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BILL COLOR, REPRODUCTION AND CONDITION EFFECTS IN WILD AND DOMESTICATED ZEBRA FINCHES

NANCY TYLER BURLEY,[1,3] DONALD K. PRICE,[1,4] AND RICHARD A. ZANN[2]

[1]*Department of Ecology, Ethology, and Evolution, University of Illinois, Champaign, Illinois 61820, USA; and*

[2]*Department of Zoology, LaTrobe University, Bundoora, Victoria 3083, Australia*

ABSTRACT.—Bill-color variability has the identical range and similar distributions in free-living Australian Zebra Finches (*Taeniopygia guttata*) and their wild-type domesticated descendants. Individual differences in bill color exist among adults of both sexes, both in nature and captivity. In laboratory birds, bill color changed over the course of the five-week breeding cycle, with lowest bill-color scores expressed at the end of the cycle. Longer-term patterns included a gradual decline of bill color over the course of multiple clutch attempts, followed by a rapid increase when resources for breeding were withdrawn. Among laboratory males, survivorship was clearly independent of bill color. Among females, bill color changed more rapidly in birds that subsequently died than in those that survived a two-year breeding experiment. High rates of reproduction were significantly associated with decline of male bill score, but not female bill score. The bill-color scores of laboratory males maintained on supplemented and basic seed diets for eight weeks did not diverge. Crowding of laboratory birds was associated with decreased bill color. For birds in nature, bill color tended to decline over the breeding season. Bill color of captive wild birds became more red over a six-week period when birds were fed *ad libitum* on the laboratory diet. Data for both laboratory and wild birds indicate that reproduction is associated with a decline of bill color in both sexes. Results of diet experiments were inconclusive, but helped to establish that the range of bill colors displayed by domesticated birds is similar to that encountered in nature. Our results, when considered in light of previous findings, suggest the possibility that bill color has different costs and benefits for the sexes and that genetic and/or physiological constraints prevent optimal phenotypic expression of bill color in Zebra Finches. *Received 4 June 1990, accepted 21 July 1991.*

THE ZEBRA FINCH (*Taeniopygia guttata*) is a sexually dichromatic estrildine with strong pair bonds and substantial biparental care. Research on domesticated Zebra Finches has established that they have mate preferences for coloration patterns (e.g. Burley et al. 1982, Burley 1985), including bill color (Burley and Coopersmith 1987). Females prefer males with relatively red, dark bills (Burley and Coopersmith 1987; Price, unpubl. data); they even prefer males whose bills are redder than any bill color known to occur among captive birds. Males, however, prefer females with relatively light, orange bills (Burley and Coopersmith 1987).

Assuming that the mate preferences and bill colors of domesticated birds are similar to those of wild birds, there are two sets of hypotheses that may account for observed mate preferences. The "good-genes" hypotheses assert that color levels serve as an accurate indicator of condition (e.g. Zahavi 1977, Hamilton and Zuk 1982, Kodric-Brown and Brown 1984). The runaway-sexual-selection hypotheses (Fisher 1930, Lande 1981) posit that color levels are not indicators of condition. Results of bill-color preference experiments were interpreted as not supporting condition-dependent hypotheses (Burley and Coopersmith 1987) on the basis of the apparent similarity of the sex roles in Zebra Finches (i.e. if red bill color were a marker of superior condition, it seemed that both sexes should have mate preferences for birds with red bills). Further research (Burley et al. 1991) examined the possibility that parasite loads affected bill color in free-living birds. A positive correlation between bill score and ectoparasite count was found, exactly opposite of the "good-genes" prediction of Hamilton and Zuk (1982).

[3] Present address: Department of Ecology and Evolutionary Biology, University of California–Irvine, Irvine, California 92717, USA.

[4] Present address: Department of Zoology, University of Tennessee, Knoxville, Tennessee 37996, USA.

We examined several other ways in which bill color might serve as an indicator of condition: (1) as a response to the intensity and duration of breeding activity; (2) as an indicator of mortality risk; and (3) as a response to diet and/or crowding.

Zebra Finches breed continuously under favorable conditions, both in captivity and in nature (Immelmann 1965). For a homeothermic vertebrate they reach sexual maturity and adult phenotype rapidly (within 90 days), and have a high intrinsic rate of reproduction. If reproduction is costly (Williams 1966), we can expect birds to lose condition over a reproductive interval.

In some birds, redness of plumage coloration and tarsal skin fades in captivity due to inadequate supplies of dietary carotenoids (Brush and Power 1976, Fox 1976). The pigment(s) responsible for conferring bill coloration in Zebra Finches have not been established, but carotenoids are generally abundant in seeds (Fox 1976), which make up the bulk of the diet of this species. Nevertheless, because diets of laboratory-housed and free-living finches differ, we sought to determine whether diet has a large impact on bill color. A similar rationale was used for examining the effect of crowding.

Our research had a dual purpose. One objective was to ascertain the correspondence of bill color in wild, free-living and domesticated, laboratory-housed birds. Given a close correspondence in the range of bill colors and mate preferences of wild and domesticated birds (Burley, unpubl. data), laboratory-housed individuals of this species, which breeds freely in captivity, can serve as an excellent tool for the empirical study of sexual selection and sexual dichromatism. Our second purpose was to search for contexts in which bill color may be an accurate indicator of condition that might explain the observed mate preferences of this species.

METHODS

Subjects and study sites.—Domesticated Zebra Finches derived from the continental subspecies (*T. guttata castanotis*) were employed in laboratory work. The laboratory colony was produced from multiple sources and stocks were regularly outcrossed (Burley 1986). Only birds with wild-type plumage characteristics and conformation were used.

We sampled wild Zebra Finches in Australia at Alice Springs (Northern Territory) and Northern Victoria, approximately 150 km north of Melbourne. Alice Springs is located in the semi-arid zone and receives an average of 250 mm of rain per year. Zebra Finches were studied there in an open-woodland habitat south of town, shortly after the end of a two-year drought. Food was not abundant during this time (May 1986–January 1987), as few grasses set seed following the winter rains of June–July 1986 (Burley et al. 1989). Breeding commenced in September, peaked at an apparently low level in November, and tapered off thereafter. Northern Victoria has a temperate climate and an annual rainfall of 450 mm. The area is flood-irrigated and subject to intensive agriculture. Birds were studied during the autumn (March–April 1987) breeding pulse. Additional details are provided in Burley et al. (1989).

Wild birds were caught primarily in walk-in traps baited with Japanese millet (*Echinochloa crus-galli*) or yellow millet (*Setaria maxima*). Birds were captured occasionally with mist nets. Bill color did not vary with trap method.

Bill-color measurements.—Bill colors were scored using the Munsell Book of Color (glossy finish collection; Kollmorgen Corporation, Baltimore) and procedures detailed by Burley and Coopersmith (1987). Bill-color measurements were standardized by using one person to record data for each aspect of the study.

The Munsell system involves separate measurements of hue, value (relative lightness or darkness), and chroma (brightness or degree of saturation). To facilitate analysis, these measurements were converted to a single number in standard decimal notation using the formula:

$$3.0(15 - z) + 1.5(6 - y) + 0.5(x - 12),$$

where x is chroma, y is value, and z is hue as scored by the Munsell system. Minor adjustments in the Munsell scoring code were made to permit this transformation. We had three reasons for using the formula: (1) redder bills tend to be darker and brighter. The three Munsell color traits are highly intercorrelated, especially hue and value (e.g. using all data for Alice Springs birds: females, $r = 0.383$, $n = 255$, $P = 0.0001$; males, $r = 0.400$, $n = 266$, $P = 0.0001$). Chroma varies less among adult birds, but also is correlated with hue (females, $r = -0.224$, $P = 0.0003$; males, $r = -0.326$, $P = 0.0001$) and value (females, $r = -0.207$, $P = 0.0009$; males, $r = -0.182$, $P = 0.0029$). In the Munsell system, colors that are redder, darker, and duller have lower scores, so the negative nature of the correlations between chroma and the other traits is a function of the scoring system. (2) Differences in the sizes of perceptual intervals in the Munsell system result in much easier discrimination of adjacent hue standards than of adjacent chroma standards. Value standards are intermediate in this respect. This is the basis for applying different weights to the three color dimensions. (3) After the above transformation, colors

that are redder, brighter, and darker have higher scores than those that are less red, duller, and lighter. Bill colors with higher scores are perceived as more striking by humans and are preferred by female Zebra Finches in heterosexual choice texts (Burley and Coopersmith 1987).

Long-term breeding experiment.—A breeding experiment was conducted with banded, never-mated adults. Birds were released into a large aviary (density of 1 adult/m^3) and, after a period of acclimation, nest sites were provided. Birds were provided with commercial finch mix, mineral grit, cuttlebone, drinking water, and a high-protein dietary supplement *ad libitum*. Vitamin supplements, hard-boiled chicken eggs, fruits, and vegetables were given on a regular basis. The photoperiod was maintained at a constant length (14L: 10D).

Reproduction occurred for approximately 22 months, at which time nesting sites were removed. Adults remained in the aviary for an additional six weeks. Throughout the experiment, juveniles were removed from the aviary at regular intervals. Reproduction was ascertained by catching birds at the nest as they engaged in parental behaviors (Burley 1986). Each nest was checked daily throughout the experiment, and the number of eggs and nestlings scored. Nestlings were banded at approximately 11 days of age.

Bill color over the course of a single breeding cycle was examined after birds had reared multiple clutches. All adults were removed weekly from the aviary for a period of eight weeks and scored by an individual who was unaware of the birds' reproductive states. Only data from successful nesting attempts (where young fledged) were used for analysis. Zebra Finches reproduce continuously under these conditions, and there were clutch attempts before and after those we measured.

Males in this experiment were banded with one of three colors. Analyses indicated no significant effect of band color on bill-color expression. Accordingly, we report results based on the aggregate male sample. Females were not color-banded.

Diet experiments.—In Australia, 20 adult finches of each sex were captured in walk-in traps, banded, and placed in an outdoor aviary (18 m^3). Artificial nest sites were provided for birds to roost. Yellow millet and other commercially available grass seeds were provided *ad libitum*, as were grit, cuttlebone, water (with liquid vitamins added), and a high-protein supplement identical to that used in the laboratory. Birds sampled all of the above items within 48 h. In addition, birds were provided with fresh fruits, vegetables and boiled chicken eggs daily. Birds were first observed to eat these items after eight days.

Bill color was measured at the time the birds were introduced to the aviary and at two three-week intervals thereafter. A number of pairs began to breed in the artificial nests provided for roosting. These clutches were destroyed shortly after they were laid. Birds were released after their bill colors were scored the third time.

In the studies of domesticated Zebra Finches, males were assigned randomly to one of two diet treatments, with 18 birds in each. The basic seed diet consisted of commercial finch mix, cuttlebone, grit, and water provided *ad libitum*. The supplemented diet consisted of the above items in addition to vitamins, a protein supplement, and daily allotments of chicken eggs, fruits, and vegetables. Birds were maintained in two adjacent, identical aviaries. Bill color of all birds was measured weekly over an eight-week span. Prior to the experiment, birds were provided with all elements of the supplemented diet except the protein supplement, although they received vitamins less often and fewer eggs, fruits and vegetables. Thus, the pre-experiment diet was more similar to the supplemented diet than the seed diet.

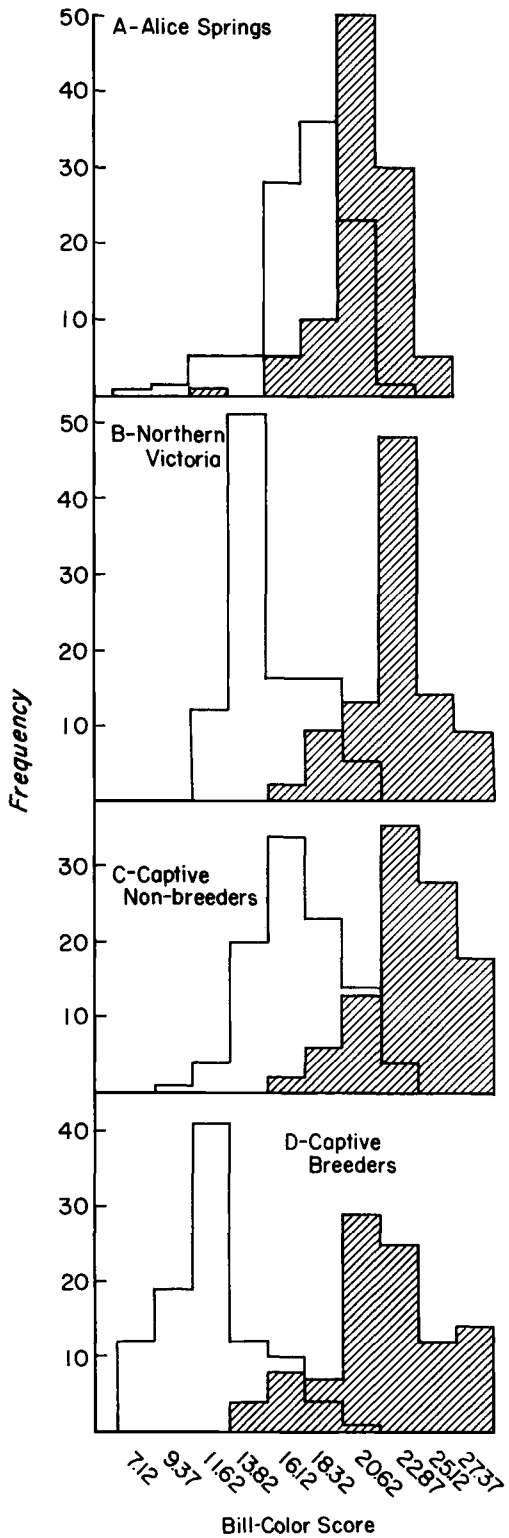
Density experiment.—Twenty adult males that had been maintained at a density of about 1 bird/0.25 m^3 for four months or more were placed in a large aviary at a density of 1 bird/2.5 m^3 for eight weeks. They were then returned to a holding cage at the previous density for an additional eight weeks. Feeding protocols were identical over all three time periods. Bill colors of birds were scored at the end of all three time periods.

Statistical analyses.—Repeatability of bill color was calculated from an analysis of variance (ANOVA) table using the equation:

$$\rho = \frac{(MS_{among} - MS_{within})/n}{[(MS_{among} - MS_{within})/n] + MS_{within}},$$

where MS is the mean sums of squares and n is the mean number of measurements per individual (a weighted mean was used when there were unequal numbers of measurements per individual; Sokal and Rohlf 1981). The multiple measurements of bill color in the density, diet, long-term breeding, and Australian aviary experiments and the Australian seasonal data were analyzed by analysis of variance or repeated-measures general linear models (GLMs; SAS Institute 1985). We also tested the linear effect of time on bill color with the first-degree polynomial in repeated-measures GLMs for experiments with more than two bill color measurements (Freund et al. 1986). This analysis allows for a test of an overall linear effect of time and the group-by-linear-time interaction.

In the long-term breeding experiment, we measured bill color 12 times (T1–T12) over the course of the experiment. The interval between measurements varied as a result of competing demands for data collection (e.g. Burley 1988) and the fact that removal of birds from the aviary for scoring was somewhat disruptive (resulting in cooling of eggs and young). We



used a principal components analysis of five reproductive measures (number of clutch attempts, number of eggs laid, number of hatchlings produced, number of fledglings produced, and number of offspring surviving to independence) to obtain a score on the first principal component for each individual during each of the 11 intervals between bill-color measurements. Prior to principal components analysis, each reproductive parameter was standardized to have a mean of zero and a standard deviation of one. All five reproductive parameters weighed positively on the first principal component (RE1) and this component explained 75% of the variation for females and 85% for males. Nested analyses of covariance (ANCOVA) were performed with the first principal component nested within individuals to examine the effect of reproductive effort on bill-color change for each sex.

RESULTS

DISTRIBUTION OF BILL-COLOR SCORES

Laboratory-housed Zebra Finches showed virtually identical ranges (Fig. 1) and similar distributions (Fig. 2) of bill color as free-living ("wild") finches. The distributions of bill color for wild birds varied somewhat between sampling intervals and locales. Populations of laboratory birds had somewhat higher variances of bill-color scores, and laboratory populations that had bred continuously for some time displayed lower means.

REPEATABILITY OF BILL COLOR

Wild birds.—We ascertained short-term repeatability under field conditions by analysis of bill-color scores on birds captured and independently scored twice within a 14-day span. Repeatability was highly significant for both sexes (for females, $\rho = 0.735$, $F = 6.54$, df = 22 and 23, $P < 0.0001$; for males, $\rho = 0.907$, $F =$

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Fig. 1. Distributions of adult bill-color scores in nature and in captivity. Open histograms represent distributions for females, hatched histograms distributions for males. (A) Alice Springs, September 1986 (198 females, 214 males); (B) Northern Victoria, March 1987 (43 females, 44 males); (C) captive nonbreeders (97 females, 103 males); (D) captive breeders (48 females, 51 males). Captive nonbreeders had not bred within previous six months; captive breeders had been breeding for 2.5–4 months at time of sampling. Data for captive breeders aggregated across populations.

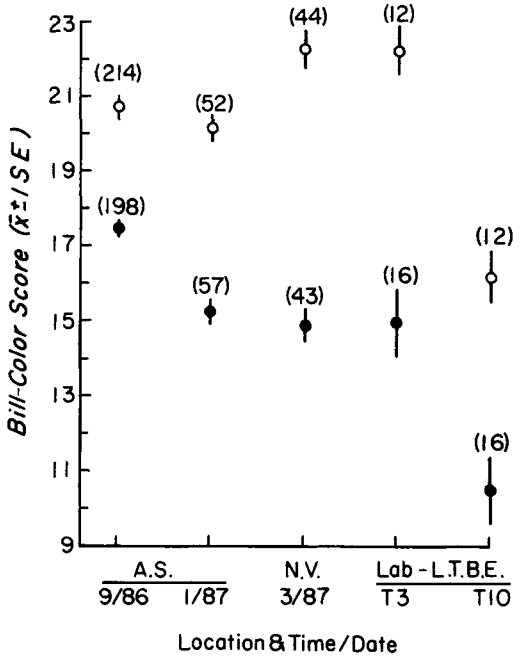

Fig. 2. Means and standard errors of bill-color scores for birds sampled at Alice Springs (A.S.) and Northern Victoria (N.V.), and for survivors of long-term (captive) breeding experiment (L.T.B.E.). T3 is 2.75 months after start of breeding in L.T.B.E.; T10 is 22.5 months after start of breeding in L.T.B.E. (see Fig. 3). Open circles represent males and closed circles females. Sample sizes in parentheses.

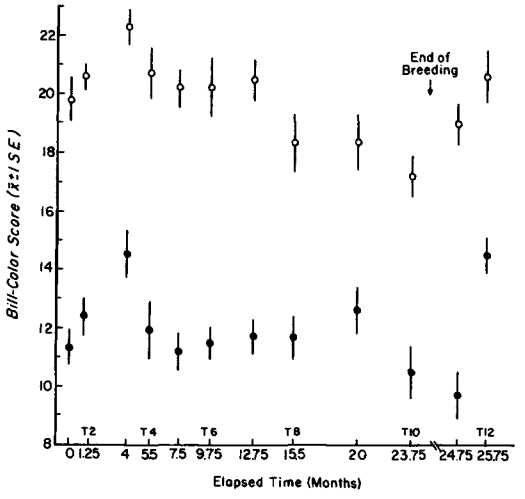

Fig. 3. Means and standard errors of bill-color scores for 23 females and 18 males during long-term breeding experiment. Reproduction commenced at T2 and ended after T10.

20.62, df = 19 and 20, $P < 0.0001$). We calculated these values as an estimate of measurement repeatability of the human observer and also to reflect short-term stability of bill color. Longer-term repeatability was estimated for birds that were measured three times between August and November 1986 (successive measurements made 3–7 weeks apart). There was a significant time effect of bill color for females (ANOVA, F = 16.50, df = 2 and 44, $P < 0.0001$), but not males (F = 2.68, df = 2 and 58, P = 0.08). Controlling for time effects in an ANCOVA, repeatability was highly significant for both sexes (for 31 females, ρ = 0.814, F = 10.71, df = 22 and 44, $P < 0.0001$; for 38 males, ρ = 0.542, F = 3.88, df = 29 and 58, $P < 0.0001$).

Laboratory birds.—Repeatability estimates are reported for bill-color measurements taken during the first four months of the long-term breeding experiment. Three measurements (T1, T2, T3 of Fig. 3) were made for each bird during this interval. Controlling for significant time effects (females, F = 3.36, df = 2 and 46, P = 0.036; males, F = 11.82, df = 2 and 36, P = 0.0001), bill-color scores were significantly repeatable for both sexes (for females, ρ = 0.527, F = 4.34, df = 23 and 46, $P < 0.0001$; for males, ρ = 0.362, F = 2.70, df = 18 and 36, P = 0.006). Thus, over a comparable time span, individual repeatability was somewhat lower for laboratory birds than wild birds, but repeatability of bill color was highly significant for both groups of birds.

Effects of Reproduction and Breeding Season

Wild birds.—Individual birds were sampled in Alice Springs at the beginning (August/September 1986) and towards the end (December 1986/January 1987) of a breeding pulse. Bill color of both sexes declined (i.e. became less red) significantly over this interval (females, n = 18, August/September $\bar{x}$ = 17.55, December/January $\bar{x}$ = 14.67; males, n = 25, August/September $\bar{x}$ = 21.80, December/January $\bar{x}$ = 19.59; repeated-measures GLM, linear time effect, F = 55.68, df = 1 and 41, P = 0.0001; linear-time-by-sex interaction, F = 0.970, df = 1 and 41, P = 0.33).

Long-term effects in laboratory birds.—Results of

TABLE 1. Reproductive effort and bill-color change in long-term breeding experiment. Analyses are nested ANCOVAs. RE1 = first principal component for five reproductive parameters.

Analysis	Sex	Individual[a]			RE1		
		F	df[c]	P	F	df[c]	P
No lag[b]	Female	0.33	22, 148	0.99	0.65	23, 148	0.89
	Male	0.48	17, 128	0.96	2.20	18, 128	0.006
Lag[b]	Female	0.23	21, 141	0.99	1.27	22, 141	0.20
	Male	0.40	17, 124	0.99	0.55	18, 124	0.93

[a] Overall model for ANCOVAs: bill-color change = individual + RE1 nested within individual.

[b] For no-lag analysis, RE1 from same time period as bill-color change used as predictor. For lag analysis, RE1 from time period previous to bill-color change used as predictor.

[c] In nested ANCOVA, degrees of freedom for numerator are $n - 1$ for individual and n for RE1, where n = number of individuals (Searle 1987).

the long-term breeding experiment indicate a significant time effect on bill color for both sexes (Fig. 3; repeated-measures GLM for survivors, T1 through T10, $F = 4.87$, df = 9 and 21, $P = 0.0013$). The time-by-sex interaction was not significant ($F = 1.75$, df = 9 and 21, $P = 0.14$). This analysis also indicates that there was a significantly negative linear effect of time ($F = 12.43$, df = 1 and 29, $P = 0.0014$), and there was no significant sex-by-linear-time interaction ($F = 1.97$, df = 1 and 29, $P = 0.17$). Generally, bill color tended to peak (become most red) for both sexes about T3 and showed an irregular decline thereafter until the end of breeding (Fig. 3). For both sexes, bill color became more red after reproduction was suspended (T10 to T12: change for females, $\bar{x} = 4.08$, $n = 15$, $t = 6.25$, $P < 0.0001$; change for males, $\bar{x} = 3.45$, $n = 12$, $t = 3.75$, $P = 0.003$).

To examine the effect of reproductive effort on changes in bill color during each time period, we performed nested ANCOVAs using scores on the first principal component based on five reproductive parameters. We found a significant within-individual effect of the first principal component for males, but not for females (Table 1). Thirteen of 18 males had negative estimates for the first principal component (mean estimate = −0.0125); bill-color score tended to decline with increasing reproductive effort.

We repeated the analysis after incorporating a time lag of one interval (using RE1 from previous time period). Results were not significant for either sex (Table 1).

Long-term survivorship in laboratory birds.—Bill color of birds that died during the long-term breeding experiment was compared with that of survivors. For females, measurements hinted at a tendency for birds that died to have redder bill colors at the beginning of the experiment, but the difference was not statistically significant (T1; Table 2). The bill colors of females that subsequently died during the experiment showed significantly more rapid change in bill color (becoming less red) than those that survived (Table 2). For males, survivorship was independent of initial bill color, and there was no difference in rate of bill-color change between males that survived and those that died (Table 2).

Short-term effects in laboratory birds.—Changes in bill color and weight were examined over the course of the five-week nesting cycle (egg-laying to fledging). Among females, both bill color and weight varied significantly over this

TABLE 2. Long-term survivorship and bill color in long-term breeding experiment. T1 = first time period (Fig. 3). Rate of bill-color change is bill color at last sampling period prior to death for birds that died (or T10 for birds that survived) minus bill color at T1, with resulting quantity divided by number of months in experiment.

Sex	Status	Initial (T1) bill color ($\bar{x}$)	n	F	P	Rate of bill-color change ($\bar{x}$)	F	P
Female	Survived	11.86	16	3.42	0.08	−0.01	4.39	0.048
	Died	14.03	8			−0.33		
Male	Survived	19.32	15	5.04	0.50	−0.03	0.01	0.91
	Died	20.50	4			−0.05		

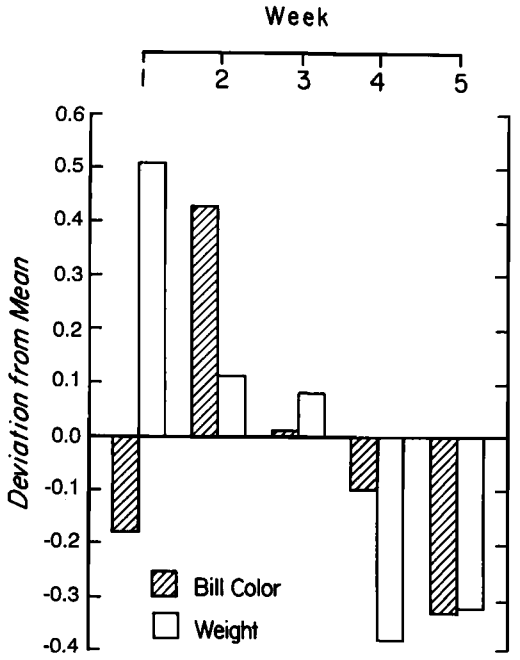

Fig. 4. Changes in mean bill-color score (n = 26) and weight (n = 27) of captive female Zebra Finches over course of nesting cycle. Egg-laying started at beginning of week 1; hatching began at start of week 3; fledging occurred during week 5. Bill-color expression on week 1 was most preferred; that on week 5 was least preferred.

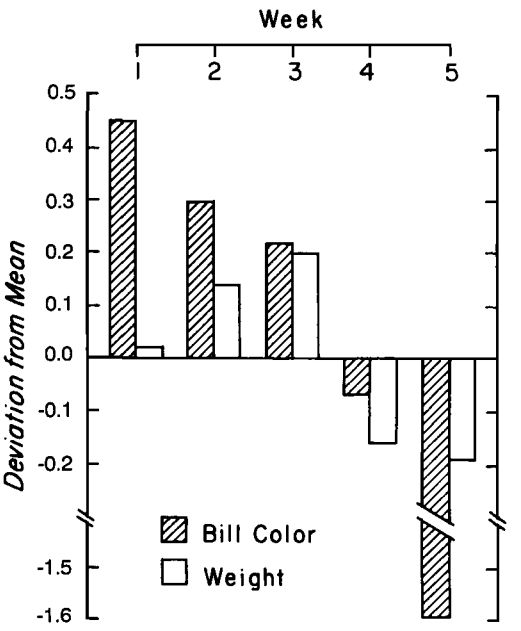

Fig. 5. Changes in mean bill-color score and weight of 29 captive male Zebra Finches over course of nesting cycle. Egg-laying starts at beginning of week 1; hatching begins at start of week 3; fledging occurs during week 5. Bill-color expression on week 1 most preferred; that on week 5 least preferred.

interval (repeated measures ANOVAs: for bill color, $F = 2.85$, $n = 26$, df = 4 and 21, $P < 0.05$; for weight, $F = 32.43$, $n = 27$, df = 4 and 22, $P < 0.0001$). Weight declined over the course of the breeding cycle; bill color, however, peaked during the second week of the cycle and declined thereafter (Fig. 4). The 29 males sampled also showed significant changes in bill color and weight (for bill color, $F = 12.12$, df = 4 and 24, $P < 0.0001$; for weight, $F = 19.08$, df = 4 and 24, $P < 0.0001$). Among males, bill color declined strikingly over the course of the nesting cycle, while weight peaked in the third week (Fig. 5).

Other Condition Effects

Diet experiment using wild birds.—To measure bill color of wild birds under conditions similar to those experienced by laboratory birds, adult males and females were captured in August 1986 in Alice Springs and held in an outdoor aviary for six weeks. Birds received a diet similar to laboratory birds. Their bill colors were scored when captured (T1) and at two three-week intervals (T2, T3) thereafter. Other adults trapped at the same time, but released after measurement, served as the primary control group. These birds were recaptured and scored at about the same times as the captive birds. Because only a portion of the birds caught during this period remained resident on the study site for any period of time, we created a second comparison group that consisted of birds caught at the same time as the aviary birds, but which were not caught again. The purpose of this group was to establish whether bill colors were similar for resident and nonresident birds, because we did not know to which group the aviary-housed birds belonged.

The bill-color distributions of aviary birds, resident controls, and nonresident birds did not differ significantly at T1 (ANOVA: for females, $F = 0.96$, $n = 57$, df = 2 and 54, $P = 0.39$; for males, $F = 0.07$, $n = 58$, df = 2 and 55, $P = 0.93$). The aviary birds' bill color dramatically increased during the two time periods and the resident birds' bill color slightly decreased dur-

TABLE 3. Change in bill-color score of birds in Australian aviary experiment. Aviary (A) birds placed in aviary after bill colors first scored (T1). Bill colors measured again after three (T2) and six (T3) weeks. Control (C) birds were free-living and caught repeatedly during same sampling periods.

		Females		Males	
Interval	Treatment	Bill-color change	*n*	Bill-color change	*n*
T2-T1	A	+2.59	19	+1.69	20
	C	−0.17	19	−0.31	16
T3-T2	A	+0.65	19	+0.85	20
	C	−0.27	19	−0.74	16

ing these two periods (Table 3). This difference in bill color change between the two groups of birds is significant (repeated measures: group-by-linear-time interaction, $F = 5.49$, df = 1 and 289, $P = 0.02$). There was no significant sex difference in bill color change (repeated measures: sex-by-linear-time interaction, $F = 0.02$, df = 1 and 289, $P = 0.88$). Bill color of aviary-held birds increased the most during the first time period, indicating that bill color can respond quickly to changing environmental conditions.

Diet experiment using laboratory birds.—There was no significant difference in bill colors of birds in the seed and supplemented-diet treatments at the beginning of the experiment (ANOVA: seed diet $\bar{x} = 23.34$; supplemented diet $\bar{x} = 23.49$; $F = 0.04$, df = 1 and 34, $P = 0.84$). A repeated-measures GLM, employing residuals from a regression of age on bill color, revealed no significant time-by-diet interaction ($F = 1.48$, df = 8 and 27, $P = 0.21$). The mean bill color of birds on the seed diet decreased by 1.00 color units during this interval, while that of birds on the supplemented diet decreased by 0.16 units. There was no linear effect of time on bill color ($F = 0.01$, df = 1 and 33, $P = 0.97$), nor a diet-by-linear-time interaction ($F = 0.02$, df = 1 and 33, $P = 0.88$).

Density experiment using laboratory birds.—One of 20 birds died during the experiment and was excluded from analysis. Repeated-measures ANOVA revealed a highly significant density effect ($F = 10.41$, df = 2 and 36, $P < 0.001$). Mean bill color increased by 2.06 color units during the eight weeks the birds were under low-density conditions and decreased by 1.11 units during the subsequent eight weeks at high density.

DISCUSSION

Comparison of laboratory and free-living birds.—For both groups of birds, bill-color distributions varied among sampling periods. For all comparisons of laboratory and free-living birds, distributions for the two groups were remarkably similar. Free-living birds did not have bill colors more extreme than those in captive populations. Thus, neither diet nor domestication has greatly altered the bill-color range in this species.

Repeatability.—Individual repeatability estimates under both laboratory and field conditions indicate the existence of persistent individual differences among adult birds even under changing conditions. It is difficult to make a meaningful comparison of the relative magnitude of individual repeatability estimates made under field and laboratory conditions, because measurement repeatability may vary. That repeatability was higher under field conditions may simply reflect the fact that the principal scorer (N.T.B.) was a novice at taking measurements at the beginning of the long-term breeding experiment, but had several years experience prior to collecting field data.

Reproduction and mortality.—Reproduction affects bill color in both wild and laboratory birds. Most of the significant results indicate that reproduction over a substantial interval is associated with a decline in bill color. Moreover, for laboratory birds, removal of opportunities to breed in the absence of other changes in resource availability resulted in a rapid rebounding of bill-color scores.

Bill-color scores appeared to increase between T1 and T3 in the long-term breeding experiment, despite the onset of reproduction at T2. This may have resulted from the fact that a reduction in density comparable to that employed in the density experiment occurred at the onset of the long-term experiment. The increase in bill color was probably not due to bird age, as birds were fully adult (4–6 months old; Burley and Coopersmith 1987) at the start of the experiment. Prior to the experiment, birds were held in unisexual groups, and it is conceivable that social interactions resulting from the change in housing conditions mediated hormonal

changes influencing bill color expression. However, Zebra Finches are hormonally primed to reproduce continuously (Sossinka 1975, 1980), and had accoustical and limited visual contact with members of the opposite sex before the experiment. Intrasexual competition may have been more intense prior to the start of the experiment, because birds were kept at much higher densities.

Short-term changes over the course of the nesting cycle observed in laboratory birds paralleled longer-term trends, with the lowest bill-color values (and weights) at the end of the nesting cycle. The predominant sex difference occurred during week 1, the period with the greatest sex-role difference. At this time, females engaged in egg laying had low bill-color scores and high weights, whereas males engaged predominately in nest building and had relatively low weights, but peak bill colors. Male bill color rebounds rapidly between the end of one nesting cycle and the beginning of the next, which often starts within 10 days post-fledging and sometimes begins before fledging of the previous brood. This suggests that variables in addition to reproductive effort (e.g. hormonal fluctuations) may contribute to bill-color change in males.

Our analyses of the effects of reproductive effort on bill-color change in males demonstrated that high reproductive effort was associated with loss of bill color. This effect was relatively rapid, as the analysis incorporating a time lag showed no significant result. Females did not show a significant effect. Unfortunately, interpretation of results of the reproductive effort analysis for females was complicated by mortality patterns. Among females, unlike males, the rate of change of bill color was not independent of mortality. Birds that showed the most rapid declines tended to die. Moreover, the recorded scores of females that died were higher than bill scores of those that lived (a result replicated subsequently; Price and Burley, unpubl. manuscript). In sum, we suggest that there may be sufficient variation in the vigor or stamina of females such that measures of numbers of eggs and young produced may be an insufficient estimate of reproductive effort. "Inferior" females with lower stamina may produce fewer offspring at greater cost to themselves. A trend that is consistent with the possibility that females suffer greater long-term effects of reproductive effort is the tendency of males to recoup peak bill color more rapidly following a substantially greater decline during the nesting cycle (compare Figs. 4 and 5).

Diet experiments.—Our experiment involving diet of wild birds was performed in ignorance of the relative quality of laboratory and natural diets. We sought to determine: (1) whether bill color would increase or decrease in wild birds held captive on a laboratory diet; and (2) if bill color increased, whether the bill colors of wild birds would exceed the bill-color scale established for laboratory birds. The answers to both these questions were clearcut. Bill color increased in both sexes; in no case did bill-color scores exceed the maxima found in captive birds (approximately 22.75 for females and 26.50 for males). This second result reinforces the conclusion that laboratory birds display the natural distribution of bill colors.

Further interpretation of this experiment is complicated by design constraints (i.e. availability of only one aviary). One interpretation is that bill color changed as the result of diet enhancement (e.g. increased abundance of substances such as carotenoids). The possibility that crowding contributed to the result is contradicted by findings in the density experiment. Also, captive birds began to lay eggs at just about the same time as free-living birds (Burley et al. 1989), which argues against the possibility that physiological changes due to reproduction were responsible for the result. The most likely alternative explanation is that the increased abundance of food and concomitant reduction in search time were responsible for increased bill color. This interpretation is inconsistent with the results of the laboratory diet experiment, which failed to show significant differences in bill-color change between birds maintained on a minimal seed diet and those on a supplemented diet. The laboratory diet experiment was inconclusive for two reasons. First, birds in both treatment groups lost bill color, which suggests the possible intervention of "seasonal" factors such as temperature and relative humidity, which varied somewhat over time. Second, results of the experiment were in the expected direction. It may be that the average condition of laboratory birds was sufficiently greater than that of the wild birds captured at the end of a drought and, therefore, that a longer experimental interval would be needed to document

effects of a restricted diet. This possibility is consistent with the apparent physical condition of wild birds prior to the start of the experiment. They were in poor feather condition (Zann and Burley, unpubl. data) and probably had suspended molt for some interval during the drought. Zebra Finches molt continuously in the laboratory and, under favorable conditions, in nature as well (Zann 1985).

Bill color, condition, and mate choice.—Our results indicate that condition affects bill color, but they are no by means sufficient to conclude that birds with certain bill colors make superior economic or genetic contributions to young, as is required by "good-genes" models of sexual selection. The results of mortality analyses for females require us to alter our interpretation of the significance of differences in the mate preferences of the two sexes. It appears likely that females with relatively red bills have low reproductive value as the result of high mortality rates, making them less desirable as mates. This could result from the occurrence of genetic correlations between the sexes for sexually dimorphic phenotypic traits (Lande 1980). A result of such a genetic correlation could be that the phenotypic expression of both sexes deviates from its optimal expression. This possibility is consistent with the findings: (1) that female mean bill color is typically redder than the range of 12–13, which is most preferred by males (Fig. 1); and (2) that females prefer males with bill colors artificially enhanced to be redder than any bills observed in the laboratory or in nature (Burley and Coopersmith 1987).

Bill color varies over the breeding cycle so that the bill colors of males (Fig. 5) and females (Fig. 4) most closely approach the mate preferences of the opposite sex at the time that fertile copulations occur (during the first few days of week 1 and a number of days before). We speculate that perhaps birds adjust physiologically in order to be of peak attractiveness at this time. Males may benefit from being maximally attractive while their mates are laying eggs to reduce the likelihood that their mates will engage in extra-pair copulations (Burley and Price 1991). Males may also attempt to attract other females after their mates' egg laying has been completed and when other demands on their time are low, as in week 2. Bill color is relatively red at this time, but not as red as in week 1 (Fig. 5).

Viewed in these terms, short-term changes in bill color may reflect not just relative reproductive effort, but strategies for temporal optimization of bill-color expression as well. This possibility further complicates interpretation of the tendency of female bill-color scores to exceed those preferred by males. In a series of experiments, Burley and Coopersmith (1987) measured male preference for most of the range of female bill scores. Most preferred were scores of 12–13. Beyond this, females with higher scores were preferred over females with even lower scores (i.e. $12.25 = 12.75 > 16.5 > 17.25 > 21.75 > 11.25 = 5.7$). Thus, for females, it is better to have a bill score higher than that most preferred than one that is lower than optimal. If female bill-color expression is constrained to drop during the later portion of the breeding cycle (Fig. 4), females whose average bill score is in the range most preferred by males will have highly nonpreferred scores by the end of a cycle. If the demands of egg-laying preclude rapid rebounding of scores, such females would be very unattractive to males at the peak of their fertile period. This, in turn, may impair female ability to gain and retain mates. Further work on the significance of mate preference and sexual dichromatism in this species would benefit greatly from information on the genetic and physiological constraints on bill color expression.

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