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# Tail size and female choice in the guppy (*Poecilia reticulata*)

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**Summary.** Under laboratory conditions, female guppies demonstrate a clear preference for males with larger tails, and this preference translates into enhanced reproductive fitness for these males. Females also prefer males with higher display rates, a behavior which appears to be linked to tail size, but which can be experimentally disassociated. This appears to be a case of female-choice sexual selection.

## Introduction

Darwin (1871) proposed that sexual dimorphism results from sexual selection, which can take two forms. In one, members of one sex, usually males, compete directly with each other for mating opportunities. In the other, members on one sex, usually females, choose mates depending on the ability of males to advertise themselves. While there is strong support for the role of intrasexual combat in producing male traits such as large size, elaborate antlers, or massive horns, support for the sole influence of intersexual selection in shaping dimorphisms is scanty.

Experiments have demonstrated that female widowbirds prefer to mate with males with the longest tails (Andersson 1982), that female moorhens prefer to mate with small fat males (Petrie 1983), that female sculpins mate with males when they are at least no smaller than the male they previously inspected (Brown 1981), and that in some anurans, females prefer males with deeper (Davis and Halliday 1977) or more rapid calls (Fairchild 1981). However, most cases of elaborate male coloration, or behavior, that have been attributed to the selective force of female choice are not convincing. The elaborate plumes of birds of paradise (Le Croy 1981), the argus pheasant (Davidson 1981), and lyrebirds (Smith 1965), or the dark plumes of the ruff (van Rhijn 1973) may stimulate the female (Ridley 1981), or may provide an indication of a male's ability to reach old age (Halliday 1978). But such functions may be secondary, as males compete throughout the year for dominance or display sites, often using the same displays. The purpose of this study was to examine in the guppy (*Poecilia reticulata*), where male-male aggression is virtually absent (Farr 1980), whether the colorful hypertrophid tail of males attracts females and subsequently affects male reproductive success.

Guppies originate from the freshwater streams of Trinidad. To attract females, males first swim parallel to females, then dart ahead and face them adopting a curved posture. This usually presents a broadside view of a fully expanded and quivering tail. In the wild there is considerable genetic polymorphism for size, fin coloration, and body spot patterns (Endler 1979). Although Farr (1980) showed that spot brightness and other markings play little or no role in female choice under laboratory conditions, Endler (1978, 1983) has demonstrated that in the absence of predation, male conspicuousness increases because of increase in spot size and pattern diversity. Since some of the spots that increased in appearance as sexual selection intensified were located on the tail, we wondered if female guppies might be discriminating among males at least in part on the basis of tail size.

## Methods

Female guppies were given the opportunity to visually inspect two males simultaneously by dividing heated, aerated 10 gal aquaria into three equal compartments, each 22 × 30 × 20 cm. A single female, previously isolated for 10 days and showing no signs of pregnancy, was introduced into the middle compartment. (In control experiments, none of 28 females meeting the 10-day isolation criterion under our conditions subsequently developed any sign of pregnancy.) A total of 20 females were used for the first set of experiments. On average each female was used 12 times, but each had at least a 1-day rest between

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trials. A single male was placed in each end compartment. The males were size-matched, and a new pair of males was selected at random from a population of 30 for each test; all fish were 4–10 months old, the time of peak reproductive activity. To insure that males could not see each other and thus to eliminate any effect of dominance or social facilitation (Farr 1980) on the display, the partitions were made of one-way mirrors. (Males display spontaneously.) Each experiment ran until a female made a choice, which took 0.5 min on average. A female was scored as having made a choice if she remained within 2.5 cm of a male's compartment for 15 s. This scoring method produced the same results as one in which males were ranked according to total number of female visits to each compartment, and latency to choice. A new female and a new pair of males was used for each choice. Males had been habituated to their mirror images for at least 10 days.

Since Farr (1980) has shown that high rates of gonopodial thrusting by non-displaying males can potentially offset female preferences, we also tested to see whether female preferences were actually translated into reproductive success by the more "attractive" male. These reproductive competition experiments were performed by removing the two partitions so that males had direct access to females. As Farr (1980) reported and we can confirm, male combat played no role in these competitions. The test was stopped after the first apparent copulation and the female was isolated. If any young were born, we reared the young to determine paternity; this was made possible because the tail characteristics are highly heritable (Endler 1978). A total of 40 females were tested.

Females were given three basic comparisons: (1) conspicuous-tailed males (TT) against inconspicous-tailed males (t); (2) conspicuous-tailed males (TT) against apparent inconspicous-tailed (T) males whose tails had been surgically shortened while anesthetized with MS-222 and treated postoperatively with methylene blue to reduce risk of infection and allowed 10 days to recover: and (3) shortened-tailed males (T) against inconspicous-tailed males (t). Care was taken to be sure all males used appeared healthy and behaved normally. Table 1 shows the average tail areas of the three classes of males, and reveals that the tails of inconspicous and the shortened males were much smaller than those of the conspicuous males. Since control comparisons between size-matched males within a class (TT vs TT; T vs T; t vs t) revealed no significant female preferences, and since no significant differences in preferences appeared among females, the result of separate experiments were combined.

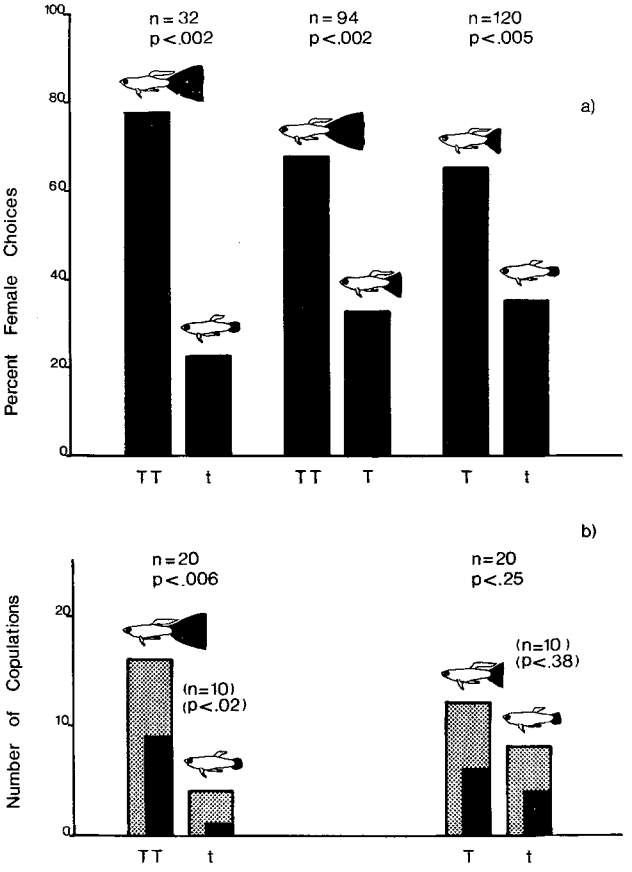


**Fig. 1.** **a** Females offered a choice between two males with different tail sizes preferred the male with the larger tail. TT = large tail; T = surgically shortened tail; t = small tail. Sample size and significance (binomial test) are given for each comparison. **b** When two males had access to a female, males with larger tails had a greater chance of obtaining the first apparent mating (wide bars) and siring offspring (narrow bars inside wide bars). Only in the case of the TT vs t comparison, however, were these differences significant. In all cases, *n* is the number of choice tests. In **b**, *n* also represents the number of different female used; in **a**, twenty females were used: in TT vs t, 12 females (selected at random) were used twice and eight were used once; in TT vs T, 14 females (selected at random) were tested five times while six were used four times; in T vs t, all twenty females were tested six times

## Results

Female guppies showed strong preferences for males with conspicuous tails (Fig. 1 a), and this initial preference was translated into enhanced reproductive success for the more conspicous males (Fig. 1 b). We noticed, however, as had Farr (1980), that conspicuous-tailed males displayed significantly more frequently than did inconspicuous-tailed males (Table 1). Thus, the observed preference could be the result of display rate, as Farr (1980) has proposed, or tail size, or some combination of the two.

To separate the effects of each component of the male display, we performed an additional series of comparisons. Since guppies are ectotherms, their activity changes with temperature. By adjusting the temperature of the male compartments we could adjust male display rate. First, we examined female preference for males of similar conspicuousness but different display rates by putting one inconspicuous-tailed male in a compartment at 32° C ($t_{32}$) and another in a compartment at 20° C ($t_{20}$). The warmer $t_{32}$ male displayed 1.8 times as often as the cooler $t_{20}$ male. The female preferred the male with the higher dispaly rate by a factor of 2.2 ($n=45$, $P<0.01$), indicating a significant role of display rate.

Next, females were given a choice among cool, conspicuous-tailed males housed at 20° C ($TT_{20}$) and warm inconspicuous-tailed males housed at

**Table 1.** Average tail areas of the three tail size classes of guppies and their display rates

| | Male tail size | | |
|---|---|---|---|
| | Conspicuous (TT) | Shortened (T) | Inconspicuous (t) |
| Tail area ($mm^2$) | 221 | 45 | 16 |
| Display rate ($n$/min) | 1.03 | 0.83 | 0.54 |
| Sample size | 40 | 40 | 40 |

32° C ($t_{32}$) in order to factor out the effect of display rate. Although the two males displayed at essentially equal rates (average $TT_{20}/t_{32}=1.07$, not significantly different from 1.00 [$t$-test]), females preferred TT males to t males by a factor of 1.5 ($n=95$, $P<0.03$), showing a significant role of tail size.

## Discussion

When the results of the female preference of the $TT_{20}$ vs $t_{32}$ tests are combined with those of the earlier TT vs t comparisons (1.5 advantage [tail size only] versus 3.7 advantage, [tail size and display rate together]), the relative importance of each factor under constant-temperature is 40.4% tail size and 59.6% display rate. If we take the residual 1.07 display-rate ratio in the $TT_{20}$ vs $t_{32}$ test into account, and assume female preference is related to display rate in a roughly linear way, at least over this narrow range, then the relative contribution of the two factors works out to 33.0% tail size and 67.0% display rate. Regardless of the method of calculation, then, female guppies choose males to a significant extent on the basis of tail size, a morphological component of their sexual dimorphism. The degree to which these two components affect female choice under natural conditions, where increased conspicuousness entails increased chances of being preyed upon, must still be examined. In large enclosures where wild-caught guppies from Trinidad and Venezuela were reared without predators, Endler (personal communication) reports that significant increases in conspicuousness and tail length (two-fold) have occurred over 9 years.

The curious linkage of tail size and display rate, if real, could have two sources: the two traits might be either genetically or phenotypically linked, or the display rate might depend on proprioceptive feedback provided by the tail. The intermediate display rate of the males with surgically shortened tails could then be interpreted in two ways. If there is a linkage between the traits, the lower display rate of T vs TT males could be an artifact resulting from some loss of vigor associated with the surgery. If the feedback is involved, however, the intermediate tail size of T males would necessarily result in an intermediate display rate. It probably makes more sense in many contexts for morphologically polymorphic animals to monitor their size and adjust their behavior accordingly (Parker 1982), particularly when ontogenetic and environmental factors contribute to morphological variability (Rubenstein 1981a, b).

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