

Experiment 1: Zebra Finches

Domesticated, wild-type zebra finches maintained in N. T. Burley's laboratory (effective population size greater than 100 individuals) were presented with opposite-sex stimulus sets composed of four individuals. Stimulus sets were matched for natural phenotypic variation (beak color, weight, and activity level). Three birds within a set were assigned crests using a stratified random design; the fourth bird was not crested.

Crest colors were selected on the basis of color-band preferences previously measured (Burley 1985) and reflect the range of responses to color bands shown by zebra finches. Each male stimulus set contained a red-crested individual (red leg bands are attractive to females), a white-crested one (white leg bands are neutral), and a green-crested bird (green is unattractive). The crest colors used for female zebra finch stimulus sets were similarly selected: black is a leg band color preferred by males, white is neutral, and light blue is unattractive.

Methods

The general methodology for measuring preferences has been previously detailed (Burley 1986*a* and references therein).

Crests were made by weaving together tiny ("seed") beads into a platform in which a feather, either a rectrix (from an estrildine or small psittacine) or contour feather (from a psittacine), was glued in an upright position. Platform color was closely matched to that of the feather, except for "black" crests, in which the bead platform was black, but the feather was dark gray. (Black feathers were not available.) Within stimulus sets, crests were closely matched for feather size and shape; trimming of feathers was sometimes employed to achieve uniformity. Feathers with uneven coloration were "touched up" with artist-quality water-based markers. When this was done, marker was lightly and uniformly applied to the entire feather. The procedure was employed for all of the red feathers used, and about half of the gray feathers, but not the blue or green ones. Crests weighed about 0.3 g, or approximately 2.4% of bird weight.

Crests were affixed with water-based glue to the crown feathers of stimulus birds (fig. 2). Most stimulus birds "accepted" (stopped trying to dislodge) their crest within 30 min of application; those that persisted in attempting to remove the crest were removed from the experiment. We repaired crests when feathers became bent, broken, or frayed. When a crest was damaged beyond repair or if a stimulus bird lost its crown feathers when its crest fell off, we discontinued use of the stimulus set.

Never-mated adults in excellent phenotypic condition were used as test birds. After test birds were acclimated to the apparatus (Burley 1986*b*), test birds received 48 h of exposure to the test phenotypes (in the experimental apparatus) before testing. Then they were tested in 2-h trials. Trials were considered successful when test birds logged 2,000 s or more of social time with stimulus type(s) and no technical failures (e.g., burned-out lightbulb) occurred. Test birds that failed to reach the 2,000-s criterion were retested up to three times (if necessary) with the same stimulus set (in no more than one trial per day); likewise, trials with technical failures were repeated on another day.

Figure 2: Artificial white crest worn by male long-tailed finch (*left*) and male zebra finch (*right*) during mate choice trials. Photo credit: Kerry Clayman.

Five stimulus sets were employed in the measurement of female choice, six for male choice, and no individual was used in more than one stimulus set. Each test bird was tested with two stimulus sets, and its response (percent of social time spent with each stimulus type) was averaged over the two trials before analysis. We attempted to use each stimulus set the same number of times, but it was often not possible to do so for reasons such as the necessity to "retire" some stimulus sets early (see above) or the availability of an odd number of test birds.

Birds were maintained on a 14L:10D photoperiod. Lighting was provided by four 100-W incandescent bulbs.

Results

Female zebra finches ($N = 15$) preferred white-crested males over other stimulus types (fig. 3*A;* Friedman test,

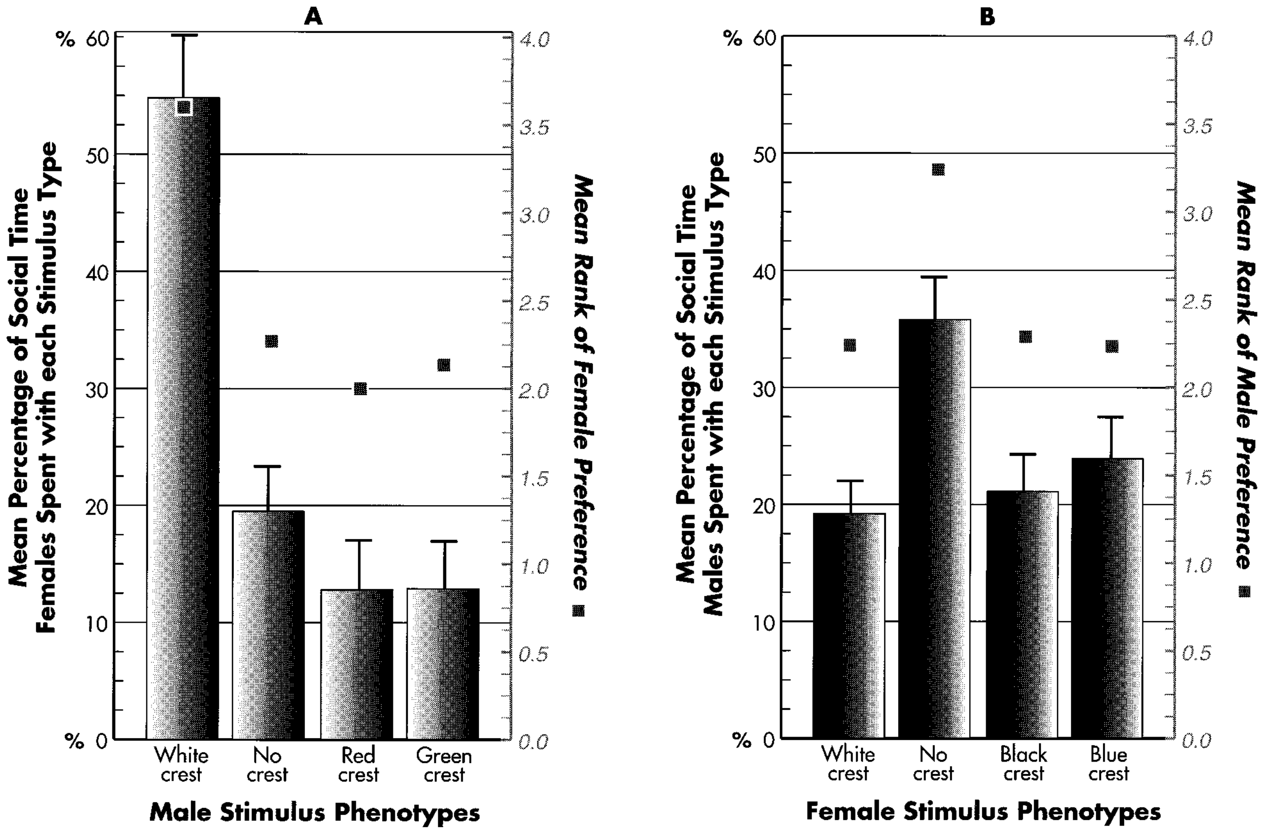

Figure 3: Mate preferences of zebra finches for nonornamented ("No crest") versus artificially crested conspecifics. Bars represent the mean proportion (+SE) of time spent in social contact with each stimulus type; dots represent mean within-trial rank of social preferences (1–4, with 4 being most preferred). *A*, Female preference for males. *B*, Male preference for females.

$\chi^2 = 14.84$, $P = .002$) and did not discriminate between uncrested males and those wearing other colors of crests. White-crested males averaged the greatest percentage of social time in four of the five stimulus sets (range of means: 47.2%–73.2% of all social time); in the fifth set, the uncrested male received the most social time (42.1%), with the white-crested male in second place (37.5%). Three sets contained males with rounded crests (including the one set with the second-place finish for white crests), and two sets contained males with vertical crests. Each stimulus set was used in four to eight successful trials ($\bar{X} = 6.0$).

Male zebra finches ($N = 21$) preferred uncrested females to crested ones (Friedman test, $\chi^2 = 9.17$, $P = .027$) and did not discriminate among crest phenotypes (fig. 3*B*). Each stimulus set was used in six to nine successful trials ($\bar{X} = 7.0$).

Experiment 2: "Larrimah" Long-Tailed Finches

Birds used in this experiment and in experiment 3 were first-generation, captive-hatched adult offspring of wild-caught birds. The effective population size in each population was about 50 birds.

Crest colors were selected (1) to determine whether preferences for white crests existed and (2) to maximize the chance of finding a preferred crest color other than white. Red was selected because birds tested from this population are attracted to red-beaked and red-banded conspecifics (N. T. Burley, unpublished data). Light blue was selected because it accentuates the distinctive blue-gray cap of the long-tailed finch.

Methods

With the following exceptions, methods used for testing were identical to those of experiment 1. In this experiment, only white finch rectrices were used: red and blue feathers were created using water-soluble marking pens. Also, the crests weighed less (about 0.15 g, or 1.4% of bird weight). Trials were of 1-h duration, and the minimum social time criterion was 1,000 s. Lighting was provided by fluorescent fixtures containing Vita-light balanced-spectrum tubes that emit near ultraviolet as well as

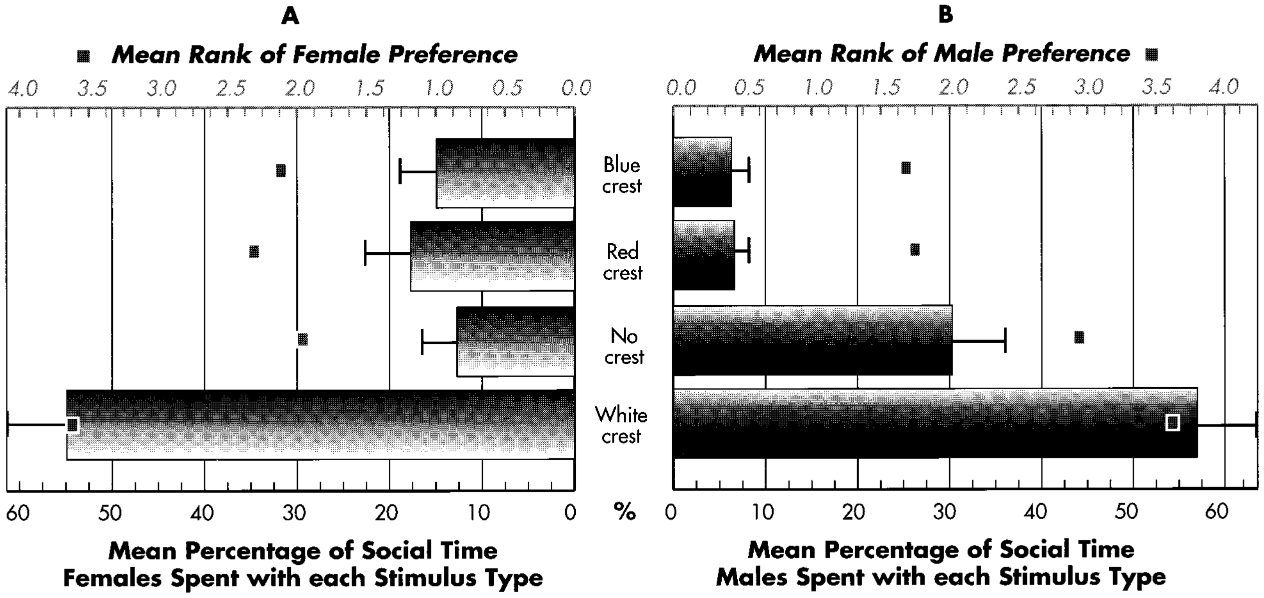

Figure 4: Preferences of Larrimah long-tailed finches for nonornamented ("No crest") versus artificially crested conspecifics. Bars represent the mean proportion (+SE) of time spent in social contact with each stimulus type; dots represent mean within-trial rank of social preferences (1–4, with 4 being most preferred). *A*, Female preference for males. *B*, Male preference for females.

wavelengths visible to humans. The fixtures were covered with diffusers, however, which probably blocked UV transmission.

Before experimentation, the sex of each individual was ascertained by repeated observation of birds (only males sing). Trials were monitored to verify that both test and stimulus birds behaved in sex-appropriate ways (Burley 1986*a*). Four male stimulus sets and five female stimulus sets were employed.

Results

Both sexes of this sexually monomorphic population displayed preferences for white crests. The response of females ($N = 13$) was indistinguishable from that of female zebra finches: white crests were strongly preferred ($\chi^2 = 13.41$, $P = .004$), and no discrimination was made among the remaining phenotypes (fig. 4*A*). Each stimulus set was used in six or seven ($\bar{X} = 6.5$) successful trials. Males ($N = 15$) displayed an aversion to red and blue crests as well as a preference for white ones vis-à-vis uncrested stimuli ($\chi^2 = 25.72$, $P < .001$; all a posteriori multiple comparisons between no crest and crest types are statistically significant; fig. 4*B*). Each stimulus set was used in four to seven successful trials ($\bar{X} = 6.0$).

Experiment 3: "Newry" Long-Tailed Finches

Females were allowed to choose between uncrested and white-crested males. This experiment had several goals: (*a*) to ascertain whether "Newry" females also prefer white-crested males; (*b*) to ascertain whether prolonged exposure to white-crested males would alter female preference; (*c*) to ascertain whether females preferred males wearing only the beaded base over uncrested males; and (*d*) to explore the possibility of individual variation in preference for white crests. This last goal was facilitated by presenting test birds with two stimulus individuals of each experimental phenotype. This test design reduces intraindividual variation in test bird response across stimulus sets, probably because the effect of a test bird's preferences for or aversions to specific stimulus individuals is reduced. That is, a test bird is less likely to find both individuals of a given stimulus type highly aversive or attractive.

Methods

In experiment 3.1, each of 13 adult females was tested with two of four stimulus sets, each consisting of two white-crested and two uncrested males. For each 1-h trial, percentage of time spent with the two males having the same phenotype (white crested vs. uncrested) was summed before analysis. Individual preference was measured as the average response over a female's two trials.

After completion of experiment 3.1, each female was housed in one of two viewing cages placed between two cages containing males from the stimulus sets used above. The six females in viewing cage A were exposed to the males from stimulus sets 1 and 2, with the crested males in a cage physically abutting one side of the female cage, and the uncrested males in a cage on the other side of the female cage. Thus, uncrested males could interact with one another, and crested males could interact with one another, but physical interactions between crested and uncrested males were not possible. At the same time, the seven females in viewing cage B were exposed to the males from stimulus sets 3 and 4 in an identical fashion. After 3 wk, the male stimulus sets were switched between female viewing sets, so that females saw a new group of males (i.e., male sets 3 and 4 were placed with females in viewing cage A, and male sets 1 and 2 were placed with females in cage B).

After an additional exposure interval of 3 wk, females were tested in experiment 3.2 for their preference of white-crested versus uncrested males. Each female was tested with one of two newly created male stimulus sets (5 and 6). None of the males in the original four sets were in the new sets.

Upon completion of experiment 3.2, the feathers of crested males in stimulus sets 5 and 6 were cut at the point of attachment to the beaded platform. Then, in experiment 3.3, each female was tested for her preference of "featherless" versus uncrested males. Here each female was exposed to the stimulus set (5 or 6) that she had not viewed during experiment 3.2.

Before the start of experiment 3, diffusers were removed from the fluorescent fixtures over the experimental chambers, making light in the near UV available. In experiment 3, feathers used in crests were white finch primaries, rather than rectrices. Primaries resist breakage better than rectrices. Previously, rectrices had been used preferentially because they appear somewhat more symmetrical than primaries.

In all steps of this experiment, each stimulus set was used in either six or seven ($\bar{X} = 6.5$) trials.

Results

In experiment 3.1, all 13 females spent a majority of social time with white-crested males (Wilcoxon $z = -3.184$, $P = .001$; mean percentage of social time spent with white-crested males ["mean preference"] = 80.4%). In experiment 3.2, 12 of 13 females spent a majority of social time with white-crested males (Wilcoxon $z = -2.909$, $P = .004$; mean preference = 86.5%). There was no difference in mean preference for white-crested males between experiments 3.1 and 3.2 (Wilcoxon matched-pairs test, $P = .53$). Averaged over all three trials, 12 of 13 females preferred white-crested males (Wilcoxon $z = -3.110$, $P = .002$; mean preference = 82.4%).

Females did not show significant between-individual variation in response in the three trials of experiment 3.1 and 3.2 (repeated-measures ANOVA: model $F = 1.803$, df = 2, 24, $P = .19$). Nor did individual females display repeatable preferences (linear polynomial $F = 0.208$, df = 1, 12, $P = .66$; quadratic polynomial $F = 2.58$, $P = .13$).

In experiment 3.3, eight of 13 females spent a majority of social time with featherless males. This result does not deviate from chance expectation (Wilcoxon $z = -0.455$, $P = .65$; mean preference for featherless males = 58.4%). Thus, female preference for crested males cannot be accounted for by a preference for the beaded platform alone.

Discussion

Alternative Explanations for Preferences

The existence of preferences for crests in a taxon devoid of them is powerful evidence that mate preferences can have their origin in nonadaptive neurophysiological processes. Moreover, the similarity of response by females of two grassfinch genera suggests that phylogeny provides structure to these preferences. All together, the series of experiments involving artificial manipulation of grassfinch phenotypes (Burley et al. 1982; Burley 1985, 1986*a;* and this article)—and the fitness consequences of bearing preferred versus nonpreferred traits (Burley 1986*c*, 1988*a;* Burley and Price 1991; Burley et al. 1994, 1996)—provides the most convincing evidence for the power of latent aesthetic preferences to date.

There are, nevertheless, several alternative/additional hypotheses that deserve attention. Two competing hypotheses that might predict a preference for crests are "rare male advantage" (see references in O'Donald 1977) and "the handicap principle" (Zahavi 1975). Both of these hypotheses, however, would predict that all crest types are preferred over the uncrested phenotype. That is, since all crest types are uncommon (in fact, novel "mutants"), a hypothesis of rare male advantage would predict that all crest types would be preferred. Moreover, a novelty hypothesis would suggest that continuous exposure to the crested male phenotype should extinguish or reduce the preference for it. In experiment 3, however, the preference for white crests was stable over an interval (12 wk, including test intervals) that is considerably greater than that typically taken by grassfinches to demonstrate formation of an enduring pair-bond. The handicap principle would not necessarily predict that all crest colors would be equally favored, but if the burden of added weight and/or reduced aerodynamic efficiency caused by upright crests confers some sort of "indicator" status to crested males, then all crest phenotypes should have been preferred over uncrested males.

Exaggeration of Courtship Posture or Species-Typical Traits. Many birds, including males of some estrildines (Goodwin 1982), commonly raise crown feathers during courtship. Perhaps the preference for a crest represents a simple exaggeration of such male display. For both species, however, the preferred crest color is atypical of the crown color. Since both species form long-term pairbonds and have high parental effort by both sexes, aversions to such species-atypical phenotypes as presented here would be consistent with much of mate choice theory (Trivers 1972). For zebra finches, one might argue that the white crest exaggerates the species-typical eye stripes (fig. 1). The aversion of male zebra finches to white-crested females, however, is inconsistent with this explanation. Long-tailed finches have white rumps but lack other conspicuous white markings.

A General Preference for "White." Two lines of evidence suggest that results reported here do not reflect a general preference for white, or a preference for all-white birds, at least in zebra finches. (No data are available for long-tailed finches.) Zebra finches find white color bands neutral (Burley 1985). There are two unlinked recessive alleles that confer all-white plumage in estrildines, but wild-type zebra finches reared by wild-type parents do not preferentially mate with white conspecifics (N. T. Burley, unpublished data).

"Artifacts." The possibility that observed preferences are an "artifactual" result of unnatural lighting conditions is discounted by the fact that similar results were obtained under a wide range of lighting conditions. Thus, for example, while white feathers may reflect UV (S. Andersson, personal communication), results indicate the preference for white crests is not contingent on UV illumination. Across the experiments, the white feathers employed came from three different species (one psittacine, two estrildines), so the feathers probably varied somewhat in reflectance spectra. One reviewer suggested that the lack of preference for colored feathers resulted from the use of markers. If so, we might expect that in experiment 1 blue and green crests would have been perceived as attractive and that black crests (less than half of which had marker applied to them) would have been found more attractive than red crests (most of which were touched up). Instead, we found that no crest color other than white was attractive regardless of whether it was naturally or artificially colored. Thus, the preference for white crests appears robust.

Attraction to White Nest Feathers: The "Spillover" Hypothesis. Both species preferentially use white feathers to line their nests. Such a preference may be functional in that a nest lining of white feathers may conceal the white eggs (Goodwin 1982). Perhaps the emergent mate preference "spills over" from an attraction to white feathers in a functional context. The plausibility of this hypothesis is weakened by the fact that while both sexes regularly collect white feathers, male zebra finches are not attracted to females with white crests. Also, neither species incorporates feathers in sexual displays, even though such display would seem an easy evolutionary "step" from estrildine stem displays (Goodwin 1982). Birds line nests with feathers only when actively breeding, roosting in unlined nests at other times. Nevertheless, this hypothesis presents the testable possibility that a preference for white crests may be absent in estrildines that do not line their nests with white feathers, and especially those species, such as ground nesters, that line their nests with dark objects (Goodwin 1982).

The spillover hypothesis suggests that latent aesthetic preferences may diverge rapidly among related species as ecology and natural history diverge (e.g., Endler 1992). This hypothesis is more easily tested than is the possibility that a latent preference is a primitive character in a tree of a lineage's phylogeny (e.g., Basolo 1990), in part because there is always the possibility that the preference was derived at some earlier time. The preference for white crests would be "derived" if it had been passed down intact from the time the two species shared a white-crested ancestor. This possibility is untestable but is seemingly remote, given the absence of extant crested estrildines and a distinct paucity of crested ploceines.

It is more likely that the preferences observed here reflect in part a general avian predilection toward facial ornamentation (Darwin 1974). This predilection appears sufficiently broad—given the diverse array of facial ornamentation that occurs in birds—that it is probably rooted in the central nervous system (CNS). In this context, it is noteworthy that the preference for white crests is sex specific in the quite dichromatic zebra finch, while both sexes are attracted to white crests in the sexually indistinguishable (Larrimah) long-tailed finch population. Similar earlier findings (Burley 1985) led to the hypothesis that responses to novel stimuli are organized by the CNS in strategic "decision-making rules." Thus, a central or higher mechanism may have evolved to organize and even override perceptual biases of sensory systems. Most Australian estrildines are relatively monomorphic, the zebra finch being one of the most dimorphic species. Results reported here, and previous results indicating that male zebra finches are attracted to only a narrow range of novel female phenotypes (Burley 1985), suggest the possibility that male zebra finches have evolved a mechanism to override latent aesthetic mate preferences. By contrast, in two monomorphic species, the aesthetic mate preferences of the sexes appear very similar (*Taeniopygia bichenovii*—Burley 1986*a; Poephila acuticauda*—this article). These species and sex differences deserve further attention as they may provide considerable insight into mechanisms of evolution of sexual monomorphism versus dimorphism.

Heritability of Preferences

Some authors have argued that critical evidence for competing models of sexual selection hinges on whether or not mate preferences are invariant and genetically fixed; by this view, aesthetic preferences must be invariant (e.g., Wilkinson and Reillo 1994; Sherman and Wolfenbarger 1995). As Christy and Backwell (1995) point out, however, there is no legitimate reason to require that aesthetic mate preferences have no heritable component. Indeed, if aesthetic mate preferences have an important role in generating sexually selected traits, then to explain the radiation of such traits, we must expect that aesthetic preferences evolve. The existence of local variation for latent preferences would provide enormous potential for speciation via sexual selection, and so it is important to determine the extent of within-species variation in latent preferences.

Unfortunately, it is difficult to ascertain individual variation in preferences because mate-choice decisions involve multiple traits (e.g., Burley 1981*b*), not just the one being experimentally manipulated. Thus, in experiment 3, between-female variation in preference was not significant, nor did individuals show repeatability of the "strength" of their preference. While an improved design might show that individual variation does exist, it does not follow necessarily that such variation is heritable. Indeed, the expression of latent preferences may be condition-dependent because females in poor condition may ill afford the consequences of mating with very attractive males (i.e., reduced paternal care that such males provide [Burley 1988*a*]); if condition-dependent mate preferences do occur, ascertaining heritability of latent preference becomes even more difficult.

Latent Aesthetic Preferences and Good Genes Models

Although it seems reasonable that latent aesthetic preferences had "accidental" origins, we doubt that this is a sufficient explanation for the readily observable diversity of aesthetic preferences found in estrildines. We hypothesize that, over evolutionary time, selection favors the broadening of mate preferences for novelty. This occurs because consensus of preference is the driving force favoring the evolution of aesthetic traits (Fisher 1930). Within a sexual population, some variation in perceptual and decision-making "apparatuses" is likely. Thus, females whose preferences for novelty encompass the spectrum of preferences displayed by conspecifics will benefit from mating with those unusual males they find attractive (i.e., their sons will be attractive to a range of females); females whose preferences are narrow and idiosyncratic will not so benefit. In turn, as preferences broaden, selection may favor enhanced mutation rates in areas of the genome affecting secondary sexual traits, resulting in a coevolutionary race between aesthetic preferences and male traits (Johnson and Burley 1998). If this scenario is valid, then it should be possible to demonstrate that other taxa besides estrildine finches have a broad range of latent aesthetic preferences. Such demonstration would be powerful evidence for our contention ("Introduction") that aesthetic preferences are an important force in the early evolution of many secondary sexual and "species-specific" traits.

Latent aesthetic preferences constitute a conceptually parsimonious explanation for the early evolution of sexually selected traits. Ironically, once preferred traits begin to evolve and the preferences are no longer latent, traits may evolve into indicators and preferences may coevolve, becoming functional. A novel attractive trait, for example, might reach fixation rapidly through the impact of aesthetic preferences. Assuming that the trait has some cost, its expression may be influenced by other loci, thus propelling the evolution of "indicator status" (e.g., a male with brighter spots that result from his condition genes could be favored). This process might be especially effective if there is nonrandom assortment of attractive individuals with mates having superior heritable traits (Burley 1986*c,* 1988*a*). These possibilities represent a sort of "reverse Fisherian" process in which traits evolve initially through aesthetic preferences but later acquire functional associations through linkage disequilibrium and coevolution. Thus, even when traits used in mate choice are found to be indicators of functional, heritable qualities, researchers should be cautious about inferring a functional origin to the preferences for those traits.

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Literature Cited

Andersson, M. 1994. Sexual selection. Princeton University Press, Princeton, N.J.

Arak, A., and M. Enquist. 1993. Hidden preferences and the evolution of signals. Proceedings of the Royal Society of London, Series B 340:207–213.

Armstrong, E. A. 1947. Bird display and behavior. Oxford University Press, New York.

Basolo, A. L. 1990. Female preference predates the evolution of the sword in swordtail fish. Science (Washington, D.C.) 250:808–810.

Burley, N. 1981*a*. The evolution of sexual indistinguishability. Pages 121–137 *in* R. D. Alexander and D. W. Tinkle, eds. Natural selection and social behavior. Chiron, New York.

———. 1981*b*. Mate choice by multiple criteria in a monogamous species. American Naturalist 117:515–528.

———. 1985. The organization of behavior and the evolution of sexually selected traits. Pages 22–44 *in* P. A. Gowaty and D. W. Mock, eds. Avian monogamy. Ornithological Monographs no. 37. American Ornithologists' Union, Washington, D.C.

———. 1986*a*. Comparison of the band-colour preferences of two species of estrildid finches. Animal Behaviour 34:1732–1741.

———. 1986*b*. Sex-ratio manipulation in color-banded populations of zebra finches. Evolution 40:1191–1206.

———. 1986*c*. Sexual selection for aesthetic traits in species with biparental care. American Naturalist 127: 415–445.

———. 1988*a*. The differential allocation hypothesis: an experimental test. American Naturalist 132:611–628.

———. 1988*b*. Wild zebra finches have band-colour preferences. Animal Behaviour 36:1235–1237.

Burley, N. T., and D. K. Price. 1991. Extra-pair copulation and attractiveness in zebra finches. Acta XX Congressus Internationalis Ornithologici, pp. 1367–1372.

Burley, N., G. Krantzberg, and P. Radman. 1982. Influence of colour-banding on the conspecific preferences of zebra finches. Animal Behaviour 30:444–455.

Burley, N. T., D. A. Enstrom, and L. Chitwood. 1994. Extra-pair relations in zebra finches: differential male success results from female tactics. Animal Behaviour 48:1031–1041.

Burley, N. T., P. G. Parker, and K. Lundy. 1996. Sexual selection and extra-pair fertilization in a socially monogamous passerine, the zebra finch (*Taeniopygia guttata*). Behavioral Ecology 7:218–226.

Christitis, L. 1987. Biochemical systematics within palaeotropic finches (Aves: Estrildidae). Emu 89:119–123.

Christy, J. H., and P. R. Y. Backwell. 1995. The sensory exploitation hypothesis. Trends in Ecology & Evolution 10:417.

Darwin, C. 1874. The descent of man, and selection in relation to sex. 2d ed. J. Murray, London.

Endler, J. A. 1992. Signals, signal conditions, and the direction of evolution. American Naturalist 139(suppl.): S125–S153.

———. 1993. Some general comments on the evolution and design of animal communication systems. Philosophical Transactions of the Royal Society of London B, Biological Sciences 340:215–225.

Enquist, M., and A. Arak. 1993. Selection of exaggerated male traits by female aesthetic senses. Nature (London) 361:446–448.

Fisher, R. A. 1930. The genetical theory of natural selection. Clarendon, Oxford.

Gill, F. B. 1990. Ornithology. W. H. Freeman, New York.

Goodwin, D. 1982. Estrildid finches of the world. Cornell University Press, Ithaca, N.Y.

Guilford, T., and M. S. Dawkins. 1991. Receiver psychology and the evolution of animal signals. Animal Behaviour 42:1–14.

Hamilton, W. D., and M. Zuk. 1982. Heritable true fitness and bright birds: a role for parasites? Science (Washington, D.C.) 218:384–387.

Johnson, K., and N. T. Burley. 1998. Mating tactics and mating systems of birds. Pages 21–60 *in* P. G. Parker and N. T. Burley, eds. Avian mating tactics: female and male perspectives. Ornithological Monographs no. 49. American Ornithologists' Union, Washington, D.C.

Johnson, K., R. Dalton, and N. T. Burley. 1993. Preferences of female American goldfinches (*Carduelis tristis*) for natural and artificial male traits. Behavioral Ecology 4:138–143.

Keast, A. 1958. Infraspecific variation in the Australian finches. Emu 58:219–246.

Kodric-Brown, A., and J. H. Brown. 1984. Truth in advertising: the kinds of traits favored by sexual selection. American Naturalist 124:309–323.

Marchetti, K. 1993. Dark habitats and bright birds illustrate the role of the environment in species divergence. Nature (London) 362:149–152.

Meyer, A., J. M. Morrissey, and M. Schartl. 1994. Recurrent origin of a sexually selected trait in *Xiphophorus* fishes inferred from molecular phylogeny. Nature (London) 368:539–542.

Morris, D. 1956. The feather postures of birds and the problem of the origin of social signals. Behaviour 9: 75–113.

O'Donald, P. 1977. Mating advantage of rare males in models of sexual selection. Nature (London) 267:151–154.

Pizzey, G. 1980. A field guide to the birds of Australia. Princeton University Press, Princeton, N.J.

Rowland, W. J. 1989. Mate choice and the supernormality effect in female sticklebacks (*Gasterosteus aculeatus*). Behavioral Ecology and Sociobiology 24:433–438.

Ryan, M. J., and A. Keddy-Hector. 1992. Directional patterns of female mate choice and the role of sensory biases. American Naturalist 139(suppl.):S4–S35.

Ryan, M. J., J. H. Fox, W. Wilczynski, and A. S. Rand. 1990. Sexual selection for sensory exploitation in the frog *Physalemus pustulosus.* Nature (London) 343:66–67.

Serle, W., G. J. Morel, and W. Hartwig. 1977. A field guide to the birds of West Africa. Collins, London.

Shaw, K. 1995. Phylogenetic tests of the sensory exploitation model of sexual selection. Trends in Ecology & Evolution 10:117–120.

Sherman, P. W., and L. L. Wolfenbarger. 1995. Genetic correlations as tests for sensory exploitation? Trends in Ecology & Evolution 10:246–247.

Sibley, C. G., and J. E. Ahlquist. 1990. Phylogeny and classification of birds: a study in molecular evolution. Yale University Press, New Haven, Conn.

Trivers, R. L. 1972. Parental investment and sexual selection. Pages 136–179 *in* B. Campbell, ed. Sexual selection and the descent of man, 1871–1971. Aldine, Chicago.

Wilkinson, G. S., and P. R. Reillo. 1994. Female choice response to artificial selection on an exaggerated male trait in a stalk-eyed fly. Proceedings of the Royal Society of London, Series B 255:1–6.

Zahavi, A. 1975. Mate selection—a selection for a handicap. Journal of Theoretical Biology 53:205–214.

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