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The guppy (*Poecilia reticulata* PETERS) as a model for evolutionary studies in genetics, behavior, and ecology *)

by

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Der Guppy (*Poecilia reticulata* PETERS) als ein Modell für Evolutionsstudien in der Genetik, Ethologie und Ökologie

S y n o p s i s : In einer monographischen Zusammenfassung werden die Ergebnisse der Untersuchungen am Guppy (*Poecilia reticulata* PETERS) dargestellt. In dem einleitenden Abschnitt wird auf die Brauchbarkeit dieses kleinen Zahnkarpfens für eine Vielzahl von experimentellen Fragestellungen hingewiesen, wobei jedoch den genetischen, ethologischen und evolutionsbiologischen Themen der Vorzug gegeben wird. Wegen seiner Anspruchslosigkeit hinsichtlich des Chemismus seiner Wohngewässer eignet sich dieser Fisch auch für vielfältige ökologische Untersuchungen. Die Mehrfachbeschreibung des Guppys in der systematischen Literatur ist eine Folge des stark ausgeprägten Männchen-Polymorphismus, der durch gonosomale Farbgenkomplexe verursacht wird, die zum Teil als "Supergene" vererbt werden. Auch Merkmale des Verhaltens wie Balzaktivität und Gonopodialstoßrate werden ebenso wie das agonistische Verhalten der Männchen Y-chromosomal, also rein holandrisch, vererbt. Selektionsdruck durch den natürlichen piscivoren Freßfeind *Rivulus hartii*, einen cyprinodontiden Zahnkarpfen, haben zu einer gemischten Balzstrategie von Balz und Kopulation ohne vorhergehende Balz (ohne Mitwirkung des Weibchens) geführt, wobei eine Selektion auch dadurch stattgefunden hat, daß die Weibchen die balzaktiveren Männchen bevorzugen. Sind alle Männchen einer Population gleich balzaktiv, so werden die bunteren Männchen von den Weibchen deutlich bevorzugt. In einer sonst monomorphen Männchen-Population führt die Einführung eines andersgefärbten Männchens zu dessen Bevorzugung durch die Weibchen ("rare male effect") selbst dann, wenn das neue Männchen weniger balzaktiv als die schon vorhandenen monomorphen Männchen ist. Allerdings kann es dann zu Mehrfachbesamungen der Weibchen durch verschieden gefärbte Männchen kommen. Die Einführung neuer Männchen in eine Population hat zwar die gewünschte Wirkung der Erhöhung des Heterozygotiegrades, kann aber auch zu der unerwünschten Wirkung der Maladaptation des neu eingeführten Y-Chromosoms in der Population führen. Wahrscheinlich erfolgt deshalb die Erhöhung des

*) Dedicated to Professor Dr. Heinz Janetschek on the occasion of his 70th birthday.

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Heterozygotiegrades nicht allein über ethologische Mechanismen, sondern zusätzlich noch durch die Inkompatabilität bestimmter Gametenkombinationen und/oder verminderte Lebensfähigkeit bestimmter Genotypenkombinationen, da in alten Laborstämmen des Guppys ein höherer Heterozygotiegrad hinsichtlich verschiedener Isoenzym-Loci auftritt, als nach der langen Inzucht zu erwarten gewesen wäre. Das Fitness-Merkmal der Balzaktivität wird durch ancestrale Röntgenbestrahlung erblich vermindert, wahrscheinlich durch Anhäufung schädlicher Gene auf dem Y-Chromosom. Außer dem leicht zu quantifizierenden Verhaltensmerkmalen des Sozialverhaltens eignet sich der Guppy auch ausgezeichnet zur Untersuchung quantitativer morphologischer Merkmale. In einem neu konzipierten Versuchsprogramm sollen populationsgenetische Veränderungen in Guppy-Populationen verwendet werden, um mutative und selektive Wirkungen von Umweltagentien auf aquatische Ökosysteme quantitativ zu erfassen.

Introduction:

The purpose of this review is to show how a small teleost might be used as a model for studying the dynamics of populations under various aspects. This poeciliid fish (*Poecilia reticulata* PETERS, 1859) is well-known as the 'guppy', 'missionary fish', or 'rainbow fish' to aquarists. It belongs to the cyprinodontiform family of livebearing tooth-carps (Poeciliidae) which consists of many species native to Middle-America, some northern states of South America as well as some southern states of North America. Some of these species are endemic to some Carribean islands such as Haiti.

The guppy is both suitable for field investigations in the natural habitat of the species, e.g. living in the freshwater systems of Trinidad, Tobago, Barbados, or Venezuela, and as a laboratory animal as well. Its suitability is prominent because its small size, short generation time of about 100 days at a temperature of about 20°C, the ecologic adaptability and versatility of this species which let the fish survive and even breed under poor environmental conditions, the relatively well-known genetics which has been under investigation for more than 60 years, the patroclineous inheritance of male sexual coloration and male sexual behavior including intermale aggressiveness, and the social behavior of the species which seems easily to quantify. Some shortcomings are due to the sperm storage of females which allows a female once inseminated to produce up to thirteen successive broods without any new insemination. Thus, only virgin females are useful for producing offspring sired by different males.

The high number of synonyms reflects the uncertainty in identifying correctly the specimens of this species caused by a high degree of polychromatism, in particular among males. The guppy was first described as *Lebistes reticulatus* PETERS 1859 (cf. DZWILLO, 1959; JACOBS, 1969). According to the systematic revision of ROSEN and BAILEY (1963), the species must now be named *Poecilia reticulata* (PETERS). Other invalid synonyms of the guppy resulting from multiple taxionomic descriptions because of misidentifiaction are *Acanthophacelus reticulatus* EIGENMANN 1907, *Acanthophacelus reticulatus* var. *gupii* EIGENMANN 1907, *Acanthophacelus reticulatus* var. *poeciloides* EIGENMANN 1907, *Acanthophacelus melanzonus* EIGENMANN 1912, *Girardinus guppii* GUENTHER 1866, *Girardinus poeciloides* BOULENGER 1912, *Girardinus reticulatus* GUENTHER 1866, *Glaridichthys (Girardinus) reticulatus* MILEWSKI 1920, *Heterandria guppyi* JORDAN 1887, *Lebistes poeciloides* De FILIPPI 1861, *Lebistes poeciloides* GUENTHER 1866, *Lebistes reticulatus* REGAN 1913, *Poecilia poeciloides* LANGER 1913, and *Poecilioides reticulatus* JORDAN and GILBERT 1883.

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Genetics:

Sex-linked inheritance plays an important role in the genetics of all poeciliid fish, emphasized particularly in the guppy. Since there are still homologous parts of both sex-chromosomes which are exchangeable by crossing-over processes, and no indication of morphological differences between the X- and Y-chromosomes could be found (WINGE, 1923), the sex-determination through different sex-chromosomes seems to be a relatively young acquisition in the natural history of this species. This is in accordance with the fact that autosomes can still be altered into sex-chromosomes and vice versa (WINGE, 1934). In other words, sex determining factors are not only located on the sex chromosomes but also to an important amount are located on the autosomes. Thus autosomally determined exceptional X/X males and X/Y females can occasionally occur, i.e. in the case of X/X males the male determining factors predominantly located on autosomes are overwhelming those of the opposite sex predominantly located on the X-chromosomes. In the case of X/Y females, however, the female determining autosomal and X-linked factors dominate those of the opposite (male) sex predominantly located on the Y-chromosome and only partly located on the autosomes (WINGE, 1930). Since in some old laboratory strains such as Wild-Maculatus (Zebrinus) exceptional X/Y females more often occur than in other strains, there seems to exist 'weak' and 'strong' Y-chromosomes. Whereas 'weak' Y-chromosomes contain only as much male determining factors as are sufficient to reach the epistatic minimum for dominating the female determining factors on the X-chromosome and the autosomes, 'strong' Y-chromosomes possess much more male determining factors. In the first case, X/Y females relatively often appear when female determining autosomal factors have been enriched by genetic recombination and random segregation on the autosomes, while in the latter case the Y-chromosomes contain so many male determining factors that exceptional X/Y females can never occur. In the same way, exceptional X/X males can be explained. Exceptional X/X males also can be produced by artificial treatment with sex hormones. Thus, DZWILLO (1962) exposed pregnant females of the gonosomal formula X_0/X_0 (hyaline fins without any pigmentation) which were inseminated by X_{NiII} (NiII causes dark pigmentation of the caudal peduncle) and Y_{Ir} sperm (Ir is responsible for a secondary sex-coloration in males) about 22 days after the last delivery of young fish for the duration of 24 hours to methyl testosterone (3 mg/l) added to the aquarium water which led to an alteration of all X/X guppies into males. Since these genotypic females but phenotypic males inherited one X from their father (X_{NiII}) and the other X (X_0) from their mother, the genosomal formula of the exceptional X/X males was X_{NiII}/X_0 and that of normal males X_0/Y_{Ir}. The expetional X/X males developed a dark pigmentation on their caudal peduncle and did not possess the orange Ir-spot on the basis of the caudal fin as was shown by the X_0/Y_{Ir} males which did not possess the dark peduncle. Thus, exceptional males (genotypic females) were phenotypically distinguishable from the genotypic males by their coloration. When breeding the X_{NiII}/X_0 males with normal X_0/X_0 females, they sired all-female broods, viz. 50 % X_{NiII}/X_0 females with a dark caudal peduncle and 50 % X_0/X_0 females without any dark pigmentation pattern. The normal X_0/Y_{Ir} males produced 50 % female (X_0/X_0) and 50 % male (X_0/Y_{Ir}) offspring after crossing them with hyaline non-pigmented (X_0/X_0) females as was expected according to the sex-linked inheritance of the guppy (WINGE, 1922a, 1922b). The particular concentration of genes on the sex-chromosomes of the guppy, however, is not yet fully understood. If taking together all known genes located on the autosomes in order to compare them with the number of genes found to

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be either X- or Y-linked (Table 1), more than fifty percent of all known genic factors of the guppy are located on the sex-chromosomes (DZWILLO, 1959; KIRPICHNIKOV, 1981). Taking into account that all of the gonosomal genes are codominant and therefore more easily detectable in comparison with the predominantly recessive genes of the autosomes, the chance of finding more recessive autosomal genes must be relatively high because of the high degree of inbreeding of the aquarium stocks of the guppy. Furthermore, the diploid chromosomal set of the guppy contains 46 chromosomes, i.e. 44 autosomes and the two sex-chromosomes (WINGE, 1922a). Thus, unter the assumption of equal chromosome length and similar genic density, about 96 % of the whole genome contains the same number of known factors as was found in only 4 % of the genome.

Table 1: Genetics of the guppy (*Poecilia reticulata*) *)

AUTOSOMAL GENES (become manifested in males and females)	GONOSOMAL GENES, causing male sexual coloration	
	only Y-linked (patroclineous)	X- or Y-linked (exchangeable)
17 isoenzyme loci	16 codominant colour gene complexes (5 of them are also effective in influencing the formation of the caudal fin)	15 codominant colour gene complexes (3 of them are also effective in influencing the formation of the caudal fin; 2 of them become weakly realised also in females)
4 recessive colour genes (defect mutants)		
5 recessive genes, causing anomalies of the vertebral column		
2 dominant genes altering fin development	1 dominant gene elongating dorsal and caudal fins	
1 dominant suppressor		
1 dominant colour gene (manifested only in males)		
30 = 48.4 %	17 = 27.4 %	15 = 24.2 %

*) For details and literature see Table 10 in Kirpichnikov (1981)

There are, however, still more genetic pecularities especially in old laboratory strains of the guppy (Table 2). As was found by FARR (1981), the percentage of male offspring depends on the laboratory age of the guppy strain. The oldest strain still kept in our laboratory was first described 62 years ago. In this strain, the sex ratio of ♂♂/♀♀ amounts 0.429, while a younger strain first described 23 years ago exhibits a sex ratio of 1.083. Since no preferential pre-or postnatal mortality occurs, the most plausible explanation seems to be the lower production and/or viability of Y-bearing sperm because of the possible accumulation of deleterious alleles on the Y-chromosome through genetic drift (NEI, 1970) or the process known as MULLER's ratchet (MULLER, 1964) as cited by FARR (1981). NEI (1970) showed that in the absence of recombination, random drift can result in a more rapid accumulation of mutations on Y-chromosomes than on X-chromosomes. The effect is accelerated at small effective population sizes as given for aquarium stocks, but dampened if the mutations are not completely recessive, an unlikely condition (CHARLESWORTH, 1978). Because the heterologous part of the Y-chromosome which is thought to contain most of the male determining factors does not recom-

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Table 2: Genetic peculiarities of old laboratory strains of the guppy (*Poecilia reticulata*)

Age of the guppy strain in years since its first description	Designation	Polymorphism of 10 isoenzymes[1]		Sex ratio[2] (♂♂:♀♀)
		Monomorph (%)	Homozygous (%)	
62	Wild-Maculatus (Zebrinus)	60	50	0.429 *)
55	Wild-Iridescense	60	60	not investigated
55	Cream-Armatus	70	60	0.630 *)
38	Gold-Maculatus	70	60	0.786
34	White-Albino	70	60	not investigated
23	Wild-Instanbul	50	50	0.744
23	Wild-Nigrocauda-tus/Filigran	70	50	1.083
23	Blond-Filigran	70	70	not investigated
20	Blond-Flamingo	80	70	not investigated

1) WU CHINGJIANG and SCHRÖDER (1983a)
2) FARR (1981)
*) Significant deviation from the 1 : 1 ratio (normal approximation of binomial probabilities with p = 0.5)

bine with the respective part of the X-chromosome, these heterologous parts of the sex-chromosomes are subject to the same disadvantages as asexual organisms with respect to the accumulation of harmful mutations. Both NEI (1970) and CHARLESWORTH (1978) suggested that Y-chromosomes have accumulated a sufficient mutation load to be completely dysfunctional in most organisms which is, however, not yet the case in the guppy.

Another peculiarity of old guppy strains is the high degree of heterozygosity of loci encoding for isoenzymes (WU and SCHRÖDER, 1983a). According to the conditions of domestication under which some old guppy strains such as Wild-Maculatus (Zebrinus) were maintained for 62 years which corresponds to at least 200 generations, a high degree of homozygosity would be expected. Since the degree of homozygosity was even higher in younger strains such as Blond-Filigran (Table 2), selection under the aquarium conditions seems to favor the heterozygotes perhaps because of a higher degree pf phenotypic polymorphism caused by heterozygous alleles.

Since it is generally accepted that isoenzymes are only a few steps removed from the nuclear genes which specify their composition and regulate the sequences of their temporal and spatial appearance (HART and COOK, 1977; HOMES and WHITT, 1970; KINGSBURG and MASTERS, 1972; PHILIPP and WHITT, 1977; SHAKLEE et al., 1974), the analysis of changes of isoenzyme patterns in different embryonic stages will provide valuable insight into the relationships between gene activation and cellular differentiation, i.e. the genetic control of protein synthesis. Using polyacrylamide gel electrophoresis, the isoenzymes alcohol dehydrogenase (ADH), lactate dehydrogenase (LDH), and glucose-6-phosphate dehydrogenase (G-6-PD) were shown to be appropriate tools for develomental genetic studies in the guppy. While LDH-E and its heteromers with LDH-B first appear after the complete differentiation of the retinal cells, the occurrence of LDH-A coincides with the contraction movement of the muscle (WU and SCHRÖDER, 1982,

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1983b). Isoenzymes ADH-B and ADH-C are not detected until fry are 16 mm, very late after complete differentiation of the retinal cells and functional vision. Because isoenzymes ADH-D und G-6-PD-B are present only in embryos and disappear suddenly after hatching, they might be regulative enzymes in some steps of cell differentiation. Tissue-specific patterns of isoenzymes (isozymes) were investigated by the use of the distribution of three dehydrogenase isozymes, viz. LDH, ADH, and G-6-PD in the adult organs and their developmental variations during ontogeny as mentioned already above. These three dehydrogenase enzymes were found to show strong tissue-specific patterns. One band of G-6-PD was exclusively detected in the liver extracts of the adult specimens, whereas the homotetramer LDH-B_4 was ubiquitous. Isozyme LDH-A_4 was detected predominantly in the extracts of the muscle, and isozyme LDH-C was uniquely observed in the eye extracts. Another form of lactate dehydrogenase, LDH-A, was found in all tissues except the heart. The isozyme of alcohol dehydrogenase, ADH-B and ADH-C, appeared only in the eye extracts (WU and SCHRÖDER, 1982, 1983b). From their exclusive presence in the vision tissues, the isozyme ADH-B and ADH-C ware speculated to play a role in the chemical process of vision. This becomes unlikely, however, because ADH-B and ADH-C are absent in the postembryonic stages up to 16 mm of length, long after the differentiation of the retinal cell and the possession of vision function. Therefore the physiological function of ADH is only poorly understood, and further investigations both on the appearance during ontogeny and the distribution in the different organs seem to be necessary.

Mutagenesis:

Because there are already three reports on the use of teleosts in mutation research (SCHRÖDER, 1973, 1979, 1980), only a brief summary should be given here. The guppy was already used as an experimental animal both for radiation and chemical mutagenesis (Table 3). As far as chemical mutagenesis is concerned, however, only triethylene-melamine (TEM) was used in order to examine the induction of dominant lethality by water-borne pollutants. TEM was found to be more effective after intraperitoneal injection than after exposing the fish to a solution of TEM. In both cases the mutational response could be described by a linear dose-effect relationship after treatment of spermatozoa (MATTHEWS, FAVOR and CRENSHAW, 1978). With respect to radiation-induced mutations, the different stages of gametogenesis were found to exert different mutagenic sensitivity similar to that already known from radiation-genetic experiments in mice, *Mus musculus* (PURDON and WOODHEAD, 1973; SCHRÖDER, 1969a, b, c, d; SCHRÖDER and HOLZBERG, 1972). With respect to the characters under investigation, both qualitative and quantitative traits were found to be influenced by radiation-induced mutations. In particular, quantitative behavioral traints such as changes of social behavior patterns seem to be a better indicator for the detection of possible mutagenic effects of environmental agents than are Mendelian traits since already the screening of only a few fish led to significant differences between control and treatment groups (SPIESER and SCHRÖDER, 1978; WERNER and SCHRÖDER, 1980). There is no doubt at all that water-borne mutagens may be checked by fish from which the guppy presents an excellent tool because of its small size, short generation time and relatively well-known genetics. We are now preparing a device suitable for the introduction of population-genetic experiments as a method to analyse the biodynamics of a natural ecosystem (cf. paragraph "Antipredator Adaptations").

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Table 3: Mutagenesis of the guppy (*Poecilia reticulata*)

Mutational Response	Mutagen	Dose	Germ-cell Stage	References
Presumed dominant mutations of gonosomal gene complexes	X-rays	750 R; 1000-2000 R	spermatozoa	SAMOKHVALOVA, 1938; PURDOM, 1966; PURDOM and WOODHEAD, 1973
Dominant lethal mutations, change of sex-ratio	chronic γ-rays	4000, 5000 or 8000R	all stages of gametogenesis	PURDOM and LINCOLN, 1973
	X-rays	500, 1000 or 2000R		SCHRÖDER, 1969a
	Triethylene-melamine (TEM)	0.1, 0.2 or 0.4 mg/kg	spermatozoa	MATHEWS, FAVOR and CRENSHAW, 1978
Recessive lethal mutations, increase in rate of anomalies	X-rays	500, 1000 or 2000R	various stages of gametogenesis	SCHRÖDER, 1969a
Induced exchange between the sex chromosomes		1000R	spermatogonia	SCHRÖDER, 1969b
Synergistic interaction of newly induced mutations with certain recessive mutant genotypes		1000R or 2 x 500R (24 h apart)	spermatogonia, oogonia or spermatozoa	SCHRÖDER and HOLZBERG, 1972
Unidirectional shift of the means values of quantitative characters (vertebral number, body proportions)		1000R	spermatogonia or oogonia	SCHRÖDER, 1969c; SCHRÖDER, 1969d
Induction and inheritance of curvatures of the vertebral column		1000R	various stages of gametogenesis	SCHRÖDER, 1969a; SCHRÖDER, 1969e
Decrease of male courtship activity in postirradiation F_2 of both seawater and freshwater substrains and increase in intermale aggressiveness		1000R	spermatogonia and oogonia	SPIESER and SCHRÖDER, 1978; WERNER and SCHRÖDER, 1980

The inheritance and mutability of quantitative characters:

Whereas qualitative or oligogenic characters are traits controlled primarily by a few genes each of which has a large contribution to the process of character formation as compared with non-hereditary fluctuations of the character concerned, quantitative or polygenic characters are controlled by many genes with small individual effects. While qualitative traits show discontinuous variation determined by counting the individuals belonging to well differentiating phenotypic classes such as different colours, the quantitative traits show continuous variation with individuals belonging to classes rather arbitrarily defined by measurements. Most of the qualitative characters are hardly being influenced by the environment, which is contrary to the quantitative characters which almost

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invariably show a large environmental component of variation (RIEGER, MICHAELIS and GREEN, 1968). If mutations occur, they exert the higher influence on the alteration of the character in question the less genes share in the phenotypic realization of the character. Thus, major or macro-mutations occur in qualitative characters which cause a drastic change of the phenotype (already in the heterozygous state when dominant and homozygous when recessive, respectively), while minor or micro-mutations are allelic changes in polygenic systems the effect of which on the phenotype concerned depends on the number of genes involved and the relative contribution to the character in question of the mutated genes. In the case of polymery (NILSSOHN-EHLE, 1908), gene interaction appears the individual effects of which are equivalent but whose action intensify each other. The production of a particular character by cooperation among several polymeric genes are of two types: dominant interaction between alleles, and nonallelic interactions. These interactions may be expressed statistically as components of genetic variance (RIEGER, MICHAELIS and GREEN, 1968). For a quantitative character controlled by polymeric genes, there are three components of genetic variance, viz. additive, dominance, and interaction variance.

A fairly simple example of additive dimery gives the inheritance of melanin patterns of the black molly, *Poecilia (Mollienesia) sphenops* var. *melanistica,* after its crossing with the wild-type form (SCHRÖDER, 1964). In this case, two different gene loci located on different autosomes are coacting with their dominant alleles in the development of black pigmentation, while their recessive alleles do not influence the respective phenotype. Thus, four dominant genes (NN MM) produce the completely black fish and four recessive genes (nn mm) are responsible for the wild-type which is uniformly grey without any black pigmentation pattern. Genotypes with only one dominant gene (Nn mm or nn Mm) produce weakly spotted fish with a few dark spots, while two dominant genes (NN mm, Nn Mm, or nn MM) are responsible for the formation of an intense dark spotting covering almost the whole body. Only the iris appears still light in specimens with three dominant factors (NN Mm or Nn MM). These genes are functioning via non-protein bound amino acids, i.e. the different phenotypes distinguish from each other by various concentrations of free amino-acids in their tissues (SCHRÖDER and YEĞIN, 1968). This holds true both for the total concentrations of all amino-acids under investigation (cystine, lysine, serine, glycine, threonine, alanine, tryptophane, methionine, valine, and leucine) and for the different percentages of the single amino-acids in the different phenotypic classes. Cystine and tryptophane were suggested to have a main position in the path-ways of melanin synthesis because of the constant product made by multiplication of the concentrations of cystine and tryptophane. In the beginning of melanogenesis, there is a high yield of cystine and a lower one of tryptophane, and at the end of it, on the contrary, the concentration of tryptophane is high and that of cystine has become low. In the growing fish, the intensity of melanogenesis is represented by the corresponding value of the ratio cystine/tryptophane concentrations.

A hypothetical example is given in Fig. 1 showing a quantitative character of six elements determined by cumulative effects of six dominant genes in which alleles and nonalleles contribute in the same manner to the formation of the character. For the sake of simplicity, six elements were thought to be determined by six dominant genes the recessive alleles of which are not effective in any way. If a recessive mutation occurs, the remaining five dominant genes are then encoding for only five elements. Of course, this kind of gene interaction may be seldom if ever realized in nature. In a natural or laboratory population, such a mutation hardly affects the frequency distribution of a given

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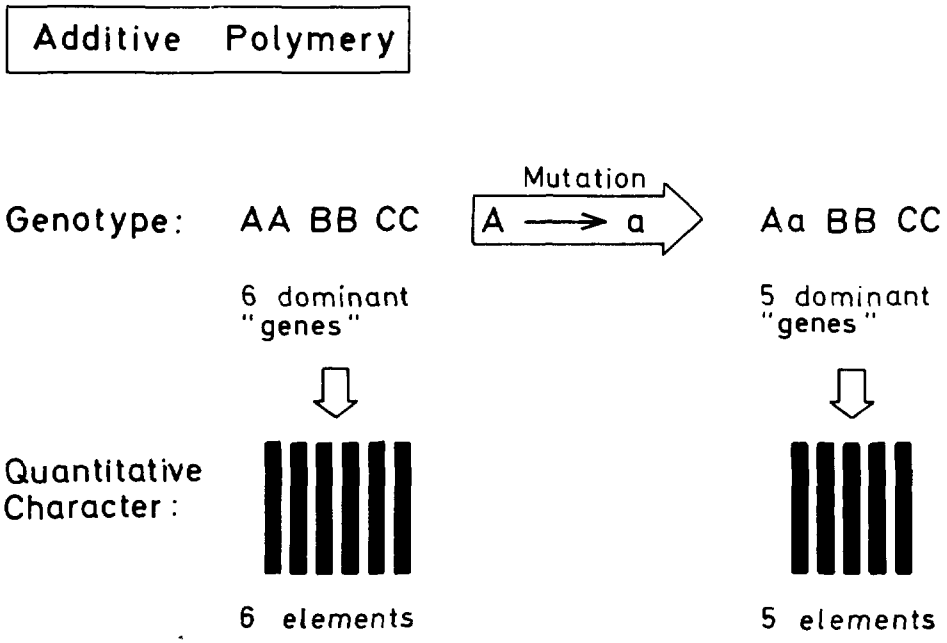

Fig. 1: A simplified model of additive polymery

quantitative character. Only if several recessive mutation occur as in the example mentioned above, some statistical parameters such as arithmetic mean and/or standard deviation may be changed indicated by a broader variation and a shift of the mean value (Fig. 2). Since by definition recessive mutations of structural genes such as nonsense or frameshift mutations are more likely to appear and give rise to the occurrence of null alleles rather than of new mutations with a new constructive gene function, most effects of micromutations are recognizable as changes of the statistic parameters of the quantitative character under investigation. The mutation of a minor gene as an individual mutational event thus cannot be analysed phenotypically. Only by means of the methods of Quantitative Genetics (e.g. FALCONER, 1960) can an analysis of the mutations in polygenic systems be done.

In the guppy, quantitative morphological and behavioral characters have been changed by radiation-induced mutations due to X-irradiation of spermatogonia and oogonia in neonatal fish. The mean number of vertebrae and the average values of some body-shape proportions were determined in F_1 and F_2 offspring. Average vertebral number increased in the F_1 and decreased in the F_2. The changes in body proportions revealed a trend towards a more compact type of fish after ancestral irradiation. The variability coefficient was greater among females of the irradiated series. Shifts of the mean values were combined with alterations of viability revealing an increase in postnatal mortality and a reduction of brood size in the backcross generation with irradiated parents. An increase in brood size and a decrease in postnatal mortality appeared in those postirradiation generations where radiation-induced detrimental mutations were less likely to become homozygous (SCHRÖDER, 1969c, 1969d). These findings agree with a hypothesis derived by

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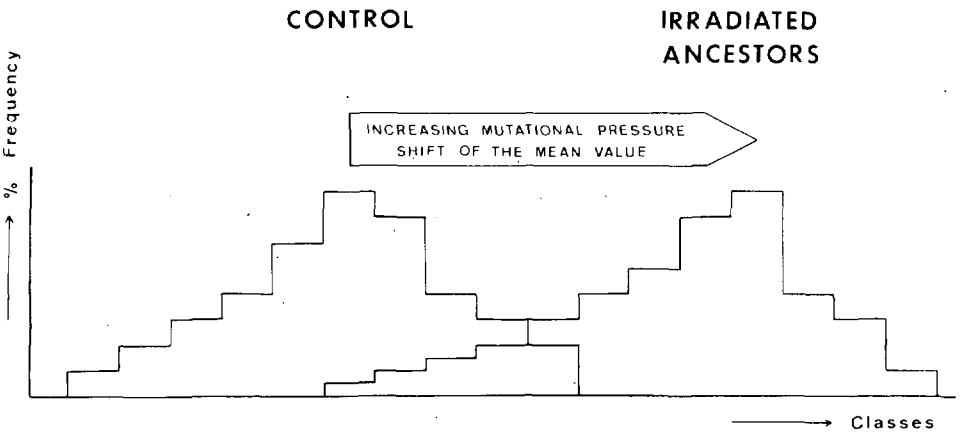

Fig. 2: The effect of increasing mutational pressure on the frequency distribution of a quantitative trait

GAUL (1967) from radiation and ethyl-methane-sulfonate experiments on barley and wheat which reads as follows: "The larger the mutation step of a given character is, the lower the average viability of the mutant, and the more seldom the mutation occurs. One can also formulate the other way around: the smaller the mutation step, the more often it occurs, and the higher the probability that mutants with improved vitality appear". Since many small mutation steps seem to occur for quantitative characters like viability which should be determined by many genes the primary function of which is unknown, brood size as a measure of viability increased in both inbred and hybrid lines in the progeny of irradiated parents (SCHRÖDER, 1968, 1969a). The radiation-induced newly arisen mutations also interact with the residual genotype of the guppies.

This was shown by the phenotypic segregation ratios in the adult F_2 after irradiation which was changed significantly in favor of wild-type and blue fish in a segregating generation, whereas the proportion of albino, blond and white (= blond + blue) guppies was lowered. In this experiment, irradiated or sham-treated fish were mated after becoming sexually mature to unirradiated mutant fish homozygous for three recessive loci, causing abinism, lack of carotinoid yellow and reddish pigmentation ("blue" constitution), and decrease in size of all melanophores ("blond" constitution). The unidirectional effect in postirradiation F_2 (cf. Fig. 2) which favored the wild-type and blue phenotype and therefore gave less blond and albino fish than in the sham-treated ontrol F_2 was greatest after exposure of spermatozoa with 1000 R fractionated into two portions each of 500 R with 24-hours interval. The next effective exposure was that with a single dose of 1000 R to spermatogonia followed by a single dose of again 1000 R to oogonia. These results were explained in terms of a synergistic interaction of recessive radiation-induced new mutations in the heterozygous state with those genotypes of the guppy which affect the formation of melanophoric patterns and the synthesis of melanins (SCHRÖDER and HOLZBERG, 1972). The overall mutation rate estimated from these radiation experiments for the guppy was calculated to lie somewhat below that of the house mouse (*Mus musculus*) (SCHRÖDER, 1968, 1969a).

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As to the inheritance of quantitative traits in fishes, no genetic analysis was provided hitherto. However, SCHMIDT (1919, 1920) demonstrated the genetic influence on the manifestation of the number of dorsal fin rays in the guppy and on the average vertebral number of *Zoarces viviparus*. For behavioral quantitative characters, however, a detailed genetic analysis was provided by FARR (1982b). In this study, FARR found that courtship activity patterns such as sigmoid display rate (open and closed display) as well as gonopodial thrusting (cf. paragraph "Behavior") of the guppy male is strongly Y-chromosome linked. In the same way, intermale aggressiveness was discovered to be inherited via the Y-chromosome. Since in an erarlier study courtship activity was shown to be a fitness character which allows more courting males to produce more offspring than can produce a less courting competitor (FARR, 1980a) and intermale aggressiveness seems to be only time-consuming and thus prevents a high-aggressive male to court the females while a low-aggressive male has a higher chance to inseminate the females, high courtship activity possesses a positive selection value while high aggressiveness reduces the fitness of the males. The descendants of irradiated guppies which were derived from X-irradiation of both spermatogonia and oogonia with 1000 R exhibited a lower courtship activity and a higher aggressiveness than was shown in the corresponding controls (SPIESER and SCHRÖDER, 1978; WERNER and SCHRÖDER, 1980; WERNER, pers. communication). Thus, a Y-linked fitness character belonging to quantitative behavioral characters was impaired by radiation-induced mutations in particular in the postirradiation F_2 offspring in which radiation-induced recessive detrimental mutations are likely to become homozygous according to the Mendelian laws while the heterozygous F_1 progeny exhibited an increase in courtship activity as compared to control F_1 (SPIESER and SCHRÖDER, 1978). Accordingly, the behavioral quantitative characters are influenced in the same way by radiation-induced mutations like morphological quantitative traits such as brood size, postnatal mortality, body proportions, and vertebral number. One can imagine that a large number of genes responsible for high courtship activity and/or low aggressiveness are located on the Y-chromosome which is partly exchangeable by cross-overs with the homologous part of the X-chromosome. Also further quantitative characters, though there is not yet any evidence for it, might be inherited as "supergenes" (DARLINGTON and MATHER, 1949) which are located on the same chromosome and usually inherited as a unit. Such genes which are not necessarily functionally related can be coadapted and then may cooperatively produce some adaptive characteristic. At least the patroclinous inheritance of male courtship behvior as well as the sex-chromosome linkage of some colour gene complexes (HASKINS et al., 1970) of the guppy provide good examples for functional supergenes whose single elements are not more exchangeable by genetic recombination when they are closely linked to the male determining factors of the Y-chromosome or to the female determining factors of the X-chromosome, respectively. These functional and spatial units may be dislocated by radiation-induced chromosome breaks leading to chromosomal rearrangements and thus to new spatial combinations of the involved genes. If so, disturbances of the supergene system regulating some neurosecretion pathways may happen and finally result in an change of aggressiveness as outlined by Fig. 3. This scheme was originally adopted in a modified form by KALLMAN and SCHREIBMAN (1973) for the explanation of the action of a sex-linked gene which controls gonadotrop differentiation and size in the platyfish (*Xiphophorus maculatus*). Since chromosome mutations in all probability occur after radiation-doses like those applied in our radiation-experiments, radiation-induced chromosome mutations may generally have led to distrubances of the endocrine system thus giving rise to the changes

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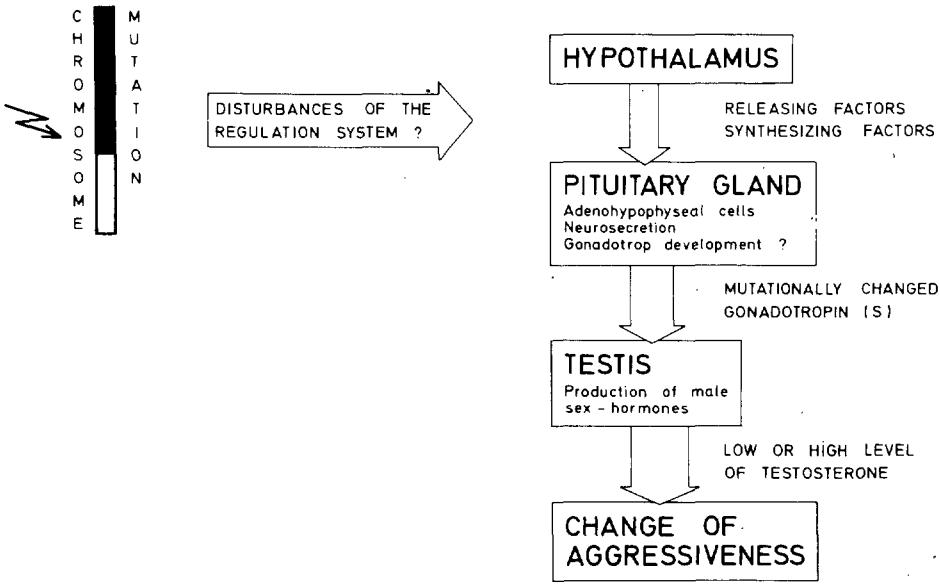

Fig. 3: A hypothetical scheme of the action of radiation-induced mutations resonsible for the change of male aggressiveness

of social behavior patterns as were observed after ancestral irradiation.

Environmental influences on the manifestation of quantitative characters:

SCHMIDT (1919, 1920) was the first author to demonstrate the influence of ecological abiotic factors on the manifestation of quantitative characters in fishes. In his experiments with the guppy (SCHMIDT, 1919) the average number of dorsal fin rays was higher where the young had been developed at a high temperature of 25°C than where their development took place at a low temperature of 18°C. Since all his experiments with the guppy gave a similar result, it may be taken as proved that the number of rays in the dorsal fin of the offspring was affected to a considerable degree by the temperature to which the mother was subjected during her pregnancy. On the other hand, the genotype of the parents influenced the number of dorsal fin rays of their offspring as well. Reared in the same aquarium, parents with 6 dorsal fin rays produced offspring with an average of 6.7 dorsal fin rays, while parents with 8 dorsal fin rays sired young with an average of 7.9 dorsal fin rays. Thus, the difference which proved to exist between the offspring of parents with respectively 6 and 9 dorsal fin rays was shown to be of hereditary nature. The same holds true for SCHMIDT's invegistations with *Zoarces viviparus* (SCHMIDT, 1920) in which he found both a genetic determinant and an environmental influence on the average number of vertebrae. While once the genotype of the mother determined at least partly the number of offspring in her progeny, the number of vertebrae also increased with increasing salinity of the environment of the wild-caught samples. Accordingly, a salt concentration of 21°/oo corresponds to an average of 117.3 vertebrae, that of 20.8°/oo to 113.2 vertebrae, that of 19.7°/oo to 112.2, and that of 11.9°/oo to

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108.0 vertebrae. In a similar manner, the number of vertebrae was higher in a seawater substrain of the guppy strain "Istanbul" as compared to the corresponding freshwater substrain of the same origin (WERNER, pers. communication). On the other hand, the brood size was reduced under seawater conditions with a salt concentration of approximately 33°/oo. Seawater guppies of this substrain showed a lower courtship activity with a decreased variability than the corresponding freshwater substrain. The response of seawater guppies to the irradiation of parental spermatogonia and oogonia with 1000 R of X-rays was more pronounced than that of the freshwater counterpart: The mean values and variances of the courtship activity of postirradiation F_1 males of seawater guppies increased, which could not be observed in postirradiation F_1 of freshwater males. In both substrains, however, the means and variances of courtship activity of postirradiation F_2 males decreased as compared to the corresponding F_2 controls (SPIESER and SCHRÖDER, 1978). Thus, one may speculate that the common rule that the influence of environment is the more pronounced the higher the number of genes involved in the manifestation of a given quantitative trait seems also to be valid in the case of quantitative characters of the guppy. Furthermore, the more genes are sharing in the determination of a quantitative character, the smaller is the contribution of a single mutation of such a polygenic system as already mentioned above. This holds true for both morphological and behavioral traits as shown for dorsal fin rays, vertebral number, and male sexual behavior.

Behavior:

The agonistic and the sexual behavior of the guppy was analysed in detail by BAERENDS et al. (1955) and by LILEY (1966). Here only a brief summary of social behavior patterns of this species can be presented which mainly refers to the description of LILEY (1966).

1. Agonistic behavior:

A situation in which agonistic behavior most commonly occurs is that where a male intrudes and attempts to court a female already courted by another male. The male already courting may threaten or attack the intruder. Another situation in which fighting occurs is when a male is introduced into a tank where a male is already well established. However, aggressive encounters were also observed not only between males, but also between females. A female's response to the courtship of a male consists often in an attack to the courting male. However, no attacks directed to females were ever observed to be delivered from males. According to BROWNE and WARREN (1982a, b), only few differences of agonistic behavior were observed between the sexes and aggressive interactions rarely resulted in physical damage to the fish.

Agonistic behavior included a lateral *threat display*, refered to as *sparring, tail-beating; attack* and *escape*. In *sparring* the two opponents take up positions parallel (or, more rarely, antiparallel) 0.5 to 1 cm apart and proceed slowly forward (or in a circle if antiparallel) with quivering bodies straight, or slightly arched laterally, and median fins fully spread. This display may last for several seconds before being interrupted by *tail-beating* in which the tail makes wide amplitude lashes directed towards the flanks of the other opponent. This may continue for several seconds before opponents *attack* each other and *whirl round one another* in a confused spiral. A fish which eventually *escapes* may flee

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into cover and hide, median fins folded (*submissive gesture*). Once dominance is established the inferior fish may escape at the approach of the other conspecific. In practice, however, very little agonistic behavior is observed in a well established group of guppies. In many cases two or more males court the same female without performing agonistic behavior.

As already mentioned above, male-female agonistic behavior is only a onse-sided affair. Males are never observed to attack or initiate sparring with a female whereas females sometimes attack or spar with courting males. The attacked male may simply re-orientate and continue courtship, or if the female is persistent and/or very aggressive, he may escape and eventually stop courting. Where male-female agonistic behavior occurs it is invariably the female which becomes dominant, no doubt largely due to the fact that the female is larger than the male.

2. Male courtship behavior:

Within two or three minutes of presentation a male may orientate to a female and, depending on her activity, begin *following* or *watching*. During *following* the dorsal fin is generally folded, but for the first few minutes of courtship the fin may be spread. A male may *watch* a female with dorsal fin normally folded from practically any position, but generally the male orientates from a position in the hemisphere around her head. From a following or watching position the male may swim in a semi-circle or a semi-ellipse around the female (*circling*) after which he may resume watching or following, or possibly begin to *display*, or he may swim away and lose interest in the female. A watching male may *retreat* slowly backwards several centimeters, with median fins folded. From the new position the male may continue to watch, move forward again, circle, swim or display. At practically any stage during courtship a male may swing his gonopodium (*gonopodial swinging*) which is the anal fin transformed to a copulatory organ to transmit sperm into the female gonopore. During this movement, the gonopodium is brought forward to one side of the mid-line, and at the same time the pelvic fin at the side is swung forward and appears to act as a support to the distal end of the gonopodium. The pelvic fin of the other side remains flattened against the male's belly. As the swing develops to its extreme form the dorsal fin spreads and the male's body becomes arched in the vertical plane, and possibly twisted into a sigmoid shape in the horizontal plane (*S-curving* or *sigmoid display*). Often it appears as if the male jerks himself into his final contorted posture. The gonopodium then returns to the rest position, the whole action being completed within a second or two. The gonopodium may be swung to either side, and gonopodial swinging may occur while watching, following, or during non-courtship in any orientation with respect to the female or even in the absence of females. However, the frequency of gonopodial swinging increases significantly when a female is present.

After orientating for some time, or possibly directly after non-courtship, a male may perform a number of displays in which the body is bent into an S or sigmoid shape in the horizontal plane. BAERENDS et al. (1955) named this the *sigmoid display* and distinguished a number of modifications on the basis of differences in orientation with respect to the female and on the extent to which the median fins are spread. During sigmoid display the caudal fin is partly or fully spread, the dorsal fin may be folded and extended to the side or erected, or it may be fully spread. The pelvics are usually pressed against the side. In general it seems that both caudal and dorsal fins are fully spread only during periods of more intense courtship, that is to say during those occasions when the male displays frequently, quivers violently and for long bouts. Two principal forms of the dis-

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play are distinguishable by BAERENDS et al. (1955) and LILEY (1966): these are the *frontal* and the *general sigmoid displays,* distinguished chiefly on the basis of their orientation with respect to the female. The *frontal sigmoid display* is described by the male's body orientated at right angles to the female's long axis, 1 - 4 cm directly in front of her. In the *general sigmoid display,* the male's orientation relative to the female is very much more variable but by far the commonest position is that in which the male is parallel to the female, head in the same or opposite direction. Since there are many intermediates between the frontal and the general sigmoid position, the distinction between these two forms seem to be rather arbitrary. Accordingly, FARR (1976 and later) recorded only two types of sigmoid courtship display which are independent on the orientation to the female. In both types, the male bends his body in an S-shape and presents himself to the females as described above. In one auf the two types, the so-called *closed sigmoid display,* the caudal fin (and mostly the dorsal fin, too) is closed. In the *open sigmoid display,* however, the caudal and dorsal fins are fully spread. BAERENDS et al. (1955) suggest that open sigmoid display is indicative of a higher motivational state of a male and that it possibly conveys a greater signal to the female, whereas the closed display may be more an appeasement gesture by which the male probes the female's receptivity. Another feature which tends to blur the distinction between frontal and general display is the fact that a displaying male may move from one position to another.

Following a closed or open display, the male may perform a *leap* in which he shoots away from the female along a straight or curved path for 10 cm or more. During the leap the median and pelvic fins are folded. The male comes to a halt, turns around and continues watching or courting.

Because of the sperm storage common to all poeciliid species by which an inseminated female can produce many successive broods without a new insemination, copulations appear very seldom in the guppy. *Gonopodial contacts,* however, are more common and can be observed regularly. There are two types of gonopodial contacts which are named *thrusts* or *gonopodial thrusts* on the one hand and *copulations* and *copulation attempts* on the other hand. They are distingushed chiefly by the fact that copulations and copulation attempts are directly preceded by a sigmoid display while thrusts occur without any preceding courtship display. In the latter case the male attempts to inseminate the female without her cooperation. In these instances, he orientates behind her, erects his gonopodium and attempts to insert it into her genital pore (FARR, 1976). These gonopodial thrusts, like courtship displays, are rarely successful (CLARK and ARONSON, 1951). At the stage at which the male actually makes contact to the female's genital pore, he rolls over onto his side. Once contact is made then it is maintained for a fraction of a second before the male jumps away and performs a series of *jerks.* This is the way to distinguish copulation attempts from true copulation: while jerks only occur after a true copulation during which the male is fixed to the female through the hooks of the tip of his gonopodium, copulation attempts are never followed by jerks (KADOW, 1954; BAERENDS et al., 1955).

3. Female sexual behavior:

Females have fewer easily defined motor patterns in their behavior and during much of the males's courtship remain passive to the males' attentions. 'Passive' is a convenient term which was used by LILEY (1966) to express the fact that no active response to male courtship was observed.

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The chief categories of female's behavior and responses are as follows: *Standing* is applied to a female remaining practically motionless, maintaining her position by means of pectoral and caudal fin activity. The median fins are usually spread. *Swimming* refers to the most commonly observed gentle swimming activity which may be seen in a courted or non-courted female. *Vigorous swimming* is an active and rapid movement to and fro. This activity, which includes the commonly observed swimming at the side in which the animal swims vigorously up and down and to and fro along the side of the tank, seems to be a form of generalised escape behavior. It may be seen in females courted persistently, or in completely isolated individuals. *Evasion* consists of a brief avoidance movement, usually in response to a thrust or copulation attempt, which may be no more than a brief, quick movement away, or possibly a short turning movement. A more vigorous avoidance movement is *fleeing*. The female swims than rapidly away, often into a corner or cover where she may hide from the male. Occasionally the female turns towards the courting male and *attacks* him, lunging towards him, and in some cases, charging him in the flanks. On a few occasions females may also *spar* with each other or with a male, interspersing lateral display with *tail beating*, attack or fleeing. In many cases a female may turn towards and swim in the direction of the male thus *approaching* him. While these behavior patterns are a loose category of female activity and certainly include both 'intentional' and 'accidental' movements in the male's direction, the following behavior patterns designated as *receptive behavior* are typical of a female which accepts copulation. Easily distinguished from approach is the response of the female termed *glide* which clearly corresponds to *drifting* described by KADOW (1954). A receptive female may glide towards a male in response to a sigmoid display or leap. Glide is not a normal swimming action, since the gliding female uses mainly the pectoral fins and caudal fin, and only very slight trunk movements are seen so that her body appears to be rigid as she slowly approaches or follows the male, with dorsal and anal fins spread. The gliding females may break off and swim away, or she may close to the displaying male, halt and rise her tail and head slightly, anal fin folded. During this activity which was named *arching* by LILEY (1966), the tail may be slightly to one side away from the male. At this point the displaying male may swim round from a position directly in front of the female and attempt to copulate. Here again she may cooperate in a positive manner: The female and male *wheel round* in a tight circle, the male on the outside, partly below and to the side of the female. At the same time as they are wheeling, the female's body is curved in the vertical plane so that her pelvic region is arched in a way which presumably exposes the genital opening. In addition the female's belly may be tilted slightly to the side of the male. The two may wheel as many as three times together before parting, but often they only complete a half-circle or less. While wheeling, the male thrusts vigorously at the female's genital opening in order to insert the tip of his gonopodium into the female's opening. The two remain in close contact momentarily (*copulation*). As soon as the male has broken contact with the female he performs *jerking* as described earlier. Frequently the pair almost jump apart the male being sometimes 'thrown' several centimeters from the female. Immediately after copulation the female may swim about rather jerkily for a few seconds but within a minute becomes quiescient, standing at the back of the tank more often near the substrate with median fins folded and *wobbling* her body with large amplitude movements. Often her body is slightly arched vertically sometimes releasing a mass of surplus spermatophores. Within a few minutes a female may begin to show receptive behavior again and cooperate in further copulations. It must be emphasized, however, that only receptive females show this rare cooperation with a courting male. Female response to

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male displays are so rare as to be virtually non-existent in natural populations (FARR, 1975). Females exhibit a well-defined ovarian cycle approximately 30 days in length; new ova are ready to be fertilized in the first 5 days following parturition (ROSENTHAL, 1952; LILEY, 1966). Thus, only virgin females and females during the first 5 days after delivery of their young are being receptive and cooperative to courting males. FARR (1982a) asked the question whether males can recognize receptive females. They do not select receptive over non-receptive females thus indicating that they possibly cannot distinguish both physiological female states. This finding does not agree with the observation of CROW and LILEY (1979) that males apparently prefer water that previously held ripe females. Thus the question whether receptive females attract courting males by sexual pheromones as found for other species of *Poecilia* (e.g. *P. sphenops;* PARZEFALL, 1970; ZEISKE, 1968) must still be kept open. Since the sexual behavior pattern which was described as *nipping* for other poeciliid species such as mollies (PARZEFALL, 1969) consisting of short snout contacts of the male to the female's genital pore seems to be rare in the guppy, olfactory releasers may play only a minor role in the recognition of receptive females by male guppies.

4. Determinants of reproductive success:

Males with higher *display rates* have a greater chance of encountering a receptive female and are preferred by females. Males adjust their display rate in such a way as to be noticeably more active than a competitor, and laboratory strains differ in the maximum rate at which males can court females. No other factor such as coloration or fin size is able to offset the disadvantage of displaying at a relatively low rate. Sexual selection has resulted in the maximization of courtship activity in natural populations (FARR, 1980a). If male court females with equal frequencies, those which also inseminate females through *gonopodial thrusting* without female cooperation (*"rape"*) have a selective advantage. Because poeciliid females store sperm, inseminations through gonopodial thrusting can reduce the reproductive success of competitor males which copulate only following a display. Accordingly, a *mixed strategy* of displaying and gonopodial thrusting is more successful than either pure strategy. The result is a mating system which partially ignores female choice mechanisms.

Intermale aggression was found to be maladaptive. Males which displayed at higher rates than competitors were less successful if they were also more aggressive than the competitors, than when they were non-aggressive or the competitors were more aggressive. Males were not able to reduce a competitor's courtship display rate through aggression. It was hypothesized that the low level of aggression in natural guppy populations is attributable to the fact that variance in size of males is low and fights would be lengthy before a winner could be determined. This would substract from time available for courtship, and female preference for high-displaying males would select against aggressive phenotypes (FARR, 1980a). PARZEFALL (1974) found an almost complete absence of aggressive behavior of a cave-dwelling form of *Poecilia (Mollienesia) sphenops* while it was well developed in its epigeous ancestor. The genetic analysis of the hybrids between the normal epigeous form of *P. sphenops* and its cave derivatives revealed that the loss of agonistic behavior is controlled by a closely linked polygenic system (PARZEFALL, 1979). Thus it was proven that under natural conditions a hereditary loss of aggressiveness really can happen when the stabilizing effect of selection favoring the maintenance of agonistic behavior has been lost. Since about 50 % of all conspecific encounters concern heterosexual meetings, mutant males which can only court all fish they meet and

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therefore do not waste their time with aggressive interactions which are of no value in the darkness of the cave will have an advantage over their aggressive competitors in inseminating the females, because during and after a fight a male is actually likely to lose contact with the female for a long time.

Normally male guppies court females at the rate of 7 - 13 displays per five minutes on the average, yet female responses to these displays are seldom if ever observed. However, FARR (1977) found that females tend to respond to the displays of a new male within 30 minutes of his introduction to a laboratory population. Further experimentation revealed that females responded to a second male added to a one-male, two-female population if he were of different coloration from the first, but that such responses were rare if he were the same coloration.

In the guppy, there was little evidence that *conspicuousness* of male coloration influences female choice of males. Dull males with high courtship display rates were significantly more successful than conspicuous males with low display rates. FARR (1980a) therefore concluded that females prefer conspicuous males only if all males exhibit equal courtship display rates.

The frequency of male colour patterns in a population did affect reproductive success in so far as males with rare colour patterns sired more offspring than expected given their frequency. The mechanisms by which a *"rare male effect"* was achieved depended on the relative mating success of phenotypes in control populations in which all phenotypes occurred with equal frequency. If a normally preferred phenotype was rare, females continued to prefer that phenotype over the common phenotype. If a normally unpreferred phenotype was rare, however, females mated with that phenotype in addition to the preferred phenotype, and the "rare male effect" was thus achieved by multiple inseminations. Females also tended to mate with more than one male in polymorphic populations, and it was concluded that certain female choice patterns with frequent multiple inseminations can maintain a polymorphism in addition to a pure rare male effect.

It was hypothesized that courtship displays and conspicuous male coloration are sexually selected characters which evolved to the occupation of invariable habitats or specialized ecological niches by a sexually monomorphic ancestor with only gonopodial thrusting as a means of inseminating females (FARR, 1980a). A subsequent reinvasion of variable habitats resulted in female choice mechanisms which maximize the level of heterozygosity of their offspring, thus resulting in polymorphic populations. The coloration of male guppies is a phenotypic cue which influences female choice in such a manner that they mate with those males with whom they most probably have the fewest genes in common.

There are also influences of *population density* on the social behavior patterns of the guppy. While populations with a single male exhibit a low level of courtship activity, the presence of a second male increases this level of activity markedly. Populations with a 1 : 1 sex ratio in densities greater than one pair exhibit a constant mean number of courtship interactions but, with increased crowding, an increasing variance in level of courtship activity. This results in a frequency profile of courtship interaction characteristic of each observed density. Each population density exhibits a density-dependent pattern of social interaction defined quantitatively by frequencies of courtship/aggressive interactions at the population level, i.e. the level of aggression rises as density increases, while the levels of initiated aggression and courtship behavior of specific individual males correlate positively at the higher density quantified. There appears to be a critical level between five and ten pairs per 17.1-litre of water volume at which aggression increases. Population

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density thus effects individual behavior in such a manner as to create a predictable quantitative pattern of social interaction at the population level (FARR and HERRNKIND, 1974).

The courtship display rate does not only depend on the population density but also on the secondary sexual coloration of males and its relative frequency in a given population. Thus, males in monomorphic (monochromatic) populations display at a lower rate than males in dimorphic (dichromatic) populations. Since the display rate is directly related to success in copulation as mentioned above (FARR, 1980a), a single male has a high probability of mating with a female when she is receptive. However, as the number of males increases, the probability of success becomes lower, so selection has favored those males which increase their display rate when in the presence of other males. Finally, if all males in a population are identical in secondary sexual coloration (monomorphic population), there is a high probability they are related; so, invoking an argument of kin selection, it is not entirely disadvantageous for a male to be unmated if his kin are successful. However, where males are different in coloration, the degree of relationship is probably less, so selection favors a further increase in display rate (FARR, 1976).

5. Influence of prior sexual experience:

There were no differences in courtship activity between males with a history of high copulation success (conditioned with virgin females) and those with low copulation success (conditioned with gravid females). Males with receptive (virgin) females exhibited higher levels of high intensity displays and fewer "rape" (= copulation attempt without cooperation of the female) attempts than males with unreceptive (gravid) females, regardless of the kind of prior sexual experience (FARR, 1980b). These findings indicate plasticity in the sexual behavior of male guppies in response to feedback from females, the result of which is optimization of frequencies of different behavior patterns and reduction in time wasted, as discussed by PARKER (1974). Since no behavior pattern is appropriate of all the time, selection should maximize the ability to determine which behavior patterns fit a particular situation.

Antipredator adaptations:

An excellent natural "laboratory" for studying potential evolutionary responses to predation is provided by certain populations of the guppy of Trinidad. Several populations are geographically isolated with no connecting fresh water by relatively short distances but are exposed to different intensities of predation (FARR, 1975; HASKINS et al., 1961; SEGHERS, 1973, 1974). At one extreme is the Guayamare River population which is preyed upon a wide diversity of fish, notably the characids, *Hoplias malabaricus* and *Astyanax bimaculatus,* and the cichlid, *Crenicichla alta.* At the other extreme, the Paria River population, about 22 km from Guayamare, is exposed to a very low density of the cyprinodontid predator, *Rivulus hartii* (Fig. 4). At Paria the main threat presumably stems from non-aquatic predators including the fish-eating bat, *Noctilio leporinus* (BLOEDEL, 1955; WORTH, 1967), and three species of kingfishers, *Chloroceryle americana, C. amazona,* and *C. aenae* (SEGHERS, 1974). The responses of laboratory-reared Guayamare and Paria guppies to a simulated aerial predator revealed significant differences between both populations insofar as Paria guppies moved a greater distance and remained inhibited from swimming longer than Guayamare guppies. The antipredator strategy of Guayamare guppies appears to be a compromise between the risk of capture from above and below the water surface. Because the Guayamare River is infested with a host of aquatic predators there must be strong selection against remaining in deep wa-

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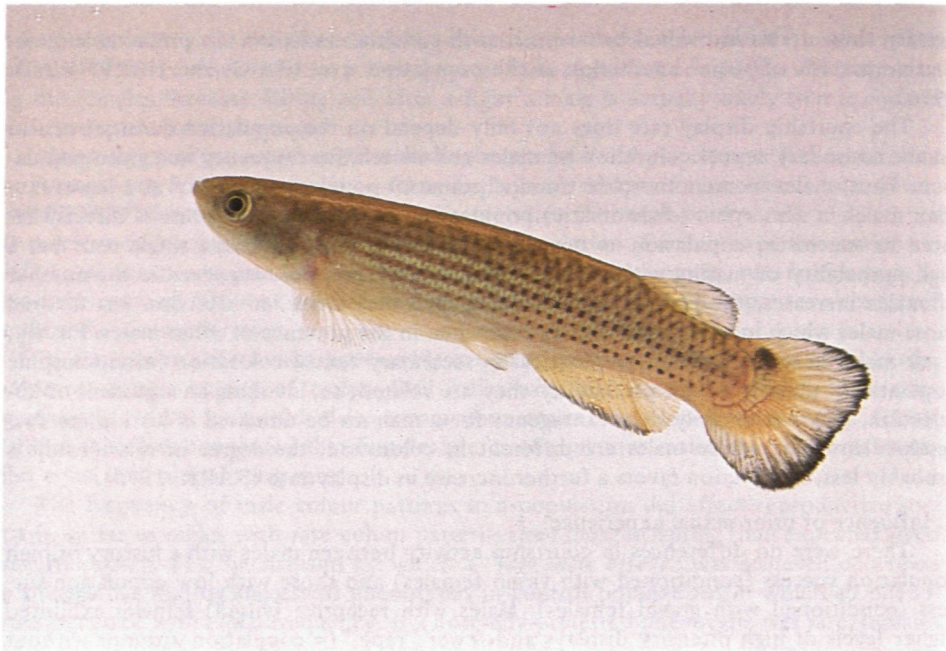

Fig. 4: *Rivulus hartii*, a piscivorous cyprinodontid tooth-carp which preys on guppies (ca. 1,2 x nat. size)

ter. With respect to aquatic predators, SEGHERS (1973) found that the sex ratio was reduced not by the larger predators as reported by HASKINS et al. (1961) but by the small cyprinodontid fish, *Rivulus hartii*. His evidence indicated that *Rivulus* selects males because they are less adept behaviorally than females avoiding predation. In conjunction with this, SEGHERS found that males coexisting with *Rivulus* tend to grow larger than in the absence of *Rivulus*. Guppies sympatric with large predators tend to live in cohesive aggregates, while this was not so for those sympatric with *Rivulus*. FARR (1975) analysed the courtship display and gonopodial thrusting rates of wild populations of guppies predated by *Rivulus* and compared their social behavior patterns with guppy populations allopatric with *Rivulus*. He found that the highest value of mean courtship displays for the *Rivulus*-type populations was still significantly lower than the lowest values for the non-*Rivulus*-types. The mean number of courtship displays for all males living sympatrically with *Rivulus* was found to be lower than that for those not sympatric with *Rivulus*.

All populations of Trinidad guppies studied by FARR (1975) were cohesive (i.e. lived in dense groups on the edges) except for four that lived in areas with high densities of *Rivulus*. Thus schooling behavior as found by SEGHERS (1973) as a response to large predators is also correlated with the coexistence or absence of *Rivulus hartii* in high densities. From FARR's (1975) observations it is apparent that there are two basic types of social organisation in the guppy closely correlated with the type of predators present. In one, the fish live in dense cohesive aggregates of individuals along the edges of streams and there is typically a high rate of male courtship display. In the second type, individuals are dispersed sparsely over the entire stream bed and the males are less active in courtship. The first type of social structure is highly disadvantageous when *Rivulus hartii* preys on

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guppies. *Rivulus* also lives in shallow water and, because of its mode of feeding, is a strong selective force against schooling and a high rate of sexual display rate. *Rivulus* hides and waits for prey to swim by, so schooling would not protect guppies from this type of predator. A concentration of prey, such as guppies in a school, would allow *Rivulus* learn where to obtain food easily. *Rivulus* individuals could lurk about a concentration of guppies and pick off those on the periphery. Hence, by spreading out, the guppies are harder to find so *Rivulus* preys on other items as well. Since *Rivulus* inhabits many small streams where guppies are not present, it is apparent that this species is polyphagous. By avoiding a concentration of conspecifics, an individual guppy lessens the probability that it will attract *Rivulus* or any other predator of this type. However, since the density of conspecifics is then greatly reduced, the chance for a male of finding a receptive female is also lessened. It then becomes much more difficult to sample the entire population for receptive females. One possible solution of this problem consists in replacing courtship displays by gonopodial thrusting thus avoiding the time-comsuming display which attracts the predator. Indeed, in *Rivulus*-type populations thrusting rate was found to be higher relative to display rate and could conceivable result in more inseminations in this manner. On the other hand, however, copulation with preceding courtship display is more effective in inseminating the female than copulation without the female's cooperation. Optimally, a balance must be found among display rate, thrusting rate, and risk of predation which would insure maximum production of offspring.

Since *Rivulus hartii* is a relatively mild predator which guarantees the survival of grown-up guppies in a large tank, this species was used for selection experiments in the laboratory. A comparison was made between a strain which exhibits a high rate of thrusting relative to courtship display rate and a strain which reversely shows a high display rate relative to gonopodial thrusting in order to determine the influence of predation by *Rivulus* on these sexual behavior patterns. For this purpose, the laboratory strains "Wild-Maculatus" with a high display rate and "Blue-Iridescense" (Fig. 5) with a low display rate were chosen because FARR (1982b) already demonstrated the hereditary nature of these behavior traits by a presumably polygenic system located on the Y-chromosome. To estimate the possible influence of living space, tanks of different volumes (630, 200 and 100 litres of water content) were used (Table 4). 541 days after the beginning of the experiment with two pairs of guppies of either strain and, in the case of presence of the predator, with one male and two females of coexisting *Rivulus hartii* (Fig. 4), the numbers and weights of the sexed guppies were counted. Except the Blue strain in the 200 and 100-litre tanks which did not contain any guppy, the remaining four laboratory populations exhibited clear effects of predation in reducing the total number of fish, the total weight of the guppy population as well as the percentage of juveniles in the *Rivulus*-containing tanks. The significant reduction of males relative to females as found in the Maculatus strain, however, has nothing to do with the predation since it was also found in non-*Rivulus*-populations and was missing in the *Rivulus*-type population of Blue guppies. As shown already above (Table 2), the aberrant sex-ratios are a characteristic of the Maculatus strains perhaps caused by less production or/and less ability to fertilize ova of Y-chromosome carrying spermatozoa. Since not only the sexual behavior patterns seem to determine the success of surviving under the conditions of predation, the preliminary experiment reveals perhaps a less complicated response to predation than expected from the previous knowledge. Further implications should play an important role such as the mean number of offspring, growth rate, and resistance against infections of the respective guppy strain. As to the fertility, no significant difference seems to exist between the two

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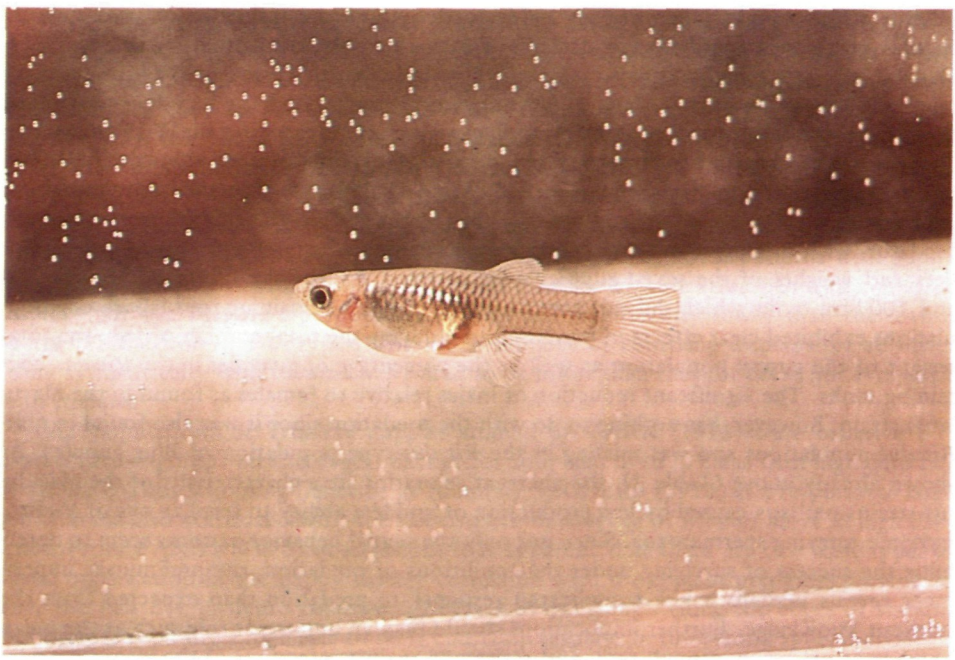
Fig. 5: Guppies of the two inbred strains as used for the selection experiments (cf. Table 4)
5a): Male of Wild-Maculatus (+/+, X_0Y_{Ma}) (ca. 2.4 x nat. size)



5b): Female of Wild-Maculatus (+/+, X_0X_0) (ca. 1.3 x nat. size)

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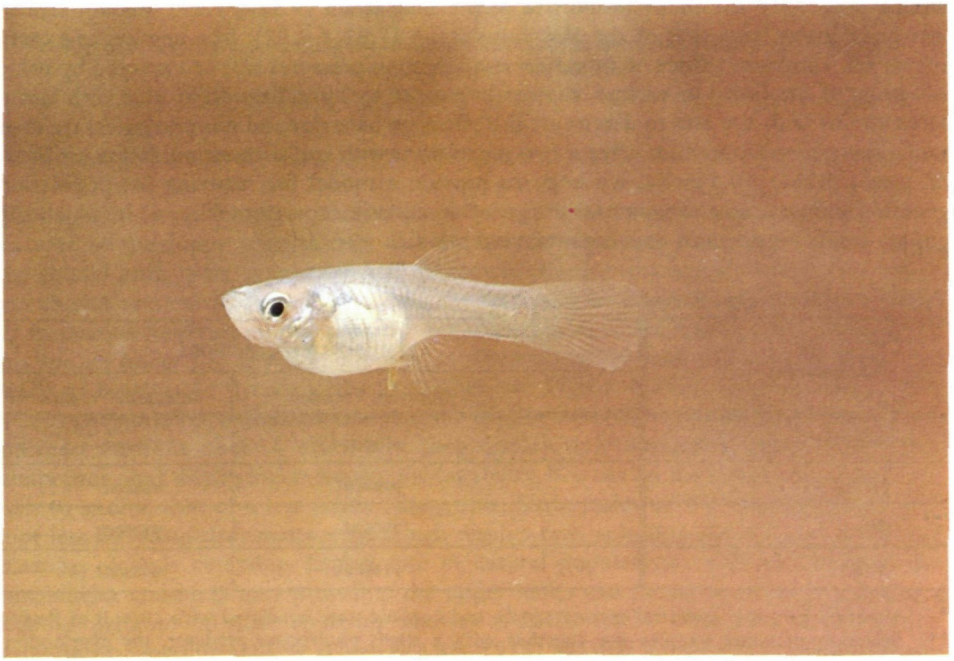
5c): Male of Blue-Iridescense (r/r, X_0/Y_{Ir}) (ca. 2.2 x nat. size)



5d): Female of Blue-Iridescense (r/r, X_0X_0) (ca. 1.4 x nat. size)

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Table 4: Results of selection experiments with the guppy (*Poecilia reticulata*). All data were collected 541 days after putting together 2 male and 2 female guppies with 1 male and 2 females of the piscivorous fish, *Rivulus hartii* (SCHRÖDER, original data)

Tank size (volume in litres)	*Rivulus hartii* **)	Guppy strain									
		Wild-Maculatus (+/+; X_0Y_{Ma})					Blue-Iridescense (r/r; X_0Y_{Ir})				
		Total number	Total weight (g)	Adults ♂♂	Adults ♀♀	Juveniles	Total number	Total weight (g)	Adults ♂♂	Adults ♀♀	Juveniles
630	absent	377	52.8	91*	118	168(44.6%)	224	19.4	57	46	121(54.0%)
	present	32	11.3	1*	17	14(43.8%)	6	2.0	4	2	0
200	absent	163	20.8	45*	85	33(20.3%)	extinguished				
	present	3	1.0	2	0	1(33.3%)	extinguished				
100	absent	113	15.1	42	31	40(35.4%)	extinguished				
	present	1	0.5	1	0	0	extinguished				

*) Significant deviation from the 1 : 1 ratio (normal approximation of binomial probalities with p = 0.5).

**) All measures of guppies made for the comparison between "*Rivulus hartii* absent and present" differ significantly from the 1 : 1 ratio within the same group as characterized by 'Strain' and 'Tank Size' (normal approximation of binomial probabilities with p = 0.5).

strains used since the mean brood size of the Blue strain (9.57 ± 1.39) was not significantly different from that of the Maculatus strain (7.92 ± 0.92). In a new set of experiments the combined effect of mutation and selection pressures will be explored by using offspring of irradiated or control guppies originated by hybridization of Blue with Maculatus strains with the aim to determine the effect on behavior and morphological traits of radiation-induced mutations after a few generations with and without predation by *Rivulus hartii* (Table 5). Finally, we hope to provide a model for studying the population genetic dynamics in a seminatural design of an aquatic ecosystem (Fig. 6) in which the guppy should be the main experimental vertebrate.

Table 5: Population experiments in the guppy (*Poecilia reticulata*)

Type of Population	Evolutionary Conditions	
	Mutation Pressure *)	Selection Pressure **)
0/0	absent	absent
M/0	present	absent
0/S	absent	present
M/S	present	present

*) Mutation pressure: ancestral spermatogonia and oogonia were irradiated with 1000 R of X-rays.

**) Selection pressure: guppies live together with a slight piscivorous predator, the cyprinodont tooth-carp, *Rivulus hartii* (1 ♂ + 2 ♀♀ and their offspring).

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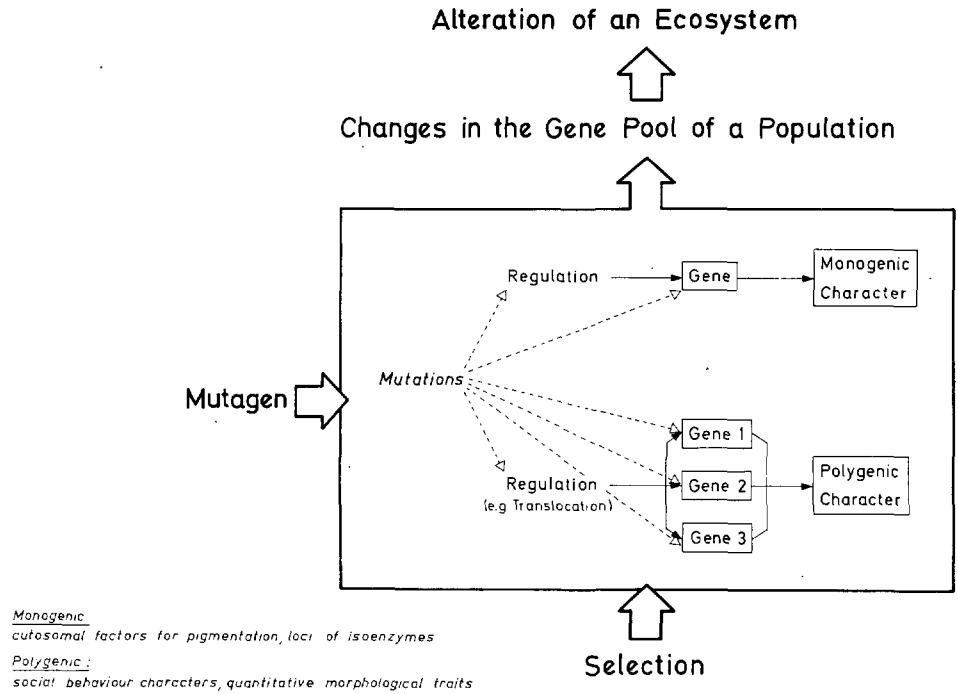

Fig. 6: A diagram representing the combined effects of induced mutations and selection on the gene pool of a population

Evolutionary consequences:

Although the evolutionary consequences of the different morphological and behavioral features of the guppy were already discussed in the respective paragraphs of this paper, one should once more summarize and emphasize this important point of why the guppy was chosen as a model for a variety of investigations. FARR (1980a) discussed in all of his numerous publications the evolutionary implications of the behavioral peculiarities of this species under the aspect of adopting the concept of *"evolutionarily stable strategies"* (ESS) as formulated by MAYNARD SMITH and PRICE (1973). In particular, FARR (1980) concluded that females compare the display rates of potential mates and choose the most vigorous ones. A male must then display only noticeably more often than a competitor, and displaying at maximum capability is wasteful if a lower display rate suffices to exceed that of a less active competitor. Since males with a low display rate produce less offspring than males with a high display rate, selection has resulted in a maximization of male courtship display rate in natural populations, with physiological and time-budget considerations providing the upper limits and predation pressure exerting a negative pressure on male courtship activity (FARR, 1975). That between-population variation in courtship activity is high (FARR, 1975) and that inbred strains exhibit significantly different levels of display activity (FARR, 1976, 1980a) which is inherited strictly

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Y-linked (FARR, 1982b)[1] suggest that heritability as the ratio of additive genetic variance to phenotypic variance is high (EHRMAN and PARSONS, 1976), and that response to selection should be fast. If courtship activity is a fitness trait as shown above, however, high heritability would contradict FISHER's (1930) genetic theory of natural selection. Anyway, the result of selection should be a rapid approach to equilibrium in any population with little within-population variability. If all males then exhibit identical display rates, mating again becomes random, and the opportunity for the evolution of "tie-breakers" arises, the first of which is gonopodial thrusting, i.e. the attempt to inseminate a female without her acceptance or cooperation. As outlined by FARR (1980a), sexual selection in all probability would lead to a mixed strategy of display and thrust which is better than either pure strategy. Similarly, sexual selection would favor less aggressive males over more aggressive ones since non-aggressive males could spend more time courting than would aggressive ones, and females would choose mostly non-aggressive males as mates. Accordingly, aggressive interactions are hardly to observe both in natural and in laboratory populations though the agonistic repertoire is well developed in both sexes (BROWNE and WARREN, 1982). Because females prefer dull but high-displaying males over brightly pigmented but low-displaying males, male conspicuousness plays only a minor role as a determinant of male reproductive success relative to male courtship activity. However, the frequency of a particular colour pattern in a population appears to be very important, because a new male introduced to an established laboratory population with gravid and normally unreceptive females successfully copulates if he carries a colour pattern different from that of the original males ("rare male effect"). There was also an indication that rare males have a long-term advantage in mating (FARR, 1977, 1980a). A frequency-dependent mating advantage with regard to colour pattern frequency is probably partially responsible for the polymorphism in coloration maintained in natural populations. Provided that all males exhibit the same display rate, females would prefer brighter males over dull males. A result of such a system in which females exert preferences for a reduced proportion of males in a population whether they are more active in courting or more conspicuous in colour is a reduction of effective population size and subsequent loss of genetic variability through inbreeding (CROW and KIMURA, 1970). Several theoretical and experimental studies have demonstrated that increased heterozygosity is an advantage in tolerating environments which can change dramatically within the lifetime of an individual or within a few generations (BRÜCKNER, 1975, 1976a, 1976b, 1976c, 1978; BRYANT, 1974; JOHNSON, 1974, 1976; LERNER, 1954; LEWONTIN, 1956, 1958; SOULÉ, 1979; TEMPLETON and ROTHMAN, 1974, 1978a, 1978b; ZOUROS, 1976), and one would expect that loss of genetic variability would be a disadvantage in species which inhabit fluctuating environments, particularly if population sizes are small. Species which live in highly variable environments should exhibit mating systems which minimize the effects of inbreeding and maximize the probability of producing heterozygous offspring. This problem of increasing the degree of heterozygosity is apparently solved by the mechanism of female choice for rare male phenotypes. Obviously, in a monomorphic population of males any male with a different pigmentation seems to be less related to the males and therefore also to the females thus guaranteeing that the rare male shares fewer genes with the females than the more frequent males of the population. Since the Y-linked patterns of secondary sexual pigmenta-

1) Added in the proof: Autosomal genes do however influence courtship activity as found in postirradiation generations (HEINRICH and SCHRÖDER, unpublished results).

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tion of a male is normally closely linked to a certain level of male courtship and thrusting activity, however, the choice of a rare male may enhance the danger of introducing a maladapted Y-chromosome into the population. If for exemple the rare male preferred by females carries a Y-chromosome with genes responsible for a high display rate while the common males of this population exert only a low display rate because of the presence of predation by *Rivulus hartii,* the desired increase in heterozygosity would be connected with an undesired maladaptation of the Y-chromosome with respect to the selective pressure by predation. One way to remove this dilemma at least partly may consist in multiple inseminations of the females by different males which was actually observed by FARR (1980a). There seem to exist still other than behavioral mechanisms to improve the degree of heterozygosity, however, since in monomorphic (monochromatic) laboratory populations where no "rare male effect" can occur the degree of heterozygosity with regard to ten different isozymes was considerably higher than expected from the degree of inbreeding (WU and SCHRÖDER, 1982a; cf. Table 2 of the present paper). Accordingly, mechanisms such as incompatibility of gametes carrying the same allele for certain isoenzyme loci or/and the inviability of homozygotes might have prevented the origin of a completely monomorphic and/or homozygous population in old laboratory strains of the guppy despite a high degree of inbreeding. Thus, natural and sexual selection have led to an evolutionary compromise between different desirable and undesirable consequences of the mating system of the guppy.

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