The Influence of a Second Y Chromosome on Social Behavior in Guppy Males, *Poecilia reticulata* Peters (Pisces: Poeciliidae)

by

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Der Einfluss eines zweiten Y-Chromosoms auf das Sozialverhalten bei Guppy-Männchen, *Poecilia reticulata* (Pisces: Poeciliidae)

Synopsis: An additional Y-chromosome in vertebrate males is suspected of promoting irregular social behavior. Because suitable Y-linked marker genes are mainly missing in mammals, XYY males cannot be recognized phenotypically. In guppies, however, hitchhiking gene-complexes are known to be inherited via the Y-chromosome. Thus genes responsible for sex determination and coloration as well as activity and strategy patterns of sexual and agonistic behavior constitute such a Y-chromosomal complex. An old aquarium stock of guppies, *Maculatus* (*Ma*), sometimes forms phenotypic females of the exceptional XY genotype, recognizable by the Y-linked codominant gene *Ma* which causes a dark spot on the dorsal fin. Crossing these XY-females with normal XY-males, in which the Y chromosomes were appropriately marked, YY-males were identified phenotypically and the effectiveness of one additional Y-chromosome on social behavior activities could be compared in the male YY-offspring with that of normal XY-brothers carrying only one Y-chromosome of the respective stock. Courtship activity was found to be enhanced in YY-males in 5 out of 7 lines, while agonistic activity of YY-males, determined as attacks delivered to and received from a standard male opponent, increased only in the 2 remaining lines which did not show any enhancement of their courtship activity.

1. Introduction:

An additional Y-chromosome is suspected of promoting social behavior alterations in vertebrates (cf. VOGEL & MOTULSKY 1979). Because suitable Y-linked marker genes are missing in mammals, XYY males cannot be recognized phenotypically. In guppies, however, hitchhiking gene-complexes ("supergenes") are known to be inherited via the Y-chromosome. Thus genes responsible for sex determination and sexual coloration as well as

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activity and strategy patterns of sexual and intermale agonistic behavior constitute such linkage groups of Y-chromosomal complexes (FARR 1983). We assume the Y-chromosome of that species and perhaps of all poeciliids to be an entity of its own characterized as a non-exchangeable hereditary complex of functionally closely related genes ("hitchhiking" genes or "supergene" complex). According to HASKINS et al. (1961), a Y-chromosome polymorphism exists also in natural habitats of this species.

2. Material and methods:

2.1. Origin of fish:

An old aquarium stock of guppies, *Maculatus* (*Ma*) (SCHMIDT 1920; WINGE 1922 a, b; 1927), sometimes spontaneously forms phenotypic females of the exceptional XY genotype, recognizable by the Y-linked codominant gene *Ma* which causes a dark spot on the dorsal fin. DNA fingerprints of these XY-females exhibit the same signal in the high molecular region (>23 kb) after hybridization with 16-mer oligonucleotide probes, as was found for normal XY-males (NANDA et al. 1990). Crossing these XY-females with normal males originated from 7 different guppy stocks with various Y-chromosomal markers, 25% of the F_1-offspring are YY-males which are fully viable and fertile. Since the X-chromosome does not contribute to the sexual behavior of males, the effectiveness of one additional Y-chromosome on social behavior activities could be compared in the male YY-offspring with that of normal XY brothers carrying only one Y-chromosome of the respective stock.

All our guppy stocks are maintained in collective breeding aquaria where fish mate at random. Although these stocks are not inbred by continuous sib-mating, several stocks are quite old (Table 1). It can be assumed that maintenance of the fish in small populations sizes and occasional "bottle-necking" of the populations over the years during establishment of new breeding stocks have resulted in a reduction of genetic variability in the stocks and a subsequent high degree of homozygosity among the individuals of a given stock. A detailed description of the Neuherberg guppy stocks was given by FARR (1980). For particular purposes, however, some of the guppy stocks are also maintained by continuous mating between sibs of the same brood for more than 20 generations, and thus constitute pure inbred strains.

Because all males and females under investigation were F_1 offspring of exceptional XY_{Ma} females crossed with males of eight different inbred aquarium stocks as listed in Table 1, they were highly heterozygous with respect to autosomal genes. Independently from their sex-chromosome markers, all test fish were named according to the abbreviations used for these eight guppy stocks (cf. Table 1).

Tab. 1: Short description of the eight laboratory stocks of the guppy, *Poecilia reticulata*, that were used in the present study[*].

Designation	Abbreviation in this study	Kept as aqua- rium stock since at least	Autosomal con- stitution	Codominant Y-chro- mosome markers
Wild - Maculatus (Zebrinus)	Ma	1922	wildtype, Zebrinus (Ze)	Maculatus (Ma)
Filigran - Nigrocaudatus	FN	1959	wildtype	Filigran (Fil)
Blond - Flamingo	FL	1963	blond (b/b)	Iridescense (Ir)
Blond - Filigran	FI	1959	blond (b/b)	Filigran (Fil)
Wild - Pauper	PA	1927	wildtype	Pauper (Pa)
Wild - Iridescense	SI	1927	wildtype	Iridescense (Ir)
Cream - Armatus	CA	1945	cream (b/b, g/g)	Armatus (Ar)
Bronze	BR	1968	gold (g/g)	Caudal pigmented (Cp) + Double sword (Ds) = fanshaped tail fin

[*]for more details cf. DZWILLO (1959), FARR (1980, 1981) and SCHRÖDER (1983)

2.2. Maintenance and breeding of fish:

The fish were kept and raised in 10 liter- capacity aquaria at a temperature of $24 \pm 3°C$ with no gravel on the floor and filled with Munich tap water, pH 7.5. All tanks were equipped with aeration and were artificially illuminated by neon lights imitating day-light on a 12:12-h light-dark cycle, but daylight was not excluded. Every day in the morning all basins containing mated pairs were routinely checked for newborn fry and dead fish. Aquatic plants, *Fontinalis spec*., were grown in all aquaria to enable newborn fish to hide in the vegetation. All fish bred in this study originated from normal 1 male/1 female matings. Food was provided daily, consisting of TetraMin® dry food and nauplia of *Artemia salina* for the fry.

2.3. Scoring behavioral activities:

Always one test male, either XY or YY, was tested with one virgin female of the same origin. Accordingly, XY-males carried the respective Y-linked marker gene as listed in Table 1, whereas YY-males carried an additional Y_{Ma}-chromosome. As standard male competitor, always one Gold-Maculatus male (g/g, XY_{Ma}) belonging to another 48-year old aquarium stock was used. While the test males' behavior was scored only once in one session of 20 min, standard males were repetitively used.

Groups of 2 males/1 female were scored for their social behavior, recording male and female behavior simultaneously with an event recorder system (EV.24) specially manufactured and equipped for our purposes. Both hard- and software was developed by a Munich

engineering office (Ingenieurbureau Erbacher, Buchenhain near Munich) for the analysis of behavioral sequences. All experiments were carried out for 20 minutes in 37.5 liter-tanks, by direct observation. Only virgin females and sexually inexperienced males were used for the behavioral observations.

For all behavioral activities both frequency (F) and duration (D, in seconds) were scored on the event recorder and subsequently transferred to a personal computer for furt-her analysis.

2.4. Description of the behavioral activities under investigation:

The courtship display of the male guppy consists of a sigmoid arching of the body with the unpaired fins either fully spread (*Open Display*, *OD*) or folded (*Closed Display*, *CD*; BAERENDS et al. 1955). Rates of Closed and Open Displays vary with changes in fema-le fertility and receptivity (LILEY 1966; FARR 1980). Both activities have been summarized as *Sigmoid Display*, (*SD*) in Fig. 1.

Fertilization in poeciliids is internal via the male's anal fin modified into a copulato-
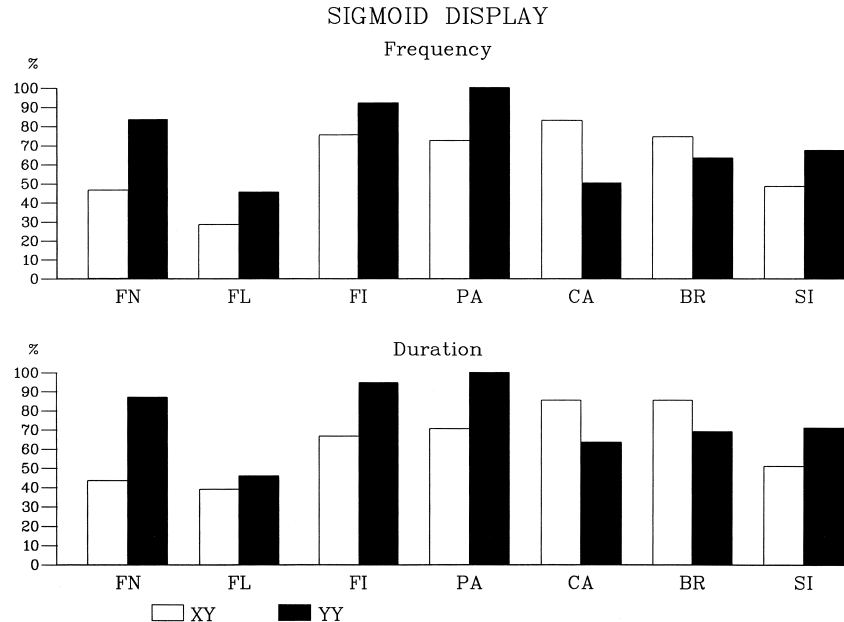

Fig. 1: Comparison of frequency and duration of sigmoid display between XY- and YY-males spent relative to the total activity.

organ, the gonopodium (PHILIPPI 1908). *Gonopodial Thrusting* (*T*) occurs either after a ry courtship display or, more often in most species (FARR 1989), with no preceding courtship. The male has to orient behind the female, brings the gonopodium to a forward position, and swims forward, attempting to insert the gonpodial tip into the female's gonopore (FARR 1989). Accordingly, a gonopodial thrust is a copulation attempt. FARR (1989) defines a gonopodial thrust as only that copulation attempt which occurs without prior display or without female acceptance of a display. In practice, however, the rate of thrusts is normally scored regardless of whether or not a display was observed before the thrust behavior.

All attacks of the test male directed toward the standard male were named *Agonistic Behavior of the Test Male* (*AT*), while attacks of the standard male which were directed toward the test male were called *Agonistic Behavior of the Standard Male* (*AS*).

If a female is not in the receptive phase of its ovarian cycle, its response to the male's courtship activity consists often of an attack on the courting male. Because it was never observed that a guppy male attacked a female, the male's aggressiveness toward a female seems to be behaviorally restrained. All attacks of the female directed toward the test male were scored as aggression behavior of the female (= *Agonistic Behavior of the Female toward the Test Male*, *AF*). Since only virgin females were used for the present experiments, female agonistic behavior was mostly nil or near nil.

3. Results:

3.1. Percent behavioral activities spent relative to total activity:

S i g m o i d   D i s p l a y (F i g . 1) : With the exception of CA and BR, the display rate of YY-males relative to the total activity was significantly higher than that of the respective XY-males. In CA and BR, however, XY males exhibited a higher rate of courtship displays. This holds true for both frequency and duration (2 x 2 chi-square contingency tables, $p < 0.013$).

T h r u s t i n g (F i g . 2) : For frequency, thrusting rates were significantly higher for FN-YY males and for CA- and BR-XY males, respectively, as compared to their counterparts. For duration, YY-males of the FN and FI line exhibited higher values. All other differences between XY and YY were not significant.

T e s t   m a l e ' s   a t t a c k s   t o w a r d   s t a n d a r d   m a l e (F i g . 3) : XY-males delivered more attacks and spent more time in attacking the standard males in FN, FL, FI, and SI lines, while YY-males did so in CA and BR lines.

S t a n d a r d   m a l e ' s   a t t a c k s   t o w a r d   t e s t   m a l e (F i g . 4) : XY received more attacks and were longer involved in attacks delivered through standard males in FN, FL, FI, PA, and SI lines, while again YY-males did so in CA and BR lines.

F e m a l e ' s   a t t a c k s   t o w a r d   t e s t   m a l e (F i g . 5) : Because of the high receptivity of virgin females which were exclusively used in this study, the level of female agonistic behavior toward the test male was nil or almost nil. Accordingly, no significant difference of female agonistic behavior directed toward XY- and YY-males was found.
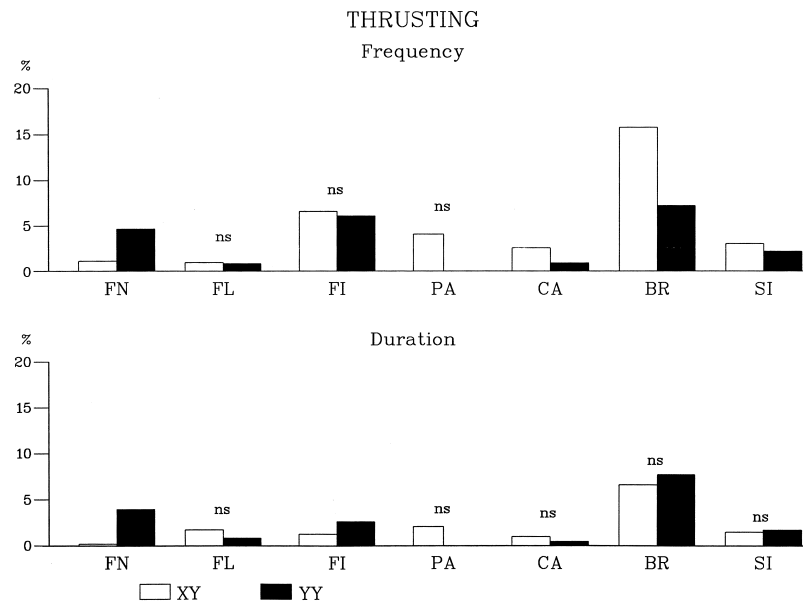
THRUSTING

Frequency

Duration

Fig. 2: Comparison of frequency and duration of thrusting behavior between XY- and YY-males spent relative to the total activity.

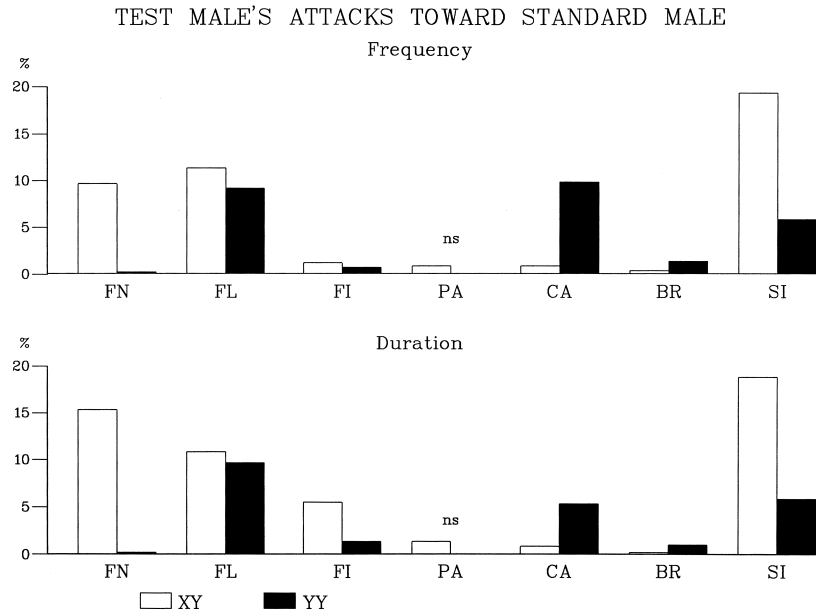TEST MALE'S ATTACKS TOWARD STANDARD MALE

Frequency

Duration

Fig. 3: Comparison of frequency and duration of test males' attacks toward standard males between XY- and YY-males spent relative to the total activity.

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STANDARD MALE'S ATTACKS TOWARD TEST MALE
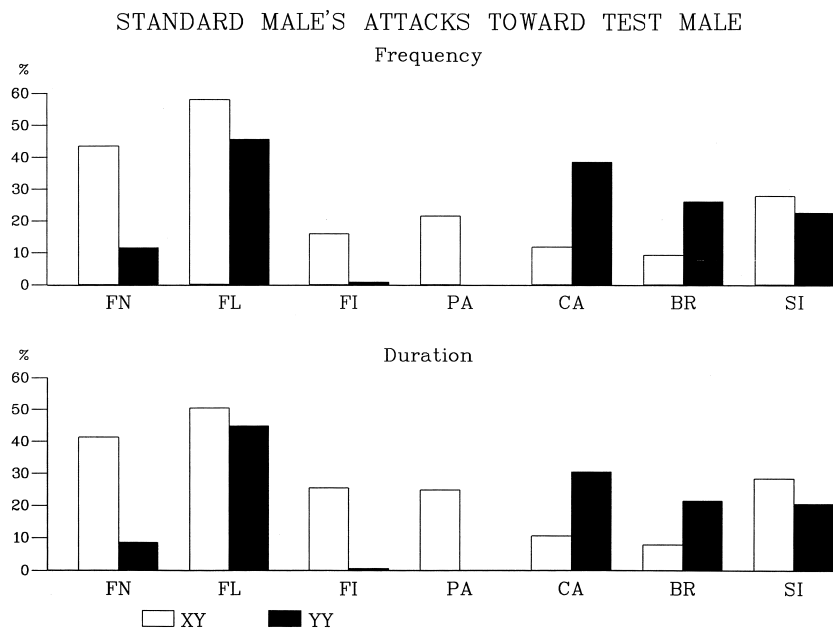
Frequency

Duration

Fig. 4: Comparison of frequency and duration of standard males' attacks toward test males between XY- and YY-males spent relative to the total activity.
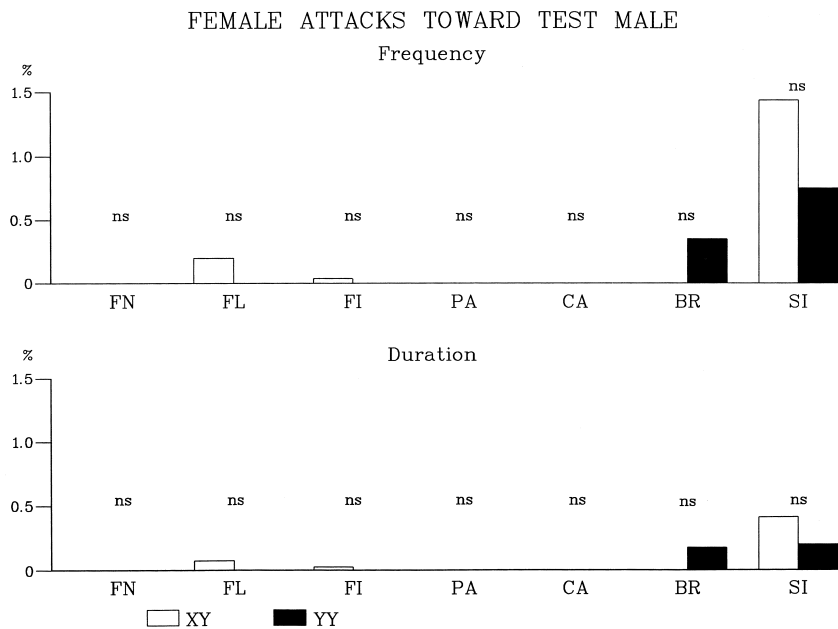
FEMALE ATTACKS TOWARD TEST MALE

Frequency

Duration

Fig. 5: Comparison of frequency and duration of female attacks toward test males between XY- and YY-males spent relative to the total activity.

3.2. Significant differences of the mean values between XY- and YY-males per 20 min observation time:

Table 2 presents the arithmetic mean (x), standard error (s_x), and range (R= Max—Min) of both frequency (F) and du ration (D) of CD, OD, SD, T, AT, AS, and AF for all XY- and YY-males of the seven different lines. Significant differences between the mean values of XY- and YY-males, however, were only found in FN, FI, CA, and SI lines (t-test, $p < 0.05$). As to display rates, the frequency of closed displays was significantly higher for YY- than for XY-males of the SI line, and the duration of open displays was again higher for YY- than for XY-males of the FI line. All other significant differences between XY- and YY-males, designated by an asterisk (*) in Table 2, refer to the male agonistic behavior. In CA, FI, and FN lines, the frequency (CA) or frequency and duration (FI and FN) of the standard male's attacks delivered toward the test male was significantly different between XY- and YY-males. Whereas CA-YY males received more attacks from the standard males than CA-XY, XY-males of FI and FN were more often involved in attacks delivered from standard males.

There were still more significant inter-line differences both between XY- and YY-males which roughly correspond to the behavioral differences already reported (FARR 1980) for the Y-linked markers of the seven lines. Because these are not of interest in the context of XY vs. YY comparisons, they are not discussed here.

Tab. 2:
Comparison of arithmetic means, standard errors, and ranges of frequency (F) and duration (D) of closed display (CD), open display (OD), total sigmoid display (SD), thrusting behavior (T), attacks of test males toward standard males (AT), attacks of standard males toward test males (AS), and attacks of females (AF) toward test males between XY- and YY-males of seven different lines.

Line	Number (n) of XY and YY males	CDF			CDD			ODF			ODD			SDF		
		$\bar{x}$	$S_{\bar{x}}$	F	$\bar{x}$	$S_{\bar{x}}$	F	$\bar{x}$	$S_{\bar{x}}$	F	$\bar{x}$	$S_{\bar{x}}$	F	$\bar{x}$	$S_{\bar{x}}$	F
FN	XY n=8	41,6	12,11	95	55,6	21,56	171,7	9,3	4,82	40	12,8	7,54	59,20	50,9	16,35	135
	YY n=7	70,3	22,40	170	84,2	29,40	206,7	19,9	11,72	88	24,9	9,26	62,50	90,1	33,42	255
FL	XY n=27	24,9	5,22	112	24,2	5,92	126,0	5,6	1,59	41	11,2	3,19	65,50	30,6	6,71	153
	YY n=15	39,5	11,59	138	46,2	14,45	173,8	6,9	2,97	40	13,7*	7,61	110,8	46,4	14,27	159
FI	XY n=24	58,1	9,97	178	77	13,59	236,6	21,3	5,45	96	42,1*	8,31	146,2	79,4	15,15	273
	YY n=16	74,4	8,81	122	81,1	11,81	178,0	35,6	6,21	79	70,8	11,01	143,8	110	13,74	192
PA	XY n=7	24,9	12,67	91	20,2	9,42	63,10	2,9	1,35	7	2,4	1,22	7,70	27,7	13,75	97
	YY n=2	25,5	16,50	33	18,6	10,20	20,40	7,0	7,00	14	4,5	4,45	8,90	32,5	23,50	47
CA	XY n=24	31,4	6,46	83	33,9	8,04	114,6	8,9	2,00	31	16,3	3,92	59,30	40,3	8,12	111
	YY n=20	28,2	5,98	85	19,6	4,31	63,90	7,1	2,43	47	11,6	4,20	60,80	35,3	7,88	120
BR	XY n=8	30,8	9,56	64	23,1	8,16	60,80	32,8	12,28	94	63,3	18,00	126,5	63,5	20,35	132
	YY n=11	27,2	7,22	82	20,1	6,67	79,40	24,8	4,02	42	53,7	10,56	106,7	52	10,75	124
SI	XY n=22	21,5*	4,49	70	31,7	7,37	122,2	6,4	1,66	31	21,5	6,66	99,60	27,9	6,02	101
	YY n=20	34,9*	4,81	85	44,6	7,31	104,4	9,7	1,93	30	26,1	5,19	78,80	44,6	6,19	101

Line	Number (n) of XY and YY males	SDD			TF			TD			ATF			ATD		
		$\bar{x}$	$S_{\bar{x}}$	F	$\bar{x}$	$S_{\bar{x}}$	F	$\bar{x}$	$S_{\bar{x}}$	F	$\bar{x}$	$S_{\bar{x}}$	F	$\bar{x}$	$S_{\bar{x}}$	F
FN	XY n=8	68,5	27,31	201,2	1,1	0,48	4	0,3	0,12	1,0	10,3	6,85	57	24,3	20,02	163,3
	YY n=7	109,1	38,19	266,9	5,0	3,74	27	5	2,43	14,4	0,3	0,29	2	0,1	0,10	0,70
FL	XY n=27	35,4	8,20	147,5	1,1	0,30	6	1,2	0,55	12,4	13,9	11,42	310	8,4	5,79	153,4
	YY n=15	59,9	21,39	284,6	0,8	0,44	6	1	0,67	9,2	8,3	4,09	62	12,0	7,83	117,7
FI	XY n=24	119,0	20,07	344,1	6,9	2,52	54	3,2	0,83	12,9	2,4	1,25	26	10,8	6,92	122,4
	YY n=16	151,9	20,53	270,3	7,3	2,41	34	4,2	1,25	14,0	1,3	0,59	9	3,9	2,17	33,20
PA	XY n=7	22,6	10,38	68,8	1,6	0,75	4	0,7	0,39	2,7	0,7	0,47	3	0,8	0,55	3,70
	YY n=2	23,1	14,65	29,3	0,0	0,00	0	0,0	0,00	0,0	0,0	0,00	0	0,0	0,00	0,00
CA	XY n=24	50,2	11,41	162,6	1,3	0,54	10	0,6	0,30	6,4	0,8	0,51	12	1,1	0,67	14,90
	YY n=20	31,2	7,96	124,7	0,6	0,46	9	0,2	0,18	3,6	6,9	5,26	106	2,8	1,97	39,10
BR	XY n=8	85,4	25,34	175,5	13,4	5,25	44	6,5	2,41	17,6	0,5	0,38	3	0,2	0,12	1,00
	YY n=11	73,9	16,49	186,1	5,9	2,11	23	7,3	2,63	23,8	2,4	0,86	7	2,2	1,20	13,10
SI	XY n=22	53,2	13,45	221,8	1,7	0,60	10	1,6	0,63	11,3	10,9	3,57	64	19,6	7,79	166,7
	YY n=20	70,7	11,01	146,4	1,4	0,35	4	1,8	0,69	11,7	4,5	1,59	27	6,9	2,84	52,30

Line	Number (n) of XY and YY males	ASF			ASD			AFF			AFD		
		$\bar{x}$	$S_{\bar{x}}$	F	$\bar{x}$	$S_{\bar{x}}$	F	$\bar{x}$	$S_{\bar{x}}$	F	$\bar{x}$	$S_{\bar{x}}$	F
FN	XY n=8	48,3*	9,15	71	65,1*	17,46	150,2	0,0	0,00	0	0,0	0,00	0,0
	YY n=7	12,1*	6,47	41	11,1*	6,65	45,7	0,0	0,00	0	0,0	0,00	0,0
FL	XY n=27	63,2	18,13	504	45,6	10,89	280,7	0,2	0,15	4	0,1	0,05	1,3
	YY n=15	45,9	5,93	95	58,4*	18,23	293,7	0,0	0,00	0	0,0	0,00	0,0
FI	XY n=24	16,4*	3,48	60	45,8*	13,38	267,4	0,0	0,04	1	0,0	0,02	0,4
	YY n=16	1,1*	0,53	7	0,6	0,26	2,6	0,0	0,00	0	0,0	0,00	0,0
PA	XY n=7	8,3	4,03	25	7,9	3,78	24,5	0,0	0,00	0	0,0	0,00	0,0
	YY n=2	0,0	0,00	0	0,0	0,00	0,0	0,0	0,00	0	0,0	0,00	0,0
CA	XY n=24	6,3*	2,05	39	7	3,65	84,6	0,0	0,00	0	0,0	0,00	0,0
	YY n=20	26,9*	9,78	184	15,2	4,76	72,5	0,0	0,00	0	0,0	0,00	0,0
BR	XY n=8	7,8	4,04	34	7,9	6,90	56,1	0,0	0,00	0	0,0	0,00	0,0
	YY n=11	21,3	11,39	118	23,1	15,05	160,2	0,3	0,14	1	0,2	0,12	1,3
SI	XY n=22	16,1	3,63	60	29,5	10,55	219,6	0,8	0,49	10	0,4	0,31	6,7
	YY n=20	14,7	3,95	47	20,3	5,84	89,8	0,5	0,21	3	0,2	0,10	1,9

3.3. Significant differences between behavioral transitions of XY- and YY- males within 20 min of observation:

The differences of sequences of every two behavioral activities between XY- and YY-males were expressed as percentages of all transitions scored within 20 min of observation time and were calculated by a 2 x 2 contingency chi-square table as the ratio of events to non-events for the two male genotypes (XY vs. YY). Although there was no unidirectional trend for the different lines under investigation, the results widely corresponded to the findings as listed in Figs. 1-5 and Table 2. According to Table 3, significant differences were found as follows:

CD follows OD: With the exception of CA where more transitions were found for XY- than for YY-males, the percent transitions were always higher for YY- than for XY-males. No significant differences were found for BR and FL lines.

OD follows CD: Again with the exception of CA, the percent transitions were always higher for YY- than for XY-males. No significant differences were found for BR and FL lines.

CD follows T: With the exception of FN where more transitions were found for YY- than for XY-males, the percent transitions were always higher for XY- than for YY-males. No significant differences were found for SI, PA, and FL lines.

T follows CD: A significant difference was only found for the BR line where percent transitions were higher for XY- than for YY-males.

OD follows T: With the exception of BR where relatively more transitions were found for XY, the percent transitions were higher for YY- than for XY-males. No significant differences were found for SI, CA, PA, and FL.

T follows OD: With the exception of FN where more transitions were found for YY, the percent transitions were higher for XY- than for YY-males. No significant differences were found for FI, SI, PA, and FL.

AF follows CD: Significant difference was only found for the SI line where percent transitions were higher for XY- than for YY-males.

CD follows AT: Significant differences were only found for the FI and SI line. In FI the percent transitions were higher for YY- than for XY-males, while in SI the value for XY was higher.

AT follows CD: A significant difference was only found for the SI line where percent transitions were higher for XY- than for YY-males.

CD follows AS and AS follows CD: In FI and FN the percent transitions were higher for XY than for YY-males, while in SI, CA, and FL the percent transitions exhibited the inverse ratio. No significant differences were found for BR and PA.

OD follows AS: The only significant difference was found in BR where the percent transitions were higher for YY- than for XY-males.

AS follows OD: The only significant differences were found in BR and FI. While in BR the YY-males showed the higher value, there was an inverse ratio in FI.

AT follows AS and AS follows AT: Only in BR and CA the percent transitions were

higher for YY- than for XY-males, while in FI, SI, FN, and FL the values were higher for XY- than for YY-males.

4. Discussion:

As all XY- and YY-males under investigation were F_1 offspring derived from two more or less inbred stocks, they exhibit a similar (high) degree of autosomal heterozygosity. Because X-chromosomal genes apparently do not contribute to the sexual activity of guppy males (FARR 1983), all differences found between XY- and YY-males of the same line should there-fore be attributed to the second Y-linked marker of YY-males.

The behavioral differences between XY- and YY-males found by the comparison of the mean values refer to the total observation time including periods of inactivity (Table 2). Accordingly, they were less significant than those differences which only refer to the time spent in activity (Figs. 1-5). Consequently, only the most conspicuous behavioral differences between XY- and YY-males are also documented by comparison of the mean values.

The percent behavioral activities spent relative to total activity, the significant differences of the mean values per 20 min observation time, and the significant differences of behavioral transitions within 20 min of observation between XY- and YY-males always reflect the same situation: While only in CA and BR lines the XY-males exhibit a higher sigmoid display rate than their YY counterparts, in the remaining five lines (FI, SI, PA, FN, FL) the YY-males show a higher courtship activity. Because only two YY-males of the PA line could be studied, these values are less reliable. As to the thrusting rate, YY-males of the CA and BR lines were again less active than their respective XY-males. The reverse ratio was found in the FI and FN lines.

As a highly aggressive test male provokes more attacks delivered by the standard male than a low aggressive test male does, the test males' aggressiveness is complementary to the response of the standard opponent. Otherwise, as already known from preceding investiga-tions (FARR 1980), guppy males courting at a high rate are less aggressive than guppy males courting at a low rate and *vice versa*. Accordingly, in the CA and BR lines, YY-test males court at a low rate and therefore deliver and provoke more attacks than XY-test males which court at high rates. In all other 5 lines, YY-test males court at higher rates than the respective XY-males and therefore spend less time in agonistic behavior provoking also fewer attacks by standard males. With respect to thrusting behavior, only FN- and FL-YY males delivered more thrusts than their XY pendants. Thus, only in the FN line the sigmoid display rate plus thrusting rate of YY-males was higher than those of XY-males. It seems most reasonable to trace these inter-line differences to the codominant marker of the second Y-chromosome of the respective line.

While the sigmoid rate of the XY-males in the present study was always considerably higher than that of XY-males with the same Y-linked markers, as in the study of FARR (1980), thrusting behavior occurred more seldom. Agonistic behavior was sometimes lower and sometimes higher than that of guppies with the same Y-linked marker genes in FARR's

study. This may be caused by the use of exclusively virgin and, therefore, receptive females in the present study, which may have provoked the males to more courting than thrusting.

Regarding the influence of the second Y-chromosome on the sexual behavior of YY-guppies, it apparently has an additional effect in 5 out of 7 lines in so far as it causes increased courtship activity. Accordingly, with the exceptions of BR and CA, in FI, SI, PA, FN, and FL lines cumulative effects of the second Y-chromosome with respect to sigmoid display rate were observed. However, as far as thrusting and agonistic behavior, which are also inherited via the Y-chromosome, are concerned (FARR 1983), gene-dosage compensation might have played a role in decreasing the rate of these behavior activities.

Apart from the investigations of FARR (1983), the influence of the Y chromosome on the sexual behavior of guppies was not investigated in details. However, in the course of a study dealing with the genetic and environmental correlates of courtship behavior in guppy males, a genetic component for sigmoid display and gonopodial swinging could be confirmed by ROUBERTOUX (1984). As to the Y-chromosomal influence on the social behavior of mammals, many investigations were carried out in laboratory mice. Most of these studies emphasize the importance of Y-chromosome genes on the agonistic and sexual behavior of males (e.g. GINSBURG 1983; GUILLOT et al. 1994, 1995; MAXSON 11994; PLATT 1986; SLUYTER & VAN OORTMERSSEN 1992) and only one research group found no evidence for a Y-chromosomal effect on mouse behavior (e.g. SLUYTER et al. 1994, 1997). Even parallels in genetic variation between intermale and predatory attacking were found (SAND-NABBA 1995). The Y chromosome also affects the open field behavior which perhaps depends on serum levels of testosterone (MONAHAN & MAXSON 1992). The same holds true for the effects of the Y chromosome on intermale aggression which are mediated by effects on testosterone metabolism (MAXSON & ROUBERTOUX 1990) in which the social signals may be pheromonal or individual urinary chemosignals (MAXSON et al. 1986). Similar to guppies, the Y chromosome of two closely related mouse strains were found to be comparable in effect on intermale aggression but different in effect on male sexual behaviors (SHRENKER & MAXSON 1981). While some authors (GUILLOT et al. 1995) give special prominence to the nonpseudoautosomal region of the Y chromosome on intermale attacking, other investigators (VAN OORTMERSSEN & SLUYTER 1994) concluded that the Y-chromosomal effect for aggression may be located on the pseudoautosomal region, which pairs and recombines with the X chromosome (MAXSON & ROUBERTOUX 1990). As to non-genetic modifications of the social environment, the postnatal maternal influence seems to affect short attack latency only to a small extent (SLUYTER et al. 1995).

Although the XYY syndrome in man is not fully comparable with the YY-genotype in guppies because, in the fish, one X-chromosome is replaced by one Y-chromosome while XYY men possess a surplus Y-chromosome, some observations are remarkable. There can be little doubt that men with chromosome constitution XYY run a higher relative risk than normal XY men to show antisocial behavior and to get into conflict with the law (VOGEL & MOTULSKY 1979). A search in the penal registration showed that 5 of the 12 XYYs

(41.7%), 3 of the 16 XXYs (18.8%), and 9.3% of all XY men had been convicted of one or more criminal offensives. The diffe-rence between XYY and XY is significant; the difference between XXY and XY is not. Both groups with abnormal karyotypes (XYY and XXY) showed a marked reduction in the indices for intellectual achievement despite the fact that the social-economic status of their parents was identical to that in the control sample (WITKIN et al., 1976). In guppies, YY-males either exhibited an increase in courtship display rate or, more seldom, an enhanced rate of intermale agonistic behavior. However, nothing is known as to whether or not this increase is caused by an enhanced level of sexual hormones as compared to re-spective XY-males.

Tab. 3: Significant differences of every two behavioral sequences ("transitions") within 20 min of observation between XY- and YY-males of seven different lines.

Line	Number of transitions	FIRST ACTIVITY FOLLOWS SECOND ACTIVITY (WITHIN 1200 SEC)													
		CD/OD	OD/CD	CD/T	T/CD	AF/CD	CD/AT	AT/CD	CD/AS	AS/CD	OD/T	T/OD	OD/AS	AS/OD	AT/AS	AS/AT
BR	424 XY			10,4%	3,5%						7,1%	14,4%	1,2%	2,6%	0,5%	0,5%
	515 YY			3,9%	1,0%						3,5%	7,6%	3,1%	7,4%	3,1%	2,1%
FI	1306 XY	22,2%	33,2%	9,9%			0,2%		9,7%	8,1%	2,0%		1,0%		3,1%	1,8%
	1056 YY	35,1%	41,3%	5,7%			1,0%		0,1%	0,7%	4,3%		0,3%		0,5%	0,6%
SI	679 XY	13,0%	18,6%			1,5%	4,4%	3,5%	3,5%	2,7%					21,2%	20,1%
	531 YY	20,5%	26,8%			0,3%	1,2%	1,1%	11,2%	9,4%					9,4%	7,8%
CA	531 XY	29,8%	36,0%	5,1%					8,7%	7,5%		4,0%			2,8%	2,6%
	597 YY	15,6%	19,6%	1,5%					17,6%	14,9%		1,5%			12,6%	11,6%
PA	74 XY	12,2%	27,0%													
	26 YY	50,0%	50,0%													
FN	418 XY	10,5%	14,6%	1,7%					21,1%	18,4%	0,2%	1,4%			14,8%	12,9%
	306 YY	30,1%	38,2%	8,2%					7,2%	6,9%	2,6%	5,2%			0,7%	0,7%
FL	1013 XY								16,7%	14,3%					19,7%	17,6%
	676 YY								21,6%	18,6%					15,7%	13,0%

5. Zusammenfassung:

Der Besitz eines zusätzlichen Y-Chromosoms bei Wirbeltiermännchen wird verdächtigt, irreguläres Sozialverhalten zu begünstigen. Da bei Säugetieren brauchbare Y-chromosomale Markierungsgene fehlen, können XYY-Männchen phänotypisch nicht erkannt werden. Beim Guppy sind jedoch Supergen-Komplexe bekannt, die über das Y-Chromosom vererbt werden. Das sind Kopplungsgruppen von Genen, die sowohl für die Geschlechtsbestimmung und Sexualfärbung als auch für die Aktivitäts- und Strategiemuster des sexuellen und agonistischen Verhaltens verantwortlich sind und in einem solchen Y-chromosomalen Komplex vereinigt sind. Ein alter Aquarium-Stamm des Guppys, *Maculatus* (*Ma*), bringt gelegentlich phänotypische Ausnahme-Weibchen des Genotyps XY hervor, die durch das Y-gebundene kodominante Gen *Maculatus* (*Ma*) erkannt werden, das für einen dunklen Fleck auf der Dorsalflosse verantwortlich ist. Wenn man diese XY-Ausnahmeweibchen mit normalen XY-Männchen, bei denen das Y-Chromosom durch ein kodominantes Farbgen entsprechend markiert ist, kreuzt, können YY-Männchen phänotypisch identifiziert und der Einfluß eines zusätzlichen Y-Chromosoms auf die sozialen Aktivitäten kann durch Vergleich mit den normalen XY-Brüdern, die nur ein Y-Chromosom des entsprechenden Stammes tragen, erkannt werden. Die Balzaktivität war bei den YY-Männchen aus 5 Linien von insgesamt 7 Linien erhöht, während die agonistische Aktivität der YY-Männchen, die durch die Anzahl der ausgeteilten und erhaltenen Angriffe von einem standardisierten männlichen Opponenten bestimmt worden war, nur bei den verbliebenen 2 Linien erhöht war, die keine Veränderung der Balzaktivität gezeigt hatten.

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