

Dedicated to the memory of William Donald Hamilton

# The effect of intrasexual fitness differences on genotype frequency stability at Fisherian sex ratio equilibrium

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Fisherian sex ratio evolution is based on a set of common assumptions which, if met, will result in the maintenance of an equilibrium sex ratio of 0.5. One of these assumptions is the absence of intrasexual fitness differences. To investigate Fisherian sex ratio selection, variation is provided by three factor sex determination systems like that found in the platyfish, *Xiphophorus maculatus*. Here, populations with genetically-based intrasexual fitness differences were established at a sex ratio predicted to be at Fisherian equilibrium. The frequency of earlier versus later maturing genotypes changed in these populations, resulting in a sex ratio of 0.5, but at a different point along a curve of Fisherian sex ratio equilibria. Thus it appears that genetic differences in fitness which are in linkage with sex-determining factors can result in evolution along the sex ratio equilibrium curve.

## Introduction

Darwin (1859) noted that selection tends to “equalise the relative numbers of the two sexes”, but ultimately concluded that “when a tendency to produce the two sexes in equal numbers was advantageous to the species, it would follow from natural selection, but I now see that the whole problem is so intricate that it is safer to leave its solution for the future.” Fisher (1930) provided a general explanation for this

evolutionary outcome; population sex ratios will stabilize at a point where the parental investment in female offspring equals the parental investment in male offspring. This Fisherian sex ratio selection results in an investment ratio of 1:1. If one sex is more common at conception, the reproductive success of the rare sex will be greater than that of the common sex. Consequently, individuals who invest more in the rare sex will be favored, and over time, the population investment sex ratio should equilibrate at

0.5. Thus Fisherian sex ratio selection is a type of frequency-dependent selection.

Fisher's basic idea has been tested mathematically (Shaw & Mohler 1953, Shaw 1958, Bodmer & Edwards 1960, Kolman 1960, Verner 1965, Crow & Kimura 1970, Nur 1974, Taylor & Sauer 1980, Bull 1983, Bull & Charnov 1988, Basolo 1994) as well as experimentally (Conover & Van Voorhees 1990, Basolo 1994, Carvalho *et al.* 1998). This body of work has provided insight on sex ratio evolution. In a population with a skewed sex ratio, selection will shift the sex ratio at conception ( $1^\circ$  sr) to the equilibrium value of 0.5 if all parental investment occurs before conception. This holds regardless of the mating system. If sons and daughters are equally costly to produce, Fisherian sex ratio selection will result in a 1:1 numerical sex ratio. If the costs differ, the numerical sex ratio should equilibrate such that the more costly sex is produced in relatively smaller proportions, resulting in numerical sex ratios deviating from 0.5, while retaining a Fisherian sex ratio equilibrium value.

Common assumptions for Fisherian sex ratio evolution models include: (1) random mating, (2) no migration, (3) no differential predation, (4) diploidy, (5) primary equals secondary sex ratio, (6) non-distorted segregation ratios of the sex-determining factors, (7) sex determined strictly by zygotic genotype (no maternal effects or cytoplasmic inheritance), (8) no mutation, (9) female fecundity is unaffected by offspring sex ratio, (10) offspring costs are additive, (11) no intrasexual fitness differences resulting from sexual genotype and (12) non-overlapping generations. Exceptions to Fisherian sex-ratio selection have been found to result from: local resource competition, local mate competition, inbreeding, kin selection, population age-structure, non-random mating, non-Mendelian inheritance and population fitness differences according to sex (Shaw 1958, Hamilton 1967, Trivers & Willard 1973, Charnov 1975, Trivers & Hare 1976, Charnov & Bull 1977, Clark 1978, Maynard Smith 1980, Clutton-Brock 1984). Yet, as recognized by Hamilton (1967), the Fisherian sex ratio is the null hypothesis to all conditions

of "extraordinary" sex ratios. Without considering the null hypothesis and its assumptions, a population may appear to be at the Fisherian equilibrium when it is not, and a population which appears to have a biased sex ratio, or an "extraordinary sex ratio", may actually be at Fisherian equilibrium.

Relative investment in offspring is an important component of studies of sex ratio evolution. Many animals have been observed to produce offspring such that the proportion of sons and daughters in the population is equal (Shine & Bull 1977, Clutton-Brock & Iason 1986, Bull & Charnov 1988, Basolo 1994). However, differential investment in sons and daughters can occur for a number of reasons (Trivers & Willard 1973, Reiter *et al.* 1978). Despite differential investment in sons and daughters resulting in numerical sex ratios other than 1:1, the Fisherian sex ratio is still expected to be 0.5 at equilibrium.

Sex ratio selection can be experimentally tested with systems with genetic variation for sex determination. Conover and Van Voorhees (1990) used the silverside fish, *Menidia menidia*, in which sex determination is a quantitative trait; populations initiated at biased numerical sex ratios evolved to a numerical sex ratio of 0.5. Using the fruit fly, *Drosophila mediopunctata*, Carvalho *et al.* (1998) also demonstrated that the numerical sex ratio evolves towards 0.5. However, these studies equated the numerical sex ratio to the Fisherian sex ratio without meeting the critical assumption that the cost of the sexes do not differ. Basolo (1994) used the three factor sex determination system in the southern platyfish, *Xiphophorus maculatus*, to test sex ratio evolution. Populations initiated at non-Fisherian values evolved towards 0.5 along trajectories predicted by computer simulations, and laboratory experiments found no difference in the cost of the sexes (A. Basolo unpubl.). In the study presented here, the *X. maculatus* system is used to investigate the effect of intrasexual fitness differences on the sex ratio as well as sex-determining allele stability in populations founded at Fisherian equilibrium. In these populations, genetically based differences in age at sexual maturation exist.

## Materials and methods

### The experimental system

The southern platyfish, *X. maculatus*, is a live-bearing, freshwater fish that ranges along the coastal plain from Veracruz, Mexico to Belize and Guatemala. On average, females produce live young 21–28 days after insemination (Tavolga & Rugh 1947, Kallman 1975). Broods may be sired by one to a number of males. There is no paternal investment after insemination, and maternal investment ends at birth. The sex-determining system consists of three commonly occurring sex factors (W, X, Y), synonymous with alleles and sex chromosomes for the purpose of this paper, which combine to form three female genotypes (XX, WY, WX) and two male genotypes (XY, YY). Four of the six possible mating combinations result, on average, in brood sex ratios of 0.5. Two mating combinations result in biased sex ratios: matings between WX females and XY males produce female-biased broods (0.25) and matings between XX females and YY males produce male-only broods. This is one of the few systems known in which sex chromosome allelic constitution affects brood sex ratios such that predictable deviations from 0.5 result. Because the cost of producing sons versus daughters does not appear to differ in this species, the numerical sex ratio appears to be representative of the Fisherian sex ratio.

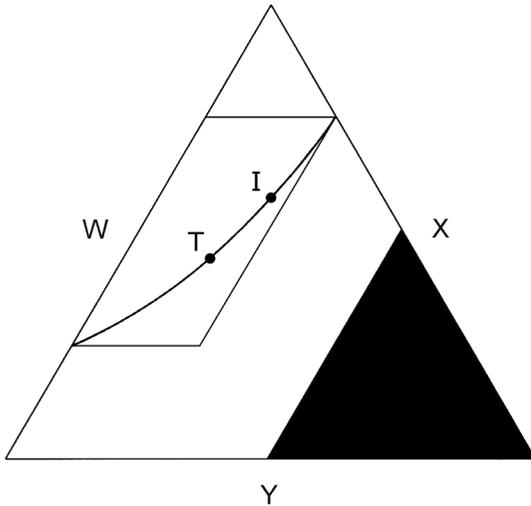
Twenty-two color patterns that code for body, fin and iris coloration are controlled by at least three sex-linked color-pattern loci in southern platyfish (Kallman 1970). Alleles at these loci are codominant. The pigment pattern loci and the sex determination locus are linked to the pituitary locus, the P-locus. The age of sexual maturity in platyfish is genetically controlled by a multi-allelic series at the P-locus (Kallman & Schreibman 1973, Kallman & Borkoski 1975). Even when tested under varying environmental conditions, individuals with different P-allele genotypes had phenotypes that were distinguishable from one another on the basis of age and weight at sexual maturation (McKenzie *et al.* 1983). Recombination between the sex factors,

pituitary alleles and sex-linked color pattern alleles is low (Kallman 1965, 1970, 1989), and these loci exhibit strong linkage disequilibrium enabling the color alleles to be used as markers in diagnosing sex factor alleles and pituitary alleles. While pigment genes facilitate identification of genotypes, they do not affect endocrine events (Kallman & Schreibman 1973) and thus do not influence the effects of P-alleles on the age at sexual maturation.

### The Fisherian sex ratio model

An equal fitness, deterministic mathematical model of a one locus, three-factor system of sex-determination to study the evolution of allele frequencies and the sex ratio has been developed and tested (Basolo 1994). A similar model is presented here which incorporates assumptions 1–11 of the previous model (Introduction), the assumption that the cost of producing a daughter equals the cost of a son, the assumption of overlapping generations, and that sex is determined by a three factor system. A set of recursion equations based on this model were utilized to determine stable sex ratio states.

Computer simulations produced a curve of sex-ratio equilibria points (Fig. 1) bounded by the two possible two factor sex determination systems. (This curve is similar to that described by Bull 1983). The curve represents an infinite set of allele and genotype frequencies at stable sex ratios of 0.5. The curve lies within a “zone of attraction” towards which populations initiated at non-Fisherian values approach and remain. This zone is defined by the area: (1)  $0.0 < W < 0.25$ , (2)  $0.0 < X < 0.75$ , and (3)  $0.25 < Y < 0.75$ . Simulations indicate that if perturbed from an allele/genotype frequency equilibrium on this curve, a population’s return to the curve does not necessarily result in the previous frequency constitution. In addition, simulations initiated at unity sex ratios with some sets of allele frequencies move away from 0.5 towards either male or female bias and then start an approach to a stable sex ratio of 0.5. Although these allele frequency sets lie within the zone of attraction,



**Fig. 1.** DiFinetti diagram showing the curve of equilibria for three sex-determining alleles. Allele frequencies are given by the perpendicular distance to the vertex. The allele frequencies sum to one. The curve originates and ends at two factor female and male heterogamety. The sex ratio is stable at 0.5 for an infinity of allele frequency sets, as indicated by the curve of equilibrium. The black area represents allele frequency combinations which are not possible with a three factor system of sex determination. The area designated by the trapezoid represents the zone of attraction. The arrow marked "I" represents the point along the curve at which the experimental populations were initiated. The arrow marked "T" represents the point along the curve at termination when the fish in both replicates were collected and assessed for genotype.

they do not lie on the curve of equilibrium. Points that lie in the area above  $Y = 0.5$  and to the left of the curve of equilibrium represent either conditions with male bias or unstable sex ratios of 0.5 which move to male-bias in one generation. The area to the left of the curve and between the area  $Y = 0.5$  and approximately  $Y = 0.32$  represents conditions when there can be male-bias, female-bias, or unstable sex ratios of 0.5. The area to the right of the curve, as well as the area below approximately  $Y = 0.32$  represents either female-bias or unstable sex ratios of 0.5 which evolve to female-bias in one generation. Such cases serve to demonstrate that an understanding of the underlying processes causing the sex ratio to move away from 0.5 is needed to accurately evaluate population sex

ratios. In the case of a three factor system, simulations suggest that populations with unstable sex ratios of 0.5 remain there for one to three generations, then move to stable sex ratios of 0.5. These findings indicate that populations in which the numerical sex ratio is 0.5 are not necessarily at Fisherian equilibrium. Thus, organismal systems in which the sex determining system is not well understood may not allow investigation of violations of Fisherian sex ratio selection. Because the genetic basis of sex determination in platyfish is known, the behavior of sex-determining factors at Fisherian equilibrium can be investigated.

Based on computer simulations, a set of sexual genotype frequencies at which the sex ratio was predicted to be at equilibrium at 0.5 was selected as the initial condition in platyfish populations. Based on the assumption that there are no intrasexual fitness differences, the sex ratio and the genotype frequencies are predicted not to change. The observed results are compared to the predicted results to determine whether populations remained at initial conditions.

### Experimental populations

Two replicate populations were established in outdoor tanks ( $3600 \pm 200$  liters each). A constant water level was maintained by a continual inflow and overflow system. A variety of plant, algae and invertebrate organisms were available as food. Water temperature was ambient. All males were sexually mature adults and all females were sexually mature virgins at the time of population establishment. The fish used to establish these populations were first and second generation offspring from genetic stock strains obtained from Dr. Klaus Kallman, Genetics Laboratories, New York. The strains used have known variation at the sex-determining locus, the pituitary locus, and sex-linked color pattern loci.

The replicate populations were both initiated with 104 individuals at the following genotype frequencies:  $WX = 0.10$ ,  $WY = 0.36$ ,  $XX = 0.04$ ,  $YY = 0.29$ , and  $XY = 0.21$ . These frequencies are predicted to be at equilibrium by the equal fitness model. The W sex-determining

allele was linked to the pituitary allele,  $P^3/P^4$  (a later maturation allele) and the color pattern allele Br (body red). The X allele was linked to the pituitary allele,  $P^1$  (the earliest known allele for maturation) and the color pattern allele Sp (spot-sided). The Y allele was linked to the pituitary allele,  $P^3$  (an intermediate maturation allele) and the color pattern allele Ir (iris red). Thus, there were intrasexual differences for age at sexual maturation. Based on previous work (Kallman & Borkowski 1978, Kallman 1989),  $X^{P^1}X^{P^1}$  females are predicted to reach maturation in 7–11 weeks, while  $W^{P^3/P^4}X^{P^1}$  females are predicted to reach maturation in 13–17 weeks. Likewise,  $X^{P^1}Y^{P^3}$  males would mature earlier than  $Y^{P^3}Y^{P^3}$  males.

The replicate populations were run simultaneously and scored for allele and genotype frequencies and sex ratio at 28 weeks ( $\pm 3$  days) post-establishment. For scoring, all individuals in each of the replicate populations were removed and transferred to inside holding pools. The fish were designated one of two classes: (1) adults and subadults, and, (2) juveniles and babies. The adults and sub-adult class were scored for sexual

genotype. The sexual genotype of juveniles and babies was not discernable because the color pattern markers had not fully developed.

## Results

### Sex ratio behavior

For both replicate A and B, the sex ratio at 28 weeks ( $\pm 3$  days) did not differ significantly from 0.5 (Table 1). However, although the sex ratios in both replicates were at equilibrium sex ratio values, the sex ratios lay at a different point on the equilibrium curve than did the initial populations (Fig. 1).

### Genotype behavior

For both replicate A and B, the genotypic frequencies at 28 weeks (Table 2) differed significantly from the founding genotype frequencies (replicate A: adjusted  $G = 16.74$ ,  $df = 4$ ,  $p < 0.005$ ; replicate B: adjusted  $G = 16.54$ ,  $df = 4$ ,  $p$

**Table 1.** Predicted and observed sex ratios (SR) for replicates A and B. The sex ratios are predicted to remain at the initiation point on the curve because the founding populations were established with genotype frequencies predicted by the equal-fitness model to be at equilibrium. Founding indicates the sex ratio at initiation of the replicate populations. Replicate indicates the sex ratio in the replicate populations at termination. T0 = time of population establishment. T1 = 200 days post-establishment.

Population	Time (weeks)	Sex ratio		95% Confidence limits		N
		Observed	Predicted	Lower	Upper	
Founding	T0	0.50	–	–	–	104
Replicate 1A	T1	0.47	0.50	45.0	55.1	410
Replicate 1B	T1	0.49	0.50	46.0	54.1	623

**Table 2.** Predicted and observed genotype frequencies for replicates 1A and 1B. The populations were founded at genotype frequencies predicted by an equal-fitness model to be at Fisherian equilibrium. Founding indicates the genotype frequencies at initiation of the replicate populations. Replicate indicates the allele frequencies in the replicate populations at termination.

Population	Time (weeks)	WX	WY	XX	YY	XY
Founding	0	0.10	0.36	0.04	0.29	0.21
Replicate 1A	28	0.09	0.30	0.14	0.21	0.26
Replicate 1B	28	0.10	0.27	0.14	0.22	0.27

< 0.0005). The genotype frequencies of replicates did not, however, differ significantly from one another (adjusted  $G = 1.39$ ,  $df = 4$ ,  $p > 0.75$ ). In both replicates, the frequency of  $XP^1XP^1$  females, the earliest maturing female genotype, increased almost four-fold while the frequency of  $WP^3/P^4YP^3$  females, the latest maturing female genotype, decreased. The frequency of  $WX$  females remained nearly unchanged. In both replicates, the frequency of  $XP^1YP^3$  males, the earliest maturing male genotype, increased, while the frequency of the  $YP^3YP^3$  male genotype decreased.

### Allele behavior

For both replicate A and B, the allele frequencies at 28 weeks (Table 3) differed significantly from the founding allele frequencies (replicate A: adjusted  $G = 6.91$ ,  $df = 2$ ,  $p = 0.032$ ; replicate B: adjusted  $G = 7.97$ ,  $df = 2$ ,  $p = 0.014$ ). The allele frequencies in replicates A and B did not, however, differ significantly from one another (adjusted  $G = 0.15$ ,  $df = 4$ ,  $p = 0.928$ ). In both replicates, the frequency of the X allele, which was linked to the early maturation allele,  $P^1$ , increased almost two-fold, while the frequency of the W allele, which was linked to the later maturation allele,  $P^3/P^4$ , decreased, but not dramatically. In both replicates, the frequency of the Y allele, which was linked to the intermediate maturation allele,  $P^3$ , decreased. In both replicates, allele frequencies at the termination of the experiment lay on the curve of equilibri-

um, however, not at the point on the curve where they were initiated (Fig. 1).

## Discussion

Genotypic frequencies were predicted to remain at the founding frequencies because the populations were established at values predicted by an equal fitness Fisherian sex ratio model to be stable at 0.5. Although the sex ratios were at 0.5 seven months post-establishment, genotypic frequencies in both replicates evolved from their initial frequencies. The low initial frequency of  $XX$  females increased dramatically in both replicates with a corresponding decrease in the frequency of  $WY$  females. Thus, there were intrasexual fitness differences for females. In addition, the number of  $XY$  males increased from the initial frequency in both replicates, with a corresponding decrease in the frequency of  $YY$  males. Thus, there were intrasexual fitness differences for males as well. When compared to the predictions from the equal fitness model, these results indicate that the sexual genotypes were not equal in fitness.

The observed changes in genotype frequencies can be explained by intrasexual variation attributable to variation at the pituitary locus resulting in differences in the age of sexual maturation in the experimental fish. The changes in the genotype frequencies corresponded with an increase in the X allele, which was linked to the earliest P-allele. This likely reflects a fitness advantage realized by  $XP^1XP^1$  females and  $XP^1YP^3$  males due to a shorter generation time. Thus, the X chromosome bearing the earliest P-allele, and to a slightly lesser degree, the Y chromosome, increased in the populations with overlapping generations because of early maturation alleles. The  $XX:XY$  is a recurrent mating pair, producing only the parental genotypes in the offspring; this factor, combined with earlier maturation, could account for the disproportionate increase in the X allele and the  $XX$  and  $XY$  genotypes.

The manner in which life history traits affect the evolution of sexual genotype frequencies at stable sex ratios is addressable with the platyfish system based on the results presented here. The

**Table 3.** Predicted and observed allele frequencies for replicates 1A and 1B. The populations were founded at allele frequencies predicted by an equal-fitness model to be at Fisherian equilibrium. Founding indicates the allele frequencies at initiation of the replicate populations. Replicate indicates the allele frequencies in the replicate populations at termination.

Population	Time (weeks)	W	X	Y
Founding	0	0.23	0.19	0.58
Replicate 1A	28	0.19	0.32	0.49
Replicate 1B	28	0.19	0.33	0.48

experimental data indicate that genotype frequencies do not remain static at the predicted neutral equilibria stable sex ratios when there are intrasexual fitness differences. Instead, they can travel along the sex ratio curve of equilibrium within the zone of attraction. Despite changes in allele and genotype frequencies, however, the values for these frequencies were on the sex ratio curve of equilibrium when scored, and thus it appears that the sex ratio is relatively insensitive to such fitness differences. Bull and Charnov (1977) demonstrated mathematically that if the YY genotype is even slightly inferior to the XY genotype, the system will lose the W factor and evolve to a XX/XY system. In addition, they have shown that increasing the intrasexual fitness of the WX genotype leads to a stable equilibrium with all three factors present (if intrasexual fitness effects of all other genotypes are equal). Decreasing the WX genotype fitness results in an unstable equilibrium and an eventual evolution to a two factor system: either XX/XY or WY/YY. In the experimental replicates, the WX female did have a fitness advantage relative to WY females, but a lower fitness relative to XX females. In these populations, the allele frequencies did not maintain a static position on the curve of equilibrium. If no other types of intrasexual advantages were present, the experimental populations may have eventually moved to the XX:XY equilibrium point. However, as the frequency of WX females did not change in the experimental populations, the combination of the P<sup>3</sup>/P<sup>4</sup> allele with the P<sup>1</sup> allele may maintain the W, making the WX genotype higher in fitness than the WY genotype and thus maintaining the three factor system. Whether or not “inner” neutral points or zones of attraction given the known fitness differences in these populations exist along the sex-ratio curve of equilibrium remains to be tested.

An understanding of the underlying genetics of sex ratio evolution is clearly important to the study of populations at Fisherian equilibrium. As the simulations indicate, not all unity sex ratios are at Fisherian equilibrium. Thus systems in which the sex determination system is not well understood are likely not good candidates for testing assumptions of Fisherian sex ratio models, such as no intrasexual fitness differ-

ences. Without considering common assumptions of Fisherian sex ratio models, a population which appears to have a biased sex ratio, or an “extraordinary sex ratio”, may actually be at Fisherian equilibrium. Likewise, a population may appear to be at the Fisherian equilibrium when it is not. In addition, if the cost of the sexes does not differ, the numerical sex ratio can be used to evaluate whether populations are at Fisherian equilibrium or at non-Fisherian values.

## Conclusions

The three-factor system of sex determination in *X. maculatus* that results in naturally occurring genetic variation in sex ratio allows for a test of common Fisherian sex ratio assumptions. The existence of the P-allele system on the sex chromosomes provides the opportunity to investigate the effect of intrasexual fitness differences on the behavior of the sex ratio, genotype frequencies and allele frequencies at sex ratio stability values. Because the cost of producing a daughter does not differ from the cost of producing a son in platyfish, the numerical sex ratio accurately reflects the Fisherian sex ratio in this system. These combined factors allow for experimental tests of Fisherian sex ratio selection and the robustness of the sex ratio at 0.5. Previous work using the *X. maculatus* system and predictions from a model assuming non-overlapping generations and no intrasexual fitness demonstrated that Fisherian sex ratios evolve toward 0.5 along predicted trajectories. The work presented here demonstrates that the sex ratio does not remain static at values predicted to be at equilibrium when fitnesses differ. The change in allele and genotype frequencies for the experimental populations is consistent with intrasexual fitness differences.

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