

*Evolution*, 60(5), 2006, pp. 000–000

## AN EYE FOR DETAIL: SELECTIVE SEXUAL IMPRINTING IN ZEBRA FINCHES

NANCY TYLER BURLEY

*Department of Ecology and Evolutionary Biology, University of California–Irvine, Irvine, California 92697-2525*

*E-mail: ntburley@uci.edu*

**Abstract.**—To investigate the idea that sexual imprinting creates incipient reproductive isolation between phenotypically diverging populations, I performed experiments to determine whether colony-reared zebra finches would imprint on details of artificial white crests. In the first experiment, adults in one breeding colony wore white crests with a vertical black stripe, while in another colony adults wore crests having a horizontal black stripe; except for their crests, breeders possessed wild-type plumage and conformation. Offspring of both sexes reared in these colonies developed mate preferences for opposite-sexed birds wearing the crest type with which they were reared; neither sex developed a social preference for crested individuals of the same sex. In a second experiment, females reared by crested parents preferred crested males versus males with red leg bands, while control females (reared in a colony of wild-type, uncrested birds) preferred red-banded males in the same test. Results of a third experiment that used sexually dimorphic crest phenotypes indicate that both sexes of offspring imprinted on maternal crest patterns. Results support the hypothesis that sexual imprinting can facilitate isolation both by engendering a preference for population-typical traits and by prioritizing such an imprinting-based preference over species-typical preferences for other traits used in mate choice. Comparison with results of other recent studies indicates that imprinting tendencies of both sexes vary with the characteristics of traits presented as an imprinting stimuli. Tendency to imprint may vary with the perceived information content (e.g., kin sex, or population indicator) of parental traits, a process dubbed selective sexual imprinting.

**Key words.**—Behavioral reproductive isolation, mate preferences, sexual imprinting, speciation, zebra finches.

Received July 19, 2005. Accepted February 8, 2006.

Sexual imprinting, a process in which early contact with parents shapes the mate preferences of offspring, occurs widely among birds and has also been reported for other taxa, notably mammals including humans (Düttmann et al. 1998; Kendrick et al. 1998; Bereczkei et al. 2004). While the topic of imprinting has been of considerable interest historically (Lorenz 1935; Hess 1973; Immelmann 1975), in recent years, the phenomenon has received less empirical attention from evolutionists (but see, e.g., Hansen and Slagsvold 2004; Albert 2005), perhaps in part because no contemporary consensus has been reached concerning the evolutionary function(s) of sexual imprinting responses (e.g., Bateson 1978; Shapiro 1980; ten Cate and Vos 1999). Also, while male birds consistently develop mate preferences for traits similar to those of their mother, the responses of females appear inconsistent. In zebra finches, a relatively well-studied species, females sometimes imprint on paternal traits (Clayton 1990; Weisman et al. 1994; Witte and Sawka 2003), other times on maternal traits (Vos 1995a), and sometimes fail to imprint (Vos 1995b; Burley 2006).

Despite these ambiguities, sexual imprinting remains important and has implications for several major topics of contemporary interest including sexual selection (ten Cate and Bateson 1988; Andersson 1994), speciation (Grant and Grant 1997a; Irwin and Price 1999; Coyne and Orr 2004; Albert 2005), and the role of learned social behaviors in evolution (Oyama 1993; Galef and Allen 1995; Dukas 1998). A phenomenon of particular relevance to understanding both causes of variability in imprinting responses and imprinting's role in sexual selection and speciation is predispositional learning, or the selective tendency to acquire information, especially that which has evolutionary salience (e.g., Nelson 2000). While numerous authors have suggested that organisms have predispositions that influence the direction and strength of imprinting responses (e.g., Schutz 1965; Bateson 1978; Im-

melmann and Suomi 1981), to date evidence for predispositional visual learning has come more from studies of filial imprinting (Lickliter 1993; Dooling et al. 1996) than from sexual imprinting studies (e.g., Kruijt 1985; Kruijt and Meeuwissen 1993; Bischof 1994). If such predispositions occur, some stimuli may elicit stronger sexual imprinting responses than others. Thus, there may exist a continuum of responsiveness toward stimuli, in which some stimuli are highly imprintable, while other stimuli evoke weak imprinting responses or perhaps none at all (e.g., Witte and Sawka 2003). Differential responsiveness based on perceived information content can be called “selective sexual imprinting.” Investigation of such imprinting responses may provide insight into how complex mating decisions involving multiple constraints and choice criteria influence population divergence and isolation (Grant and Grant 1997b; Payne et al. 2000).

Imprinting has been hypothesized to facilitate reproductive isolation by generating positive assortative mating for traits that differ between populations, and to do so without requiring changes in the genetic bases of mate preferences (e.g., Kalmus and Maynard Smith 1966; Payne 1973; Laland 1994; Grant and Grant 1997a; Irwin and Price 1999; ten Cate 2000). To investigate this hypothesis, I reared zebra finches in colonies in which otherwise wild-type parents wore gray- or white-feathered crests (Burley 2006). Males developed preferences for the crest phenotype of their mother (gray, white, or none), and did not respond to their father's crest phenotype. By contrast, females reared in all treatments failed to imprint; instead they displayed the aesthetic preference for white-crested males previously shown for zebra finches reared with noncrested parents (Burley and Symanski 1998). This result suggested that a latent predisposition for a trait or trait value can override an imprinting response to other trait values, a tendency that might interfere with establishing reproductive isolation between incipiently divergent popu-

## SELECTIVE SEXUAL IMPRINTING

lations (e.g., Basolo 1998). Thus, for example, if a white-crested phenotype were to arise in nature, its attractiveness to females might lead it to quickly sweep across zebra finch populations distributed over the continent of Australia, and might even result in hybridization between zebra finches and other estrildines also attracted to white crests (Burley and Symanski 1998).

Here I report results of experiments designed to test whether addition of species-salient information to the white crest phenotype affects the tendency of offspring to imprint on white crests. Because the adult phenotype of the species contains two (in females) or three (in males) types of black-and-white stripes, I elected to add black stripes to white crests in a population-specific manner. In one captive breeding population, I added crests with horizontal black stripes to the crowns of founders, and crests with vertical black stripes were applied to founders of another population. Crests were built entirely from human-made materials.

While previous experiments had established that normally reared females are attracted to males wearing white-feathered crests, it was necessary to determine whether birds of either sex would show such preferences for conspecifics wearing white featherless crests (crests made from plastic material that is painted white). The first experiment explored this question and measured the tendency of birds reared in aviaries in which all adults wore one crest type to develop preferences to associate with opposite- and/or same-sex individuals wearing that crest type. To further explore possible divergences in mate preferences between populations, I performed a second experiment. This experiment investigated whether rearing experience influences the strength of a latent preference for a novel attractive trait (red leg bands) in a way that would further to contribute to population divergence. In the third experiment, sex-specific crest phenotypes were introduced to one of the experimental breeding populations to determine which parent the offspring used as an imprinting stimulus.

I adopted the experimental approach of adding crests to otherwise wild-type zebra finches for several reasons. The major objective was to leave existing species- and sex-indicating traits of breeders intact, so that offspring could imprint on those traits as naturally as possible, and so that the types of imprinting stimuli would be reasonably similar to those that might be experienced by avian young in naturally diverging populations. A second objective was standardization of the imprinting stimulus within populations; such standardization is difficult to achieve by modifying the natural plumage with bleach or dyes (e.g., Calkins and Burley 2003). Although zebra finches are naturally uncrested, crests and other types of elongated facial feathers have evolved in numerous avian lineages (Darwin 1871; Armstrong 1965), and thus crests constitute a reasonable trait for study. Crests also have practical advantages for this sort of study; chief among them is the inability of an experimental subject to remove its crest by preening.

## MATERIALS AND METHODS

*Experimental Subjects*

Breeding populations were established from an outcrossed, captive-bred colony having an effective population size of

about 150 birds. Only birds with wild-type plumage and conformation were employed as breeders or participants in mate-choice experiments. Experiments were performed in 2003 and 2004.

*Artificial Crests*

Crests were made from artificial fingernails cut to standard dimensions. They were painted with white fingernail polish and trimmed with commercial (Letraset, Ashford, U.K.) drafting tape. Two styles of crests were manufactured: vertically striped (V) crests were taller than they were wide, whereas horizontally striped (H) crests were wider than tall (Fig. 1). Crest shapes were designed so that the black horizontal and vertical stripes were of approximately equal length and so that the crest types were of similar area. All crests were mounted on platforms (minimum 1 cm<sup>2</sup>) also made from artificial fingernails; the top surface of platform was painted gray to blend with the birds' plumage. Finished crests weighed 1 g and were applied to birds' crowns using non-toxic, water-based glue.

Crest whiteness conferred by nail polish appeared somewhat less bright or saturated than that conferred by white feathered crests; this was confirmed by spectrophotometric measurements, which also revealed no UV reflectance of the crest types used in these experiments. Previous experiments (Burley and Symanski 1998) indicated that zebra finch responsiveness to white feather crests was independent of whether lighting conditions permitted UV perception.

*Breeding Protocol*

In the course of these experiments, up to four breeding populations were maintained simultaneously in large (94 m<sup>3</sup>) outdoor aviaries. Each experimental population consisted of 18 to 20 pairs and was visually isolated from the others. Avicultural management procedures ensured that the genetic background of all experimental populations was similar and precluded close inbreeding (full- or half-sib mating).

Birds were allowed to choose mates and reproduce freely. In aviaries in which breeders wore crests, crests were applied after pairs formed but before the first eggs hatched. Breeders were captured twice a week and crests were reglued or replaced as needed. Food (commercial seed mix), oyster shell, and water were available ad libitum throughout experiments. Other resources (grass and feathers for nest-building and a protein supplement) were regularly supplied. At least two nest sites were available for each breeding pair.

When offspring produced in these populations reached 50–54 days of age, they were captured and housed inside their natal aviary in unisexual cages. This procedure prevented young birds from attempting to reproduce as subadults (Zann 1996). The acquisition stage of sexual imprinting (Bischof 1994) is thought to be complete before 50 days of age, and dispersal around this age often occurs in nature (Burley et al. 1989). Although caged subadults were visually isolated from opposite-sexed birds also held in cages, they were in visual contact with free-flying adults in their natal aviary. The caged birds interacted frequently with free-flyers and were regularly observed to engage in heterosexual courtship as adulthood approached (during the consolidation phase of

NANCY TYLER BURLEY

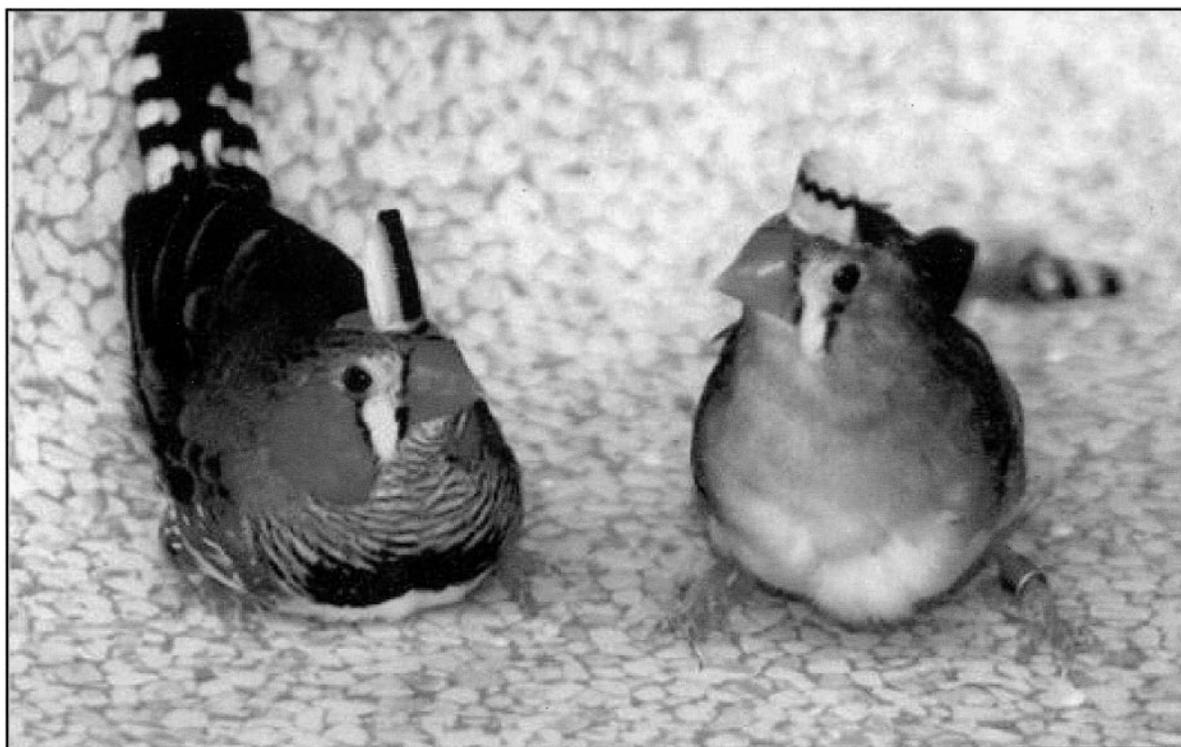


FIG. 1. Crest phenotypes used in this study. The female zebra finch (right) wears the horizontally striped crest type (H); the male wears the vertically striped phenotype (V). H crests measured approximately 8 mm tall  $\times$  10 mm wide; comparable measurements for V crests were 10.5 mm  $\times$  7.5 mm.

sexual imprinting; Bischof 1994). When the caged birds reached 90 days of age (i.e., young adults), they were removed from their natal aviary and housed in the facility used for measuring social preferences.

At the end of a breeding experiment, and after all potential test birds had been removed from the aviary, I stopped maintaining the crests of breeders until they eventually fell off.

#### *Social Preference Trials*

Soon after young adults were removed from their natal aviary, they were acclimated to the test apparatus. The apparatus, and the acclimation and exposure procedures, are described in detail elsewhere (Burley 1986b; Burley and Symanski 1998). Lighting was provided by natural spectrum bulbs, and stimulus and test birds were physically separated by wire mesh. After acclimation, test birds received 2 days of exposure to the range of experimental phenotypes with which they would be tested (test sequence exposure). Finally, test birds received 4 h of pretrial exposure to stimulus sets with which they were actually tested; this exposure occurred the day before they were tested. During acclimation and test sequence exposure, test birds were never exposed to stimulus birds used in actual experiments. Pretest exposure periods served to provide birds an assessment phase of mate choice; stable preferences are not observed during these periods, as birds spend significant time with all stimuli before reaching decisions. Once birds have had pretest exposure, decisions recorded during mate choice trials are repeatable (Burley, unpubl. data). At all times (acclimation, exposure, and pref-

erence testing), all stimuli presented to test birds were housed in individual cages, so that physical interaction among stimulus phenotypes was not possible.

Prior to a trial, a single test bird was released into an apparatus and allowed to recover from handling for 10 min. The subsequent 30-min trial was continuously monitored by a human observer, who watched from an adjacent room and scored test bird movements throughout the apparatus. Social time was the time (in seconds) the test bird spent on perches that permitted viewing of stimuli; only one stimulus could be viewed at any time. A trial was considered unsuccessful when a test bird accumulated less than 600 sec of social time during a trial, or when a stimulus bird lost a crest during a trial. Failure to meet the 600-sec criterion is more common in trials examining same-sex social preferences; sometimes test birds rest throughout most of a trial, for unknown reasons. Following an unsuccessful trial, the test bird was retested with the same set at a later date. About 5–10% of all trials failed in these experiments.

Birds were typically tested with two stimulus sets per experiment or subexperiment (an exception is noted below), and their preferences were averaged across tests. This procedure was carried out in part to reduce effects of preferences for other traits on the results. Although individuals within stimulus sets were matched for age, beak color, and body size, individual test birds retain idiosyncratic preferences or aversions for particular stimulus birds (N. T. Burley, unpubl. data). Ideally each stimulus bird would be used in only one trial, but this would require an unfeasibly large population

## SELECTIVE SEXUAL IMPRINTING

size. (To meet this criterion, more than 900 stimulus birds would have been needed for the first experiment alone.) By averaging each test bird's response across two stimulus sets and testing different test birds with different combinations of stimulus sets, pseudoreplication is minimized.

All birds within a stimulus set came from the same natal aviary; test birds were never exposed to stimulus birds from their own natal aviary. An individual bird participated in only one stimulus set. To offset any position effects, which are uncommon in my test apparatus, the positions of stimulus phenotypes around the apparatus were changed regularly.

For various methodological reasons, it was not possible to use all stimulus sets the same number of times. When a stimulus bird lost its crest midway through a planned sequence, for example, the set was retired if crown feathers were also lost. Instead, stimulus sets were used a maximum number of times (which varied between experiments based on bird availability) and then retired. Whenever possible, a given stimulus set was tested with test birds from more than one treatment; constraints on this procedure were imposed by the rule that a stimulus set must come from a different aviary from the test birds exposed to it. Test birds intended for use in more than one experiment were sometimes unavailable for later experiments due to injury or a decline in condition. Only birds judged to be in peak condition were used, as condition influences selectivity of test birds (Burley and Foster 2006).

*Experiment 1*

Test birds belonged to one of three rearing treatments. Controls were reared in two aviaries in which all breeders were wild-type and uncrested. Treatment VV birds were reared in an aviary in which all wild-type breeders wore V crests, while HH birds were reared in an aviary containing wild-type breeders that wore H crests (Fig. 1). In the first set of trials, test birds were exposed to opposite-sex stimulus sets containing three adult birds matched for phenotypic characteristics (beak color, body size, age). Prior to testing, one stimulus bird in each set was randomly assigned to wear a V crest, and a second one was assigned to wear an H crest. The third stimulus bird was uncrested. Each test bird was tested with two stimulus sets and its social time with each stimulus phenotype was summed across trials prior to statistical analysis.

Following completion of the first set of trials, additional tests were performed. For birds reared in experimental treatments, subjects were tested for their isosexual social preference using the same range of crest phenotypes (V, H, and none). This was to determine if observed preferences were general social ones, or specifically sexual in nature. Each bird was tested with two stimulus sets.

Control birds received a heterosexual follow-up test when at least half their test cohort had showed a preference for crested phenotypes in the first round of testing. In these follow-up trials, each test bird was presented with stimulus sets containing two individuals, one of which was uncrested and one of which wore the crest type other than that which the chooser had accumulated the most social time during the first round of trials; each test bird was tested with two stimulus

sets. The heterosexual follow-up was performed because previous research has shown that when zebra finches are given more than two simultaneous social choices, they often spend so much time with their first choice that differences in preferences for the remaining stimuli cannot be measured (Burley 1985). The follow-up was necessary, then, to determine whether birds that preferred one crest phenotype over wild-type (the noncrested phenotype) also preferred the other crest phenotype over wild-type.

Because I planned to use birds from control and VV treatments in experiment 3, I trained and tested a greater number of test birds from these cohorts than from the HH cohort. Test subjects were drawn from as many breeding pairs as possible within treatments, with the exception that I avoided using offspring of birds that tended to lose their crests between the crest repair sessions that occurred twice weekly.

*Experiment 2*

Females from the control and VV treatments of experiments 1 were tested to measure heterosexual preference for red-banded males versus V males. Previously studies have shown that normally reared females have a mate preference for red-banded males (Burley et al. 1982; Burley 1986b); I wished to ascertain whether this preference was modified by rearing condition. Methods were identical to those of experiment 1, except that, to maximize comparability, all subjects were tested with the same two stimulus sets. In a follow-up experiment, birds from these cohorts were tested for their preference of red-banded versus green-banded males. In the follow-up, each test bird was tested twice with a given stimulus set; between trials with the same set, the leg bands were switched between stimuli.

*Experiment 3*

After all crests had fallen off breeders in the VV flight of experiment 1 and the birds had been rested for two months, they were recreted—females with H crests and males with V crests—and allowed to breed again. Rearing procedures within the aviary were identical to those of experiment 1. Offspring of both sexes were tested as adults for their heterosexual preferences for H, V, and uncrested phenotypes using methods described for experiment 1. Each stimulus set consisted of one bird with no crest, one H bird, and one V bird. Due to a shortage of test females in this treatment that arose through experimenter error, each test female was tested with three of six heterosexual stimulus sets.

## RESULTS

*Experiment 1*

*Control treatment.*—In the first round of trials, 19 females were each tested with two of eight stimulus sets. Although 16 of 19 females spent most of their social time with one of the crested phenotypes, there was not a consensus preference for a single stimulus phenotype in the three-way analysis (median social time = 1472 sec of 1800-sec trial; Friedman  $\chi^2_r = 2.48$ ,  $df = 2$ ,  $P = 0.29$ ; Fig. 2). Nevertheless, in a post hoc comparison, females did accumulate somewhat more time with crested phenotypes (median percent time = 44%)

NANCY TYLER BURLEY

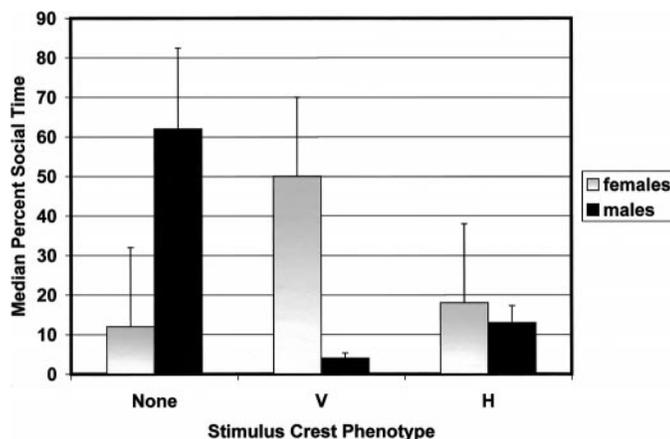


FIG. 2. Heterosexual social preferences of control female ( $N = 19$ ) and male ( $N = 21$ ) zebra finches in experiment 1. None, uncrested stimulus; V, stimulus wearing vertically striped crest; H, stimulus wearing horizontally striped crest. Error bars are semi-interquartile ranges (Sokal and Rohlf 1981). Control test birds were derived from 19 breeding pairs.

than they did with uncrested males (median = 12%;  $\chi^2 = 4.26$ ,  $df = 1$ ,  $P = 0.039$ ). V males were the first choice of nine females, and H males were the first choice of six females; one female spent equal time with males having the two crest phenotypes. I compared the relative strength of choice of those birds that spent the most time with V versus H crests in these trials. In a post hoc comparison, females that preferred V males accumulated a somewhat greater fraction of social time with V males ( $N = 9$ ; median time = 85%) than those that preferred H males spent with H males ( $N = 6$ ; median time = 54%; Mann-Whitney  $U = 44$ ,  $df = 1$ ,  $P = 0.045$ ).

In the second round of trials, 14 of these 15 females were then tested for their choice between uncrested males and males with the crest-type they did not prefer in the first round. Twelve of 14 females preferred the crested phenotype in this round (median time with: crested stimuli = 93%; uncrested stimuli = 7%;  $\chi^2 = 4.57$ ,  $df = 1$ ,  $P = 0.033$ ). Thus, a majority of females preferred male stimuli wearing either crest phenotype over the uncrested stimulus.

Control males ( $N = 21$ ) displayed a strong tendency to associate with uncrested females (median social time = 1377 sec; 11 stimulus sets;  $\chi^2 = 14.2$ ,  $df = 2$ ,  $P = 0.001$ ; Fig. 2). Sixteen of 21 males accumulated the most time with uncrested females.

**Vertical crest (VV) treatment.**—In heterosexual choice tests among the three stimulus phenotypes, test females ( $N = 15$ ) displayed a strong preference for V males (median social time = 1574 sec; eight stimulus sets;  $\chi^2 = 15.6$ ,  $df = 2$ ,  $P < 0.001$ ; Fig. 3). The preference of VV-reared females for V males was stronger than that shown by control females ( $U = 167$ ,  $df = 1$ ,  $P = 0.023$ ). In isosexual tests, VV-reared females ( $N = 12$ ) showed no tendency to associate with a particular stimulus type (median social time = 1538 sec; six stimulus sets;  $\chi^2 = 0.125$ ,  $df = 2$ ,  $P = 0.94$ ; Fig. 4).

Male test subjects ( $N = 20$ ) given heterosexual tests preferred to associate with V females (median social time = 1412 sec; seven stimulus sets;  $\chi^2 = 8.12$ ,  $df = 2$ ,  $P = 0.017$ ;

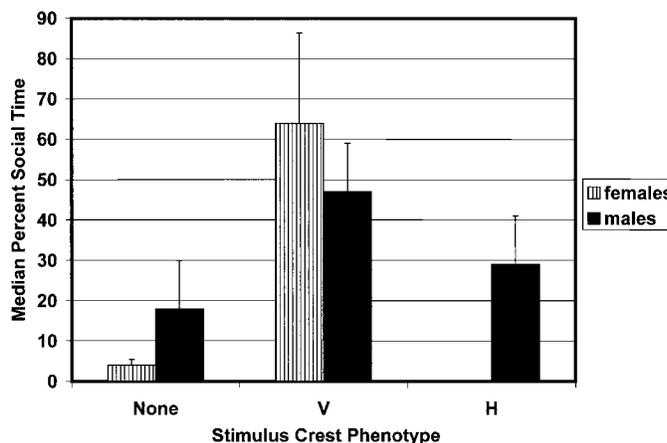


FIG. 3. Heterosexual social preferences of test female ( $N = 15$ ) and male ( $N = 20$ ) zebra finches reared in treatment VV (parents of both sexes wearing vertical crests) of experiment 1. VV test birds were derived from 15 breeding pairs.

Fig. 3). Their preference for V females was significantly stronger than the preference of control males for V females ( $U = 364$ ,  $df = 1$ ,  $P < 0.001$ ). In isosexual tests, males ( $N = 10$ ) showed no significant preference for associating with V males (median social time = 1686 sec; seven stimulus sets;  $\chi^2 = 3.65$ ,  $df = 2$ ,  $P = 0.16$ ; Fig. 4).

**Horizontal crest (HH) treatment.**—Test females ( $N = 12$ ) preferred to associate with H males (median social time = 1436 sec; nine stimulus sets;  $\chi^2 = 6.17$ ,  $df = 2$ ,  $P = 0.046$ ; Fig. 5). The preference of HH-reared females for H males was stronger than that shown by control females ( $U = 167$ ,  $df = 1$ ,  $P = 0.032$ ). In isosexual tests, females ( $N = 8$ ) showed no tendency to associate with any stimulus type (median social time = 1542 sec; four stimulus sets;  $\chi^2 = 1.56$ ,  $df = 2$ ,  $P = 0.46$ ; Fig. 6).

Test males ( $N = 10$ ) showed a strong preference to associate with H females (median social time = 1204 sec; five stimulus sets;  $\chi^2 = 10.0$ ,  $df = 2$ ,  $P = 0.007$ ; Fig. 5). Their preference for H females was significantly stronger than that of control males for H females ( $U = 20$ ,  $df = 1$ ,  $P < 0.001$ ).

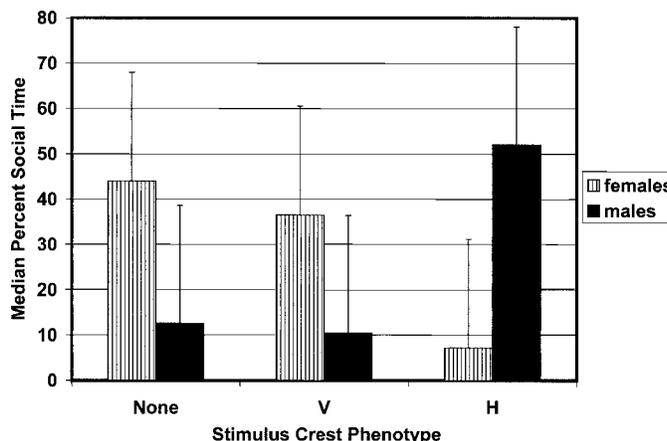


FIG. 4. Isosexual social preferences of female ( $N = 12$ ) and male ( $N = 10$ ) zebra finches from treatment VV (parents of both sexes wearing vertical crests) of experiment 1.

## SELECTIVE SEXUAL IMPRINTING

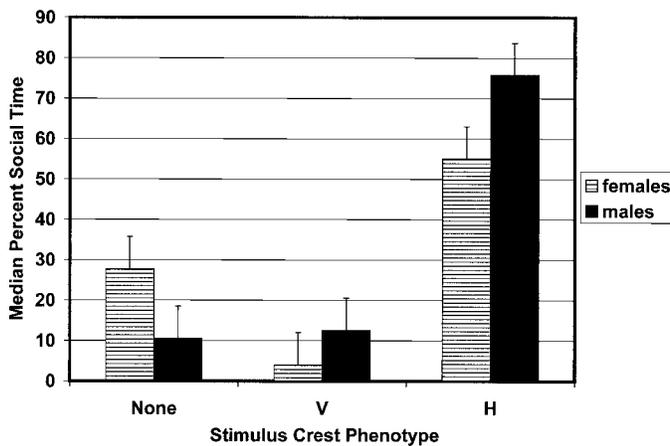


FIG. 5. Heterosexual social preferences of test female ( $N = 12$ ) and male ( $N = 10$ ) zebra finches reared in treatment HH (parents of both sexes wearing horizontal crests) of experiment 1. HH test birds were derived from 11 breeding pairs.

In isosexual tests, males ( $N = 9$ ) showed no significant tendency to affiliate with a stimulus type (median social time = 1256 sec; seven stimulus sets;  $\chi^2 = 2.67$ ,  $df = 2$ ,  $P = 0.26$ ; Fig. 6).

*HH versus VV rearing treatments.*—Mann-Whitney tests were performed to compare the relative heterosexual tendency of VV-reared versus HH-reared birds to associate with V, H, and uncrested stimulus birds. For both sexes, birds from the two rearing treatments differed in the percentage of time they associated with V stimuli (females:  $U = 160$ ,  $df = 1$ ,  $P = 0.001$ ; males:  $U = 176$ ,  $df = 1$ ,  $P = 0.001$ ) and H stimuli (females:  $U = 12$ ,  $df = 1$ ,  $P < 0.0001$ ; males:  $U = 20$ ,  $df = 1$ ,  $P < 0.001$ ). Neither sex differed in its tendency to affiliate with uncrested opposite-sex stimuli based on rearing treatment (females:  $U = 70$ ,  $df = 1$ ,  $P = 0.32$ ; males:  $U = 116$ ,  $df = 1$ ,  $P = 0.48$ ).

*Relative strength of preferences for crest types.*—I compared the percent time accumulated with V stimuli by VV birds with the percent time accumulated with H stimuli by HH birds in heterosexual tests. VV females ( $N = 15$ ) spent a larger fraction of their social time with V males (median = 95%) than HH females ( $N = 12$ ) accumulated with H males (median = 55%;  $U = 132$ ,  $df = 1$ ,  $P = 0.040$ ). By contrast, HH males ( $N = 10$ ) accumulated more time with H females (median = 76%) than VV males ( $N = 20$ ) spent with V females (median = 46%;  $U = 39$ ,  $df = 1$ ,  $P = 0.007$ ).

## Experiment 2

There was a significant difference between control and VV treatments in tendency to affiliate with crested versus banded males (median social time = 1508 sec;  $U = 75.0$ ,  $df = 1$ ,  $P = 0.002$ ). Females reared in the vertical crest treatment ( $N = 10$ ) spent a median of 88% of their social time with the crested stimuli, while control females ( $N = 8$ ) spent a median of 14% of their social time with crested males.

When females from the two test cohorts were given a choice between red-banded and green-banded males, there was no difference in strength of preference displayed ( $N = 5, 7$ ;  $U = 18$ ,  $df = 1$ ,  $P = 0.94$ ) and the overall average

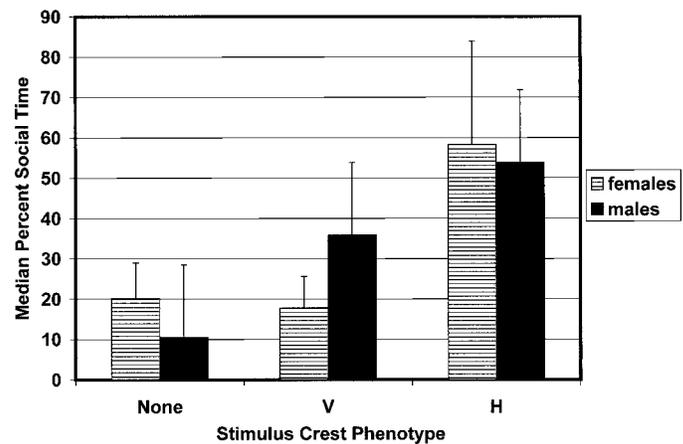


FIG. 6. Isosexual social preferences of female ( $N = 8$ ) and male ( $N = 9$ ) zebra finches from treatment HH (parents of both sexes wearing horizontal crests) of experiment 1.

preference was similar to that previously reported (Burley et al. 1982; Burley 1986b; median = 67%,  $N = 12$ ,  $\chi^2 = 5.33$ ,  $df = 1$ ,  $P = 0.021$ ).

## Experiment 3

Ten test females preferred to associate with H males (six stimulus sets;  $\chi^2 = 13.9$ ,  $df = 2$ ,  $P = 0.001$ ; Fig. 7). Sixteen test males preferred to associate with H females (seven stimulus sets;  $\chi^2 = 24.0$ ,  $df = 2$ ,  $P < 0.01$ ; Fig. 7).

## DISCUSSION

Results of these experiments support the idea that visual phenotypic divergences among populations of a given species may increase behavioral reproductive isolation via sexual imprinting. In the first experiment, control females showed a predisposition toward white crests as previously reported, even though the human-made materials the crests were constructed from were quite different from the natural feathers used previously. Control females showed no consensus of

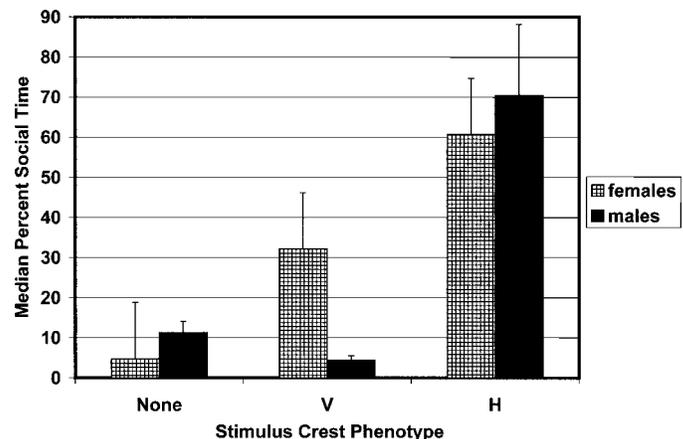


FIG. 7. Heterosexual social preferences of female ( $N = 10$ ) and male ( $N = 16$ ) zebra finches from experiment 3, in which mothers wore horizontal crests and fathers wore vertical crests. Test birds were derived from 15 breeding pairs.

NANCY TYLER BURLEY

preference for V or H crests; both phenotypes were preferred over the uncrested stimulus. As previously reported (Burley and Symanski 1998), control males preferred uncrested females. In the HH and HV treatments, both sexes preferred the phenotype of their natal population, and the strength of their preference for that phenotype was stronger than the corresponding preference of birds reared in control aviaries.

That the imprinting response observed in experiment 1 represents a mate preference rather than a more general social preference is indicated in part by the difference in response of VV- and HH-reared birds in isosexual versus heterosexual tests. In all four comparisons (two sexes, two treatments), birds showed heterosexual preferences for stimuli wearing crests corresponding to rearing treatment but failed to show significant isosexual preferences. Also, the heterosexual test protocol employed here has repeatedly been demonstrated to document mate preferences (e.g., Burley 1986a, 1988; Price and Burley 1994).

A limitation of experiment 1 was that all test subjects within a treatment were drawn from the same experimental aviary. Conceivably, some variable might have differed between the flights other than parental crest phenotype that caused differential responsiveness to V and H crests. The physical set up and resources provided to the two aviaries were virtually identical, however, and the founders were drawn from the same outcrossed stock, so this possibility is remote. Moreover, how a random, uncontrolled variable could accidentally predispose birds in the HH treatment to be attracted to H crests and those in the VV treatment to be attracted to V crests (*vis-à-vis* the responses of birds from two control flights, also of the same design) is difficult to imagine. Regardless, the results of experiment 3 eliminate this possibility, as offspring of both sexes altered their imprinting response within a flight based on parental crest characteristics. Specifically, offspring reared in the flight when parents were both crested V preferred V-crested potential mates, whereas when the maternal phenotype was switched to H, offspring of the same parents (and reared in the same breeding aviary) developed a mate preference for H-crested birds. Thus, in experiment 1 an individual's early experience created a mate preference for a specific crest trait value (horizontal or vertical stripe) like that of its parents and typical of the population in which it grew up.

Results of experiment 2 suggest that imprinting not only influences the mate preference for a specific stimulus or trait value that is imprinted upon, but also changes preference priorities for different traits. Females reared in the VV treatment preferred V males over red-banded ones, while control females showed the reverse ranking, even though both cohorts of females were attracted to both red-banded and white-crested males. The imprinting experience affected both preferences for specific features of white crests as well as relative preferences for crests versus a different ornamental trait. This experience-based change in female mating priorities would tend to further increase isolation between phenotypically diverging populations by creating a tendency to focus on different ornamental traits. A result with similar consequences was obtained for female Javanese mannikins, *Lonchura leucogastroides*, which imprinted on conspecific males wearing artificial red crests. Plenge et al. (2000) found that this pref-

erence was generalized by the imprinted females to include preferences for red tail stripes.

### *Selective Sexual Imprinting*

Results of these experiments may provide an illuminating comparison to other recent studies of zebra finch tendencies to imprint on parental traits. I found that while male zebra finches readily imprint on gray or white maternal crests, females fail to imprint on either crest color (Burley 2006); instead, females in all rearing treatments showed a preference for white-crested males quantitatively indistinguishable from that shown by females reared with uncrested parents (Burley and Symanski 1998). Thus, this behavioral trait—a predisposition for males with white-feathered crests—seems to resist or override imprinting responses, at least when females are reared with parents that are otherwise phenotypically wild-type. In the present study, however, both sexes did imprint on population-typical details of white crests (experiment 1); additional results (experiment 3) indicate that the major imprinting response of both sexes was to maternal crest characteristics.

The only other study to report a tendency of female zebra finches to imprint on a maternal trait focused on plumage color. Experiments involved rearing young birds with conspecific parents having wild-type (gray) or white body plumage, and as in this study, both sons (Immelmann 1985; Vos et al. 1993) and daughters (Vos 1995a) imprinted on maternal traits. (As these authors used somewhat different methodologies than those employed in my lab, one must be careful in drawing comparisons. Here I am assuming that qualitatively similar results would be obtained using a range of apparatuses.) It is noteworthy that gray and white zebra finches differ in additional details besides the ground color of their plumage; of particular interest here is the observation that the pure white morph lacks the species-typical eye stripes (Rogers 1977). Perhaps young birds in the gray versus white “plumage color” imprinting studies attended to differences in parental eye stripe phenotypes and adopted a preference for their mother's type (eye stripe present or eye stripe absent). The tendency of both sexes to imprint on maternal crest stripes found here may be an extension of attentiveness to maternal eye stripes.

Zebra finch eye stripes display variation among individuals and families (fig. 3 in Burley and Bartels 1990), and experiments suggest that adult zebra finches may practice phenotype matching of this trait to recognize kin (Burley et al. 1990). Why offspring should be more attentive to maternal eye stripes is not clear, but perhaps zebra finches use different traits to recognize maternally and paternally inherited kin (e.g., Clayton 1988, 1990). Further work should be undertaken to explore this possibility and the possible significance of eye stripe variation. Such an exploration might illuminate the apparent sex difference in response to V crests (upon which females tended to imprint somewhat more frequently in experiment 1) and H crests (to which males showed a greater imprinting response); additional work would be needed to establish that the subtle sex difference in tendency to imprint on H and V crests observed here is robust.

Another study produced quite different results. While nor-

## SELECTIVE SEXUAL IMPRINTING

mally reared zebra finches do not display preferences for red-crested conspecifics (Burley and Symanski 1998; Witte and Sawka 2003), Witte and Sawka (2003) reported that female zebra finches sexually imprint on red crests worn by male parents; moreover, males did not imprint on maternal or paternal red crests. This result differs strikingly with imprinting experiments reported here, and earlier ones in which males imprinted on white or gray crests worn by mothers, but females failed to imprint on either sex (Burley 2006). In sum, for a given trait (crest color), imprinting response of both sexes varies with trait value (white, red, gray, black-and-white striped).

The tendency of females to imprint on paternal red crests is probably an extension of their general receptivity to the color red (Witte and Sawka 2003). Zebra finch beak color naturally ranges from orange to red, and males' beaks are generally redder than those of females; normally reared female zebra finches are attracted to males with bright red beaks (Burley and Coopersmith 1987; Houtman 1990; de Kogel and Puijs 1996). Females are also attracted to males wearing bright red leg bands (Burley et al. 1982; Burley 1986b). Normally reared males, in contrast, are attracted to females with orange beaks (Burley and Coopersmith 1987; Price and Burley 1994). These results suggest that both sexes have predispositions to imprint on sex-appropriate traits or trait values (see also Clayton 1988, 1990; Weisman et al. 1994). While males appear to find a wider range of novel maternal phenotypes appropriate for imprinting than females do, both sexes seem to fail to imprint on opposite-sex parental traits deemed inappropriate. The tendency of females to imprint on maternal traits in some cases and paternal traits in others also suggests that imprinting is an actively selective process.

*Sexual Selection and Sexual Imprinting*

Some of the apparent discrepancies among studies discussed here might be explained by the existence of evolved sets of decision rules that regulate the tendency to imprint on parental traits. As suggested above, such rules might be designed to respond to a trait partly on the basis of whether it is naturally sexually dimorphic. This possibility is consistent with the apparent female tendency to imprint on paternal traits that are naturally secondary sexual characteristics. However, it seems unlikely that females generally imprint on the specific values of their fathers' secondary sexual traits. If, for example, females of a population have a consensus mate preference favoring a certain male phenotype, female offspring of males that deviate most from the preferred phenotype will make poor mating decisions if they imprint on their father's deviant trait value. Thus, any mechanism that lowers tendency to imprint on parental values of traits that are strongly sexually selected may be advantageous. Indeed, if such a mechanism does not exist, and females develop mate preferences for trait values identical to their fathers', the occurrence of consensus mate preferences would simply mean that females tend to prefer the most common male phenotype in a population. In sexually dimorphic species in which males possess more ornamental traits than females do, selection will thus be stronger on females to resist imprinting on a wider range of trait values than will selection on males.

For both sexes, however, we can expect some structure in imprinting responses of normally or quasi-normally reared birds; otherwise, offspring might imprint on all sorts of parental traits that are both unusual and maladaptive. In short, both consensus preferences and consensus aversions may override imprinting responses. The failure of rearing treatment to influence strength of female preference for plain (unstriped) white crests (Burley 2006) appears to be an example of a consensus preference that overrides imprinting responses. Evidence of consensus aversions is suggested by the failure to imprint on species-inappropriate traits reported for another estrildine (Hörster et al. 2000; but see Plenge et al. 2000).

Under selective imprinting, the fate of new traits and trait values emerging in populations will likely depend on organism perception of their information content (e.g., kin, sex, or population indicator). Of course, that perception may not be accurate, especially when a novel trait or trait value arises by mutation or experimental manipulation. Thus, for example, while zebra finches may respond to striped crests because such stripes have been meaningful indicators of kinship in their recent history, the striped crests used here provided no such information. Similar mistaken perceptions may lead to evolutionary divergences in real populations. This logic implies, however, that only a subset of novel traits may possess the sorts of information that lead to imprinting responses facilitating behavioral reproductive isolation (Burley 2006).

Experimenters seeking to investigate the occurrence and consequences of selective sexual imprinting need to be attentive to the signal value of existing traits. Thus, for example, imprinting on kin traits would require the occurrence of traits or suites of traits that are accurate indicators of kinship. These traits include environmentally based, learned traits, such as songs (e.g., Clayton 1987), but may also include genetically based traits (Lehman and Perrin 2002). In zebra finches, eye stripe variation may function as a genetically based trait (Burley and Bartels 1990; Burley et al. 1990). This possibility is implausible for beak color, however, as beak color, while heritable (Price and Burley 1993), does not naturally provide reliable information about kin status (Burley and Coopersmith 1987; Burley and Bartels 1990) any more than eye color variability typically provides such information in humans. Finally, to avoid inferential errors, experimenters must also be attentive to the possibility that subjects select different traits as imprinting stimuli than those that are categorized by the experimenter (e.g., Calkins and Burley 2003).

## ACKNOWLEDGMENTS

I thank K. Ortiz, K. Vo, and C. Que for running mate choice trials and students in Biology 199 for helping to maintain the crested experimental population. N. Pohl assisted with spectrophotometric analysis. T. Slagsvold and an anonymous reviewer provided useful comments on the manuscript.

## LITERATURE CITED

Albert, A. Y. K. 2005. Mate choice, sexual imprinting, and speciation: a test of a one-allele isolating mechanism in sympatric sticklebacks. *Evolution* 59:927–931.

NANCY TYLER BURLEY

Armstrong, E. A. 1965. Bird display and behavior: an introduction to the study of bird psychology. Dover, New York.

Andersson, M. 1994. Sexual selection. Monographs in Behavior and Ecology. Princeton Univ. Press, Princeton, NJ.

Basolo, A. 1998. Evolutionary change in a receiver bias: a comparison of female preference functions. *Proc. R. Soc. Lond. B* 265:2223–2228.

Bateson, P. 1978. Sexual imprinting and optimal outbreeding. *Nature* 273:659–660.

Bereczkei, T., P. Gyuris, and G. E. Weisfeld. 2004. Sexual imprinting in human mate choice. *Proc. R. Soc. Lond. B* 271:1129–1134.

Bischof, H.-J. 1994. Sexual imprinting as a two-stage process. Pp. 82–97 in J. A. Hogan and J. J. Bolhuis, eds. Causal mechanisms of behavioural development. Cambridge Univ. Press, Cambridge, U.K.

Burley, N. 1985. The organization of behavior and the evolution of sexually selected traits. Pp. 22–44 in P. A. Gowaty, D. W. Mock, eds. Avian monogamy. Ornithology Monograph 37. American Ornithologists' Union, Washington, DC.

———. 1986a. Sexual selection for aesthetic traits in species with biparental care. *Am. Nat.* 127:415–445.

———. 1986b. Comparison of the band-colour preferences of two species of estrildid finches. *Anim. Behav.* 34:1732–1741.

———. 1988. The differential allocation hypothesis: an experimental test. *Am. Nat.* 132:611–628.

Burley, N. T. 2006. Oedipus, yes; Electra, no: sex differences in sexual imprinting on artificial crests in zebra finches. *Behav. Ecol. In press.*

Burley, N., and P. J. Bartels. 1990. Phenotypic similarities of sibling zebra finches. *Anim. Behav.* 39:174–180.

Burley, N., and C. B. Coopersmith. 1987. Bill color preferences of zebra finches. *Ethology* 76:133–151.

Burley, N. T., and V. S. Foster. 2006. Variation in female choice of mates: condition influences selectivity. *Anim. Behav. In press.*

Burley, N. T., and R. Symanski. 1998. "A taste for the beautiful": latent aesthetic mate preferences for white crests in two species of Australian grassfinches. *Am. Nat.* 152:792–802.

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

Burley, N., R. A. Zann, S. C. Tidemann, and E. B. Male. 1989. Sex ratios of zebra finches. *Emu* 89:83–92.

Burley, N., C. Minor, and C. Strachan. 1990. Social preferences of zebra finches for siblings, cousins and non-kin. *Anim. Behav.* 39:775–784.

Calkins, J. D., and N. T. Burley. 2003. Mate choice for multiple ornaments in the California quail, *Callipepla californica*. *Anim. Behav.* 65:69–81.

Clayton, N. S. 1987. Song tutor choice in zebra finches. *Anim. Behav.* 35:714–721.

———. 1988. Song discrimination learning in zebra finches. *Anim. Behav.* 36:1016–1024.

———. 1990. Subspecies recognition and song learning in zebra finches. *Anim. Behav.* 40:1009–1017.

Coyne, J. A., and H. A. Orr. 2004. Speciation. Sinauer, Sunderland, MA.

Darwin, C. 1871. The descent of man and selection in relation to sex. John Murray, London.

de Kogel, C. H., and H. J. Priejs. 1996. Effects of brood size manipulations on sexual attractiveness of offspring in the zebra finch. *Anim. Behav.* 51:699–708.

Dooling, R. J., S. D. Brown, K. Manabe, and E. F. Powell. 1996. The perceptual foundations of vocal learning in budgerigars. Pp. 113–137 in C. F. Moss and S. J. Shettleworth, eds. Neuroethological studies of cognitive and perceptual processes. Westview Press, Boulder, CO.

Dukas, R. 1998. Evolutionary ecology of learning. Pp. 129–174 in R. Dukas, ed. Cognitive ecology: the evolutionary ecology of information processing and decision making. Univ. of Chicago Press, Chicago.

Düttmann, H., H.-H. Bergmann, and W. Engländer. 1998. Development of behavior. Pp. 223–246 in J. M. Stark and R. E. Ricklefs, eds. Avian growth and development. Cambridge Univ. Press, Cambridge, U.K.

Galef, B. G., Jr., and C. Allen. 1995. A new model for studying behavioral traditions in animals. *Anim. Behav.* 50:705–717.

Grant, P. R., and B. R. Grant. 1997a. Genetics and the origin of bird species. *Proc. Natl. Acad. Sci. USA* 94:7768–7775.

———. 1997b. Hybridization, sexual imprinting and mate choice. *Am. Nat.* 149:1–28.

Hansen, B. T., and T. Slagsvold. 2004. Early learning affects social dominance: interspecifically cross-fostered tits become subdominant. *Behav. Ecol.* 15:262–268.

Hess, E. H. 1973. Imprinting: early experience and the developmental psychobiology of attachment. Van Nostrand Reinhold, New York.

Hörster, A., E. Curio, and K. Witte. 2000. No sexual imprinting on red bill as a novel trait. *Behaviour* 137:1223–1239.

Houtman, A. M. 1990. Sexual selection in the zebra finch (*Poephila guttata*). Ph.D. diss., University of Oxford, Oxford, U.K.

Immelmann, K. 1975. Ecological significance of imprinting and early learning. *Annu. Rev. Ecol. Syst.* 6:15–37.

———. 1985. Sexual imprinting in zebra finches: mechanisms and biological significance. Pp. 156–172 in V. D. Ilyichev and U. M. Gavrillov, eds. Proceedings of the XVIII International Ornithological Congress. Nauka, Moscow.

Immelmann, K., and S. J. Suomi. 1981. Sensitive phases in development. Pp. 395–431 in K. Immelmann, G. W. Barlow, L. Petrionovich, and M. Main, eds. Behavioural development. Cambridge Univ. Press, Cambridge, U.K.

Irwin, D. E., and T. Price. 1999. Sexual imprinting, learning, and speciation. *Heredity* 82:347–354.

Kalmus, H., and J. Maynard Smith. 1966. Some evolutionary consequences of pegmatic mating systems (imprinting). *Am. Nat.* 100:619–635.

Kendrick, K. M., M. R. Hinton, K. Atkins, M. A. Haupt, and J. D. Skinner. 1998. Mothers determine sexual preferences. *Nature* 395:229–230.

Kruijt, J. P. 1985. On the development of social attachments in birds. *Neth. J. Zool.* 35:45–62.

Kruijt, J. P., and G. B. Meeuwissen. 1993. Consolidation and modification of sexual preferences in adult male zebra finches. *Neth. J. Zool.* 43:68–79.

Laland, K. N. 1994. On the evolutionary consequences of sexual imprinting. *Evolution* 48:477–489.

Lehman, L., and N. Perrin. 2002. Altruism, dispersal, and phenotype-matching kin recognition. *Am. Nat.* 159:451–468.

Lickliter, R. 1993. Timing and the development of perinatal perceptual organization. Pp. 105–123 in G. Turkewitz and D. A. Devenny, eds. Developmental time and timing. Erlbaum Associates, Hillsdale, NY.

Lorenz, K. 1935. Der Kumpan in der Umwelt des Vogels. *J. Ornithol.* 83:137–213, 289–413.

Nelson, D. A. 2000. A preference for own-subspecies' song guides vocal learning in a song bird. *Proc. Natl. Acad. Sci. USA* 97:13348–13353.

Oyama, S. 1993. Constraints and development. *Neth. J. Zool.* 43:6–16.

Payne, R. B. 1973. Behavior, mimetic songs and song dialects, and relationships of the parasitic indigobirds (*Vidua*) of Africa. *Ornithol. Monogr.* 11:1–133.

Payne, R. B., L. L. Payne, J. L. Woods, and M. D. Sorenson. 2000. Imprinting and the origin of parasite-host species associations in brood-parasitic indigobirds, *Vidua chalybeata*. *Anim. Behav.* 59:69–81.

Plenge, M., E. Curio, and K. Witte. 2000. Sexual imprinting supports the evolution of novel male traits by transference of a preference for the colour red. *Behaviour* 137:741–758.

Price, D. K., and N. T. Burley. 1993. Constraints on the evolution of attractive traits: genetic (co)variance of zebra finch bill colour. *Heredity* 71:405–412.

———. 1994. Constraints on the evolution of attractive traits: selection in male and female zebra finches. *Am. Nat.* 144:908–934.

Rogers, C. 1977. Zebra finches. John Bartholomew and Son, Edinburgh.

## SELECTIVE SEXUAL IMPRINTING

- Schutz, F. 1965. Sexual Prägung bei Anatiden. *Z. Tierpsychol.* 22: 50–103.
- Shapiro, J. L. 1980. Species identification in birds: a review and synthesis. Pp. 69–111 in M. A. Roy, ed. *Species identity and attachment: a phylogenetic evaluation*. Garland STPM Press, New York.
- Sokal, R. R., and F. J. Rohlf. 1981. *Biometry*. 2nd ed. W. H. Freeman, New York.
- ten Cate, C. 1984. The influence of social relations on the development of species recognition in zebra finch males. *Behaviour* 91:263–295.
- . 2000. How learning mechanisms might affect evolutionary processes. *Trends. Ecol. Evol.* 15:179–181.
- ten Cate, C., and P. Bateson. 1988. Sexual selection: the evolution of conspicuous characteristics in birds by means of imprinting. *Evolution* 42:1355–1358.
- ten Cate, C., and D. R. Vos. 1999. Sexual imprinting and evolutionary process in birds: a reassessment. *Adv. Stud. Behav.* 28: 1–31.
- Vos, D. R. 1995a. Sexual imprinting in zebra-finch females: Do females develop a preference for males that look like their father? *Ethology* 99:252–262.
- . 1995b. The role of sexual imprinting for sex recognition in zebra finches: a difference between males and females. *Anim. Behav.* 50:645–653.
- Vos, D. R., J. Pijls, and C. ten Cate. 1993. Sexual imprinting in zebra finch males: a differential effect of successive and simultaneous experience with two colour morphs. *Behaviour* 126: 137–154.
- Weisman, R., S. Shackleton, L. Ratcliffe, D. Weary, and P. Boag. 1994. Sexual preferences of female zebra finches: imprinting on beak colour. *Behaviour* 128:15–24.
- Witte, K., and N. Sawka. 2003. Sexual imprinting on a novel trait in the dimorphic zebra finch: sexes differ. *Anim. Behav.* 65: 195–203.
- Zann, R. A. 1996. *The zebra finch: a synthesis of field and laboratory studies*. Oxford Univ. Press, Oxford, U.K.

Corresponding Editor: T. Tregenza