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Report

Sexual Imprinting Can Induce Sexual Preferences for Exaggerated Parental Traits

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Summary

Sexual preferences in animals are often skewed toward mates with exaggerated traits. In many vertebrates, parents provide, through the learning process of "sexual imprinting," the model for the later sexual preference [1–3]. How imprinting can result in sexual preferences for mates having exaggerated traits rather than resembling the parental appearance is not clear. We test the hypothesis [4] that a by-product of the learning process, "peak shift" [5, 6], may induce skewed sexual preferences for exaggerated parental phenotypes. To this end, zebra finch (*Taeniopygia guttata*) males were raised by white parents, with beak color as the most prominent sexual dimorphism. We manipulated this feature with nail varnish. At adult age, each male was given a preference test in which he could choose among eight females with beak colors ranging from more extreme on the paternal to more extreme on the maternal side. The males preferred females with a beak of a more extreme color than that of their mothers, i.e., they showed a peak shift. Sexual imprinting can thus generate skewed sexual preferences for exaggerated maternal phenotypes, phenotypes that have not been present at the time of the learning. We suggest that such preferences can drive the evolution of sexual dimorphism and exaggerated sexual traits.

Results and Discussion

Many animals possess exaggerated and often sexually dimorphic traits. As suggested by Darwin [7], such traits are likely to have evolved by sexual selection under the influence of skewed sexual preferences. Whereas this explanation is largely undisputed [8], far less clear is how such preferences arise in the choosing individual, i.e., which mechanisms and processes underlie these preferences [8–11]. However, to understand trait evolution, it is essential to understand these mechanisms, because theoretical models have shown that the direction and speed of evolutionary change in a sexually selected trait depend crucially on how the preference for such a trait is determined [12–14]. Sexual preferences are often assumed to be unlearned and to result from selection favoring preferences for traits that indicate mate quality. However, in most birds [1] and several mammals [2], including humans [3], sexual preferences are affected by the learning process of sexual imprinting. Young animals in species with sexual imprinting use the parental phenotype to model the later sexual preference. As an explanation of skewed sexual preferences in species showing sexual imprinting, it has been postulated that an additional perceptual bias, unconnected to the learning process, should be present [15], for instance for specific colors or patterns (e.g., spots [16]). In contrast, another, thus far untested hypothesis [4] suggests that skewed preferences may result as a by-product, called "peak shift," of the learning process itself.

Peak shift is a form of skewed overgeneralization [5, 6] induced by discriminative learning about two similar stimuli that are differentially reinforced, one leading to a reward (S^+), the other to punishment or no reinforcement (S^-). The stimuli may, for instance, be two colored lights differing in wavelength, or two tones of differing frequency. In most cases, the strongest responses in a discrimination task will be to the training stimuli. However, if these stimuli are very similar in appearance (e.g., lights differing slightly in wavelength), the peak in responding is often shifted away from the training stimuli in directions that increase the contrast between them, i.e., toward more extreme stimuli (e.g., lights of lower and higher wavelengths than the training stimuli). This can be demonstrated by testing animals with a range of stimuli (e.g., light stimuli covering a range of wavelengths) and comparing the frequency or intensity of the responses to these novel stimuli with those to the training stimuli.

Peak shift is an inherent consequence of the learning process [5, 6]. Although the precise mechanisms underlying peak shift are still not fully understood [17], the phenomenon is well documented in many studies over a wide range of taxa [6], albeit predominantly for very artificial learning tasks and simple stimuli. However, some studies indicate that peak shift may also occur in more naturalistic settings [18], such as in learning to avoid aposematic prey [19] or in the learned flower color preferences of bumble bees [20]. The sexual preferences that result from sexual imprinting in birds arise from a natural learning context involving complex stimuli. Although the presence of peak shift has been hypothesized for this context [4], it has not been demonstrated so far. If present, it would show that sexual imprinting itself can generate skewed preferences for specific novel types of mates. This would expand the range of naturalistic settings in which peak shift occurs to the important domain of mate choice. It would also be a clear example of how "receiver psychology" [9, 21, 22] may drive the evolution of sexually selected signals, a process analogous to the manner in which "sensory exploitation" may drive the evolution of sexual selection [10, 11].

Sexually dimorphic species with biparental care expose the offspring to two phenotypically different

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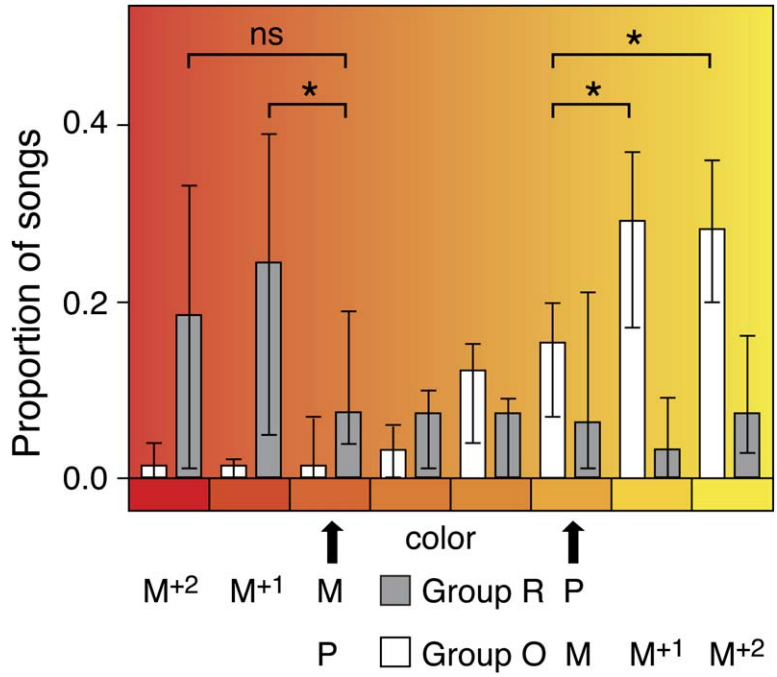

Figure 1. Beak Color Preferences in Choice Test

Proportion of songs (median, 1st quartile, and 3rd quartile ranges) directed to females with beaks in eight different colors ranging from extremely red to extremely orange (background color does not match the real color, but provides an impression of the range). Group O refers to males for which the mother had an orange painted beak and the father a red one; group R are males raised with a red-beaked mother and an orange-beaked father. Arrows indicate the third and sixth colors of the range, which were used as the maternal (M) and paternal (P) beak colors for each group. M^{+1} and M^{+2} indicate more extreme versions of the maternal beak color for each of the two groups. Statistically significant differences are indicated with *.

parents as imprinting stimuli. This provides a natural context in which peak shift can be expected. This should be reflected in adult offspring showing a sexual preference for mates that possess traits that exaggerate the sexual dimorphism. The aim of our experiment was to test this prediction.

We used the prime model species for studies of sexual imprinting: the zebra finch [23]. This is a sexually dimorphic species in which males and females normally differ in plumage characteristics and in beak color. However, we used an all-white plumage color morph, in which beak color is the most conspicuous sexually dimorphic trait. Zebra finches are monogamous, and both sexes have a role in mate choice [23]. For both males and females, the initial choice is based on the appearance of the potential partner [23] and is affected by sexual imprinting (e.g., [1]). Beak color is one factor involved in mate choice, but its effect seems more clear-cut in males than in females [24]. Also, because male mate preferences, which are expressed by singing toward the female [23], can be more readily assessed than those of females [1], we confined our experiments to tests of male mating preferences. We controlled beak color by painting the beaks of parents and potential mates with nail varnish. One group of males was raised by parents of which the mother's beak was painted orange and the father's beak red (group O). These beak colors are close to the natural parental colors. In a second group, the mother's beak was painted red and the father's beak orange (group R). Previous studies showed that zebra finch males raised by white parents develop a learned sexual preference for females with the maternal beak color and a dislike for females with the paternal color, irrespective of whether the parents had beaks painted in colors similar to the unpainted beaks or were painted in the opposite way [25, 26]. For this reason, we consider the beak color of the mother as a positive stimulus (S^+) and that of the father as a negative one (S^-). We examined the male preference for different beak colors in a choice test. The experimentally raised adult males could choose simultaneously among eight females that differed in beak color from extremely red (i.e., more toward the red end of the spectrum than the red of the red-beaked parent) to extremely orange (i.e., more toward the orange end of the spectrum than the orange-beaked parent) (see Experimental Procedures). If peak shift is present, this should be reflected in stronger sexual preferences for females with beaks with the extreme colors at the maternal end of the spectrum than for the other females.

Figure 1 shows the proportion of courtship songs that males directed to each of the differently colored females. Males from both groups did not differ in the number of songs to all females together during the tests (median number of songs per male over both tests was 80.5 by group O males and 73.0 by group R males, Mann Whitney U test $Z = 0.461$, $n = 34$, $p = 0.64$). In general, males directed a larger proportion of songs to the females with the most extreme beak colors at the maternal end of the spectrum (maternal^{+1} and maternal^{+2}). These females received more songs than females with the maternal beak color (group O: maternal versus maternal^{+1}, $p = 0.026$, $t = 2.400$, degrees of freedom [d.f.] = 21; maternal versus maternal^{+2}, $p = 0.021$, $t = 2.488$, d.f. = 21. Group R: maternal versus maternal^{+1}, $p = 0.013$, $t = 2.883$, d.f. = 13; maternal versus maternal^{+2}, $p = 0.159$, $t = 1.494$, d.f. = 13. Groups combined: maternal versus maternal^{+1}, $p = 0.002$, $t = 3.374$, d.f. = 34; maternal versus maternal^{+2}, $p = 0.006$, $t = 2.940$, d.f. = 34). There was no effect of brood on the preferences.

An additional analysis addresses the preference peaks of the individual males, i.e., to which particular female type each male sang most. Sixteen out of the twenty-one males in group O sang most to one of the two females that had a more extreme beak color than their mother. Only two males sang most to a female at