
Sex Ratio Manipulation and Selection for Attractiveness

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Source: *Science*, New Series, Vol. 211, No. 4483 (Feb. 13, 1981), pp. 721-722

Published by: American Association for the Advancement of Science

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12. J. R. Hayes, M. U. K. Mgbodile, T. C. Campbell, *Biochem. Pharmacol.* **22**, 1005 (1973).
13. D. S. Davies, P. L. Gigon, J. R. Gillette, *ibid.* **17**, 1865 (1968).
14. J. Yanai, *ibid.* **28**, 1429 (1979).
15. R. I. Salganik, I. M. Gryaznova, A. L. Markel, N. M. Manankova, N. A. Solovyeva, *Experientia* **36**, 43 (1980).
16. R. Faris and T. C. Campbell, unpublished observation.
17. C. Heidelberger, in *Annual Reviews of Biochemistry*, E. E. Snell, P. D. Boyer, A. Meister, C. C. Richardson, Eds. (Annual Reviews, Palo Alto, Calif., 1975), vol. 44, p. 79.
18. J. A. Miller, *Cancer Res.* **30**, 559 (1970).
19. E. Huberman and L. Sachs, *Int. J. Cancer* **19**, 122 (1977).
20. W. K. Lutz, *Mutat. Res.* **65**, 289 (1979).
21. We thank I. Barbeau for valuable technical assistance and D. Roe for valuable suggestions. Supported by PHS grant 5 R01 CA23913 and T2E50705A.

20 October 1980

Sex Ratio Manipulation and Selection for Attractiveness

Abstract. *Laboratory experiments performed on a monogamous estrildid, the zebra finch (Poephila guttata), indicate that sex ratio of offspring is affected by nongenetic markers (colored plastic leg bands) that vary in attractiveness to birds. Results suggest that natural selection favors individuals that produce offspring of the sex of the more attractive parent within a breeding pair.*

Trivers and Willard (1) advanced the provocative hypothesis that natural selection favors parental control over the sex of offspring, but empirical support for their idea is limited (2). I now report that the sex ratio of progeny is affected by nongenetic (human-made) "attractive" traits in a social estrildid, the zebra finch (*Poephila guttata*).

Zebra finches are nomadic opportunistic breeders that reach sexual maturity quickly (3) and form long-term pair bonds (4). They are principally granivorous and breed in loose colonies of variable size (5). Both sexes contribute to all phases of offspring care. Size dimorphism is slight, but plumage dimorphism is striking, with males much more colorful than females.

Experiments have indicated that zebra finches are sensitive to the color of plastic leg bands worn by opposite sex conspecifics (6). To measure preferences for bands, individuals are permitted to perch next to any of four birds, three of which wear color bands, while the fourth is unbanded. Preference is measured as relative time spent with each bird during a 30-minute test interval. In an experiment in which males had red (R), orange (O), or light green (g) bands, females perched most often in view of R males and least often in view of g males. In a sequence in which females had black (Bl), pink (P), or light blue (b) bands, males preferred to perch in view of Bl and P and spent least time perching near b females. Thus Bl, P, and R are attractive colors (preferred to bandless) to at least one sex, whereas b and g are unattractive (bandless preferred). The natural leg color is orange.

To determine whether band color influences reproductive success, I released 30 adults of each sex into an aviary (8 by 5 by 2 m) containing abundant food and nesting sites. Ten females each were

banded Bl (attractive), b (unattractive), and O (intermediate). Ten males each were banded R (attractive), g (unattractive), and O (intermediate). Birds were permitted to select mates and reproduce freely. Data were collected on the reproductive patterns of each color type.

The nine possible pair combinations produced 125 offspring that reached sexual maturity between December 1979 and July 1980 (7). Mortality during the interval between fledgling and molting into adult plumage was about 6 percent, so the figures presented below approximate relative parental investment and secondary sex ratios.

By 1 January 1980, 49 offspring had hatched that survived to adulthood. Of these, 29 were fathered by R males ($\chi^2 = 17.8$, $P < .005$), and 36 had O mothers ($\chi^2 = 36.6$, $P < .005$). This trend continued through July, so that, overall, R males and O females achieved disproportionate reproduction (Table 1) (male $\chi^2 = 8.9$, $P < .05$; female $\chi^2 = 26.9$, $P < .005$) (8).

Sex ratio varied according to pair combination (Table 1). Attractive (Bl) females that were mated with less attractive O and g males produced a lower fraction of male offspring than did attractive (R) males mated with less attractive (O and b) females (6 males, 11 females versus 30 males, 16 females; $P = .03$ by the Fisher exact test) (Table 1). This

trend is more striking when only the extremes are considered (g males with Bl females versus R males with b females; $P = .003$). Overall, R males produced a higher proportion of sons than g males ($P = .03$), and Bl females produced a higher proportion of daughters than b females ($P = .007$). Thus, individuals wearing colors that were found to be attractive in preference experiments were more likely to produce offspring of that sex than were those judged unattractive. Pairs with traits of similar attractiveness produced a balanced sex ratio (Table 1).

A determination of the overall association between disparity in attractiveness within pairs and sex ratio of the clutches produced was made with a rank-order correlation test (9), performed by ranking individuals from 1 (unattractive) to 3 (attractive). For each pair, the female's rank was then subtracted from the male's, with resulting pair rankings that varied from $+2(R \times b)$ through $-2(g \times Bl)$. The correlation between this measure and the sex ratio for all clutches is significant ($\gamma = .334$; $P = .03$ by a two-tailed test) and reinforces the conclusion that birds adjust the sex ratio to reflect differences in attractiveness within pairs. At present the mechanism of sex ratio manipulation is unknown, but observations suggest that adults may recognize the sex of young shortly after hatching.

These results suggest that epigamic selection (mate choice) (10, 11) has contributed to the evolution of dimorphism in zebra finches, but they do not exclude the possibilities that intrasexual competition (10, 12) and ecological specialization (13) by the sexes have also occurred. A possible function of preferences for attractive traits is enhanced confidence of appropriate mate selection when related species occur sympatrically (14). Zebra finches breed in several habitats and have by far the widest distribution of any Australian estrildid (15). The array of species encountered by individuals is variable and somewhat unpredictable (16).

Quantitative models of the evolution

Table 1. Number of offspring of each pair combination to reach maturity by 30 June 1980. Band colors: R, red; O, orange; g, light green; Bl, black; and b, light blue.

Female parent	Male parent					
	R (attractive)		O		g (unattractive)	
	Male	Female	Male	Female	Male	Female
Bl (attractive)	5	6	5	3	1	8
O	21	14	4	4	13	13
b (unattractive)	9	2	9	6	1	1

of dimorphism through epigamic selection assume that offspring inherit attractive traits in Mendelian proportions (17). So, for example, one-quarter of all offspring of a male that is heterozygous for a dominant attractive allele with sex-limited expression displays the father's trait. However, if individuals are able to practice facultative sex ratio manipulation, a larger fraction of the progeny of attractive individuals will display the attractive trait and enjoy enhanced mate-getting abilities. One effect of this process should be that the rate of evolution of sexually selected traits is accelerated.

Patterns of sex ratio manipulation for attractiveness probably vary among mating systems and as a function of the genetics of inheritance of attractive traits. In promiscuous and moderately polygynous mating systems, females may benefit from biasing their offspring's sex as a reflection of their mate's attractiveness. In monogamous or somewhat polygamous mating systems, where males as well as females exert selectivity of mates, the attractiveness of both partners may be important, thus complicating the problem of optimal production. For example, while it may be relatively clear that an unattractive female mated to an attractive male should produce an excess of sons, it is less evident, a priori, what two attractive individuals should produce. If males' reproductive opportunities are more affected by attractiveness than are females', then (i) it may benefit females mated to attractive males to produce sons regardless of their own attractiveness, and (ii) it may be less advantageous for males to reproduce with attractive individuals. The latter possibility is supported by data indicating that attractive males have a reproductive advantage over other males, whereas attractive females have fewer offspring than females of intermediate attractiveness (Table 1). Under these circumstances selection for attractiveness in females should be more constrained, and female attractiveness should evolve more slowly.

These results indicate that birds can respond to novel nongenetic traits. Presumably they would display a similar capacity if mutations altered leg coloration or other aspects of species appearance. Thus by manipulating artificial indices of attractiveness, it would seem possible to investigate behavioral processes that affect the evolution of species traits.

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References and Notes

1. R. L. Trivers and D. E. Willard, *Science* **179**, 90 (1973).
2. G. C. Williams, *Proc. R. Soc. London Ser. B* **205**, 567 (1979). For a criticism of Trivers and Willard's data, see J. H. Myers [*Am. Nat.* **112**, 381 (1978)]. Evidence for facultative sex ratio variation has been presented for Hymenoptera by W. D. Hamilton [*Sexual Selection and Reproduction Competition in Insects*, M. S. Blum and N. A. Blum, Eds. (Academic Press, New York, 1979), p. 167] and by J. H. Werren [*Science* **208**, 1157 (1980)].
3. A. J. Marshall and D. L. Serventy, *J. Exp. Biol.* **35**, 666 (1958).
4. These bonds are evidenced under both natural and laboratory conditions [see (5) and P. A. Butterfield, in *Social Behaviour in Birds and Mammals*, J. H. Crook, Ed. (Academic Press, London, 1970), p. 249].
5. K. Immelmann, *Zool. Jahrb. Ab. Syst. Oekol. Geogr. Tiere* **90**, 1 (1962); *Ostrich Suppl.* **6**, 371 (1966).
6. N. Burley, G. Krantzberg, P. Radman, in preparation. Experimental procedures were modified from those of M. J. Walter [*Behaviour* **46**, 154 (1973)] and P. Sonneman and S. Sjölander [*Z. Tierpsychol.* **45**, 337 (1977)].
7. Data on 11 "white" birds are excluded because birds with this plumage mutation cannot be accurately sexed on the basis of external appearance. Data are also excluded for one homosexual female couple (orange-blue) that raised four clutches with no apparent male assistance.
8. From January on, the aviary contained offspring that were physiologically capable of reproduction. However, they were not observed to make nesting attempts during the interval for which data are reported here.
9. A. W. Ghent, *Biologist* **58**, 41 (1976); L. A. Goodman and W. H. Kruskal, *J. Stat. Assoc.* **49**, 732 (1954).
10. C. Darwin, *The Descent of Man, and Selection in Relation to Sex* (John Murray, London, 1871).
11. R. A. Fisher, *The Genetical Theory of Natural Selection* (Clarendon, Oxford, 1930).
12. M. Ghiselin, *The Economy of Nature and the Evolution of Sex* (Univ. of California Press, Berkeley, 1974); G. Borgia, in *Sexual Selection and Reproductive Competition in Insects*, M. S. Blum and N. A. Blum, Eds. (Academic Press, New York, 1979), p. 19.
13. R. K. Selander, in *Sexual Selection and the Descent of Man, 1871-1971*, B. Campbell, Ed. (Aldine, Chicago, 1972), p. 180.
14. C. G. Sibley, *Condor* **59**, 166 (1957); E. Mayr, in *Sexual Selection and the Descent of Man, 1871-1971*, B. Campbell, Ed. (Aldine, Chicago, 1972), p. 87. The reproductive isolation hypothesis is subject to criticism on the grounds that evidence for character displacement is weak [P. R. Grant, *Biol. J. Linn. Soc.* **4**, 39 (1972); *Evol. Biol.* **8**, 237 (1975)]. However, as Grant (1975) pointed out, negative evidence for character displacement is based on characters that might be involved in ecological specialization in sympatry. Grant felt that evidence for reproductive isolation is much stronger.
15. Zebra finches are found in most parts of continental Australia and on some neighboring islands. They are excluded only from wet sclerophyll forest and rain forest [J. A. Keast, *Emu* **58**, 219 (1958)].
16. In captivity they have formed hybrids with at least 15 species [K. Immelmann, *Australian Birds in Bush and Aviary* (Halstead, Sydney, 1965)].
17. P. O'Donald, *Heredity* **22**, 499 (1967); *ibid.* **31**, 145 (1973); *Theor. Popul. Biol.* **12**, 298 (1977); J. Maynard Smith, *J. Theor. Biol.* **57**, 239 (1976); G. Bell, *Evolution* **32**, 872 (1978).
18. I thank C. Coopersmith for assistance with data collection and the following people for advice: A. W. Ghent, S. Rohwer, R. Symanski, and M. F. Willson. Supported by the University of Illinois Research Board.

4 November 1980

Neural Correlates of a Nonjammable Electrolocation System

Abstract. *The detection of objects by the electrosensory system of weakly electric fish is subject to electrical interference such as that produced by the electric organ discharges emitted by neighboring electric fish. Most electric fish species have a behavioral reflex, the jamming avoidance response, which protects their electrolocation system against jamming. Sternopygus is unique in that it has no jamming avoidance response, yet can electrolocate even in the presence of jamming. It appears that Sternopygus protects electrolocation not by a behavioral strategy but by first-order central processing mechanisms that can distinguish between localized changes in the amplitudes of electric organ discharges caused by objects and large-field amplitude modulations caused by jamming. This mechanism acts as a local contrast detector and is functionally similar to the one used by retinal cells to respond to local contrast in light but not to overall changes in illumination.*

Weakly electric fish (Gymnotiformes and Mormyriiformes) perceive objects in their immediate surroundings by emitting electric signals and evaluating small distortions of these signals as they are bent by objects. The emission of electric organ discharges (EOD's) generates an electric field around the animal. Electroreceptors, the primary sensory organs of the electrosensory system, detect objects as a local change in the amplitude of the electric field. Any extraneous signals that can distort the electric field (including EOD's emitted by a neighbor) can therefore alter the amplitude modulations caused by objects and "jam" electrolocation. Various behavioral modifications minimize this interference. The most studied is the jamming avoidance

response (JAR), in which a fish shifts the frequency of its electrolocating signal to maximize the difference between it and the jamming frequency (1). Since the JAR protects an individual's electrolocation against interference by its neighbors, it is not surprising to find that it is a widespread behavior within the weakly electric fish. With the exception of the gymnotiform *Sternopygus*, all weakly electric fish so far tested demonstrate JAR's (2).

Behavioral experiments have shown that, even without JAR's, *Sternopygus* can electrolocate even in the presence of unnaturally strong jamming stimuli (3). In contrast, electrolocation in all other species tested, including the *Eigenmannia* spp. studied here for com-