



This work is licensed under the Creative Commons Attribution-Noncommercial-Share Alike 3.0 United States License. To view a copy of this license, visit <http://creativecommons.org/licenses/by-nc-sa/3.0/us/> or send a letter to Creative Commons, 171 Second Street, Suite 300, San Francisco, California, 94105, USA.

EVIDENCE FOR GENETIC CONTROL OF SEX RATIO DISTORTION IN TWO
COLONIES OF *GLOSSINA MORSITANS SUBMORSITANS* NEWSTEAD (DIPTERA:
GLOSSINIDAE)

R. H. Gooding
Department of Entomology
University of Alberta
Edmonton, Alberta T6G 2E3
Canada

Quaestiones Entomologicae
22: 19-28 1986

ABSTRACT

Males of Glossina morsitans submorsitans Newstead sired families which had only females or which had both males and females (with males usually comprising 20 to 70% of the offspring). The phenomenon occurs in two colonies, one originating near Komoé, Burkina Faso, and the other from Yankari Game Preserve, Nigeria. A single generation of selection for or against sex ratio distortion, using flies from both colonies, resulted in shifting the sex ratio in the expected direction. The data indicate that sex ratio distortion in G. m. submorsitans is controlled by an X chromosome-linked factor. A breeding program designed to increase the proportion of males in a colony is proposed.

RÉSUMÉ

Des mâles de Glossina morsitans submorsitans Newstead ont produit des progénitures comprenant seulement des femelles, ou bien des progénitures mixtes mais dont les mâles représentaient généralement de 20 à 70% du total. Ce phénomène a lieu dans deux colonies, l'une provenant des environs de Komoé au Burkina Faso, et l'autre provenant de la réserve faunique de Yankari au Nigéria. En effectuant avec des mouches des deux colonies une sélection pour ou contre ce déséquilibre du rapport des sexes, une seule génération suffit pour ramener le rapport des sexes dans la direction prévue. Les données indiquent que le déséquilibre du rapport des sexes chez G. m. submorsitans est sous le contrôle d'un facteur lié au chromosome X. L'auteur propose un programme d'élevage visant à accroître la proportion des mâles d'une colonie.

INTRODUCTION

In most animal populations there are equal numbers of males and females. This is believed to result from the selective advantage that would accrue to an individual producing offspring of the sex which is in short supply since such an individual would have a greater chance of having "grandchildren" than would an individual producing offspring of the sex which is in excess. (For a recent discussion of this see J. Maynard Smith, 1978.)

Among the exceptions to occurrence of equal numbers of males and females are colonies of *Glossina morsitans submorsitans* Newstead, which originated from Burkina Faso (Gooding, 1984; 1985) and from Nigeria (Gooding, 1984; 1985; Rawlings and Maudlin, 1984). In these colonies an excess of females occurs because some males sire daughters only, while others sire both sons and daughters (Rawlings and Maudlin, 1984). Rawlings and Maudlin (1984) presented no experimental evidence concerning the genetic mechanism(s) by which sex ratio distortion occurs in *G. m. submorsitans*, but they alluded to "experiments in progress" which indicated that "temperature stress and decreased frequency of feeding can [change] the sex

ratio towards normality”.

As well as being of theoretical interest, knowledge of the mechanism(s) of sex ratio distortion in *G. m. submorsitans* may be of practical value. Where sterile males are released as part of an integrated control program, sex ratio distortion resulting in an excess of females will increase the size of the colony necessary for production of a given number of males and thus increase the cost of each sterile male released. Environmental manipulations or breeding programs which increase the proportion of males in a colony of *G. m. submorsitans* could contribute to the cost effectiveness of an S.I.T. program for this species.

Because of the dearth of published information on the mechanism(s) of sex ratio distortion in *G. m. submorsitans*, the present study was undertaken to determine whether the tendency of males to sire families with a distorted sex ratio is inherited. Here I compare the magnitude of sex ratio distortion in two colonies of *G. m. submorsitans*, I present evidence that the tendency for males to sire families with a distorted sex ratio is inherited as an X chromosome linked trait, and I propose a breeding program designed to create a line of *G. m. submorsitans*, with an increased proportion of males.

MATERIALS AND METHODS

Two colonies of *Glossina morsitans submorsitans* Newstead were maintained at approximately 24°C by feeding on rabbits five or six days per week. In this paper the colony which originated from Komoé, Burkina Faso, is designated Gms(BF) and the one originating from Yankari Game Preserve, Nigeria is designated Gms(N). The histories of these colonies were described previously (Gooding 1982; 1985).

Sex ratio among offspring of each male was determined as follows. Each male was placed in a cage with five or six virgin females from the same colony and the flies were maintained as indicated above. (Females in each cage emerged within a three day period and thus could not be full-sibs, but any female in a cage could have been a full-sib of the male placed in that cage and she could be the half-sib of any of the other females in the cage.) Puparia were collected at intervals until at least 11 were produced by each cage of females. The sex of each emerging adult was recorded. Progeny of a single male are referred to as a “family”. Data are presented for those families in which 11 or more adults were obtained.

F₁ females from those families which had no males were mated individually with colony males, from the appropriate colony, and placed in cages designated “Gms(BF) distorter” or “Gms(N) distorter”. (To set up “Gms(BF) distorter” 55 females, from the first four families listed in column 1 of Table 1, were used. For “Gms(N) distorter” 77 females, from the first five families listed in column 1 of Table 2, were used. The females in each family were at least half-sibs and since the father of each female had been with five or six females, between 16.7 and 20% of the females in each family were full-sibs.) Male offspring thus obtained (designated Gms(BF)-D-F₂ and Gms(N)-D-F₂) were mated with several colony females and the sex ratio among their offspring was determined as indicated above.

F₁ females from those families which had both males and females were mated individually with males from these families (designated Gms(BF)-N-F₁, or Gms(N)-N-F₁) and maintained as above. (To set up Gms(BF)-N-F₁ 88 females from the last 11 families listed in column 1 of Table 1 were used, whilst for Gms(N)-N-F₁ 143 females from the last 16 families in column 1 of Table 2 were used. Sib-ships are the same as stated in the above paragraph.) The sex ratio in families sired by their sons (i.e. Gms(BF)-N-F₂ and Gms(N)-N-F₂ males) was determined as

above.

Sex ratios in the various groups of families were compared using the Wilcoxon two-sample test (Sokal and Rohlf, 1981).

RESULTS AND DISCUSSION

Colonies of *G. m. submorsitans* originating from Burkina Faso and from Nigeria have males which sire families of females only or families having various proportions of males and females (Tables 1 and 2). The colonies were not significantly different from each other with respect to sex ratios in families sired by individual males (Table 3).

A single generation of selection for or against sex ratio distortion affected (in the expected direction) the average sex ratio in families produced by males in the selected lines (Tables 1 and 2). However, in three of the four experiments the ranks of sex ratios in the selected lines were not significantly different from those of the original colonies (Table 3). Although the selected lines Gms(BF)-D-F₂ and Gms(BF)-N-F₂ did not differ significantly from each other, the two lines selected from Gms(N) (*i.e.*, Gms(N)-D-F₂ and Gms(N)-N-F₂) were significantly different from each other (Table 3). Similarly, the combined values for sex ratios of families sired by Gms(BF)-D-F₂ and Gms(N)-D-F₂ are significantly lower than the combined values for Gms(BF)-N-F₂ and Gms(N)-N-F₂ (Table 3).

The fact that a single generation of selection shifted the average sex ratio in the expected direction in all four experiments indicates that sex ratio distortion is an inherited trait in *G. m. submorsitans*. Sufficient data have been gathered to test three genetic models (an X chromosome locus, an autosomal recessive, and an autosomal dominant) to see which best explains the genetic basis of sex ratio distortion in *G. m. submorsitans*. None of the four data sets reject the X chromosome model but one data set rejects the autosomal recessive model and two data sets reject the autosomal dominant model (Table 4). Thus it appears that sex ratio distortion in *G. m. submorsitans* is controlled by the X chromosome. However until either suitable genetic markers are obtained, or an inbred line free of the distorter X chromosome is established, it is not possible to test this hypothesis. (See Gooding (1984) for a recent review of tsetse genetics, including current status of information on *G. m. submorsitans*.) Nor is it possible, at this moment, to offer an adequate explanation of why X chromosomes carrying the gene(s) for distortion do not sweep through the population creating fewer and fewer males in each generation. We are currently attempting to establish lines which are genetically marked on each chromosome in hopes of investigating these phenomena.

Sex ratio distortion resulting in an excess of females is known to occur in several species of *Drosophila*. (See Ehrman and Powell (1982) and Lakovaara and Saura (1982) for recent brief reviews.) In some species a maternally inherited spiroplasma or virus causes females to produce daughters only, whilst in others (mainly in the *Drosophila obscura* species group) inversions on the X chromosome cause males to produce mainly, or exclusively, sperm which carry X chromosomes. Evidence obtained in the present study suggests that sex ratio distortion in *G. m. submorsitans* is similar in its inheritance pattern to the latter type of sex ratio distortion in *Drosophila*. Whether the details of the mechanism(s) of sex ratio distortion will be the same remains to be determined.

Evidence that sex ratio distortion in *G. m. submorsitans* is genetically controlled suggests that it may be possible to increase the proportion of males in a colony by removing offspring produced by males who sire families which are predominantly or totally female. This may be

done by setting up cages consisting of one male and several females, keeping puparia from each cage as a group and retaining (for breeding purposes) only adults from families which have a reasonably high proportion of males. The process must be continued through several generations since there is no simple way of identifying females which carry the "distorter X chromosome". Such a breeding program is currently underway in my laboratory in preparation for further studies on sex ratio distortion.

ACKNOWLEDGEMENTS

I thank K.A. Foster for maintaining the tsetse colonies during these experiments. This work was supported, in part, by a grant (No. A-3900) from Natural Sciences and Engineering Research Council of Canada and was performed as part of a research agreement (No. 4044/CF) with International Atomic Energy Agency.

REFERENCES

- Ehrman, L. and J.R. Powell. 1982. The *Drosophila willistoni* species group. Chapt. 14, pp 193-225 in M. Ashburner, H.L. Carson and J.N. Thompson, Jr. The Genetics and Biology of *Drosophila*. Vol. 3b. Academic Press, N.Y. xiv + 428pp + xxxix.
- Gooding, R.H. 1982. Classification of nine species and subspecies of tsetse flies (Diptera: Glossinidae: *Glossina* Wiedemann) based on molecular genetics and breeding data. *Canadian Journal of Zoology* 60: 2737-2744.
- Gooding, R.H. 1984. Tsetse genetics: a review. *Quaestiones Entomologicae* 20: 89-128.
- Gooding, R.H. 1985. Electrophoretic and hybridization comparison of *Glossina morsitans morsitans*, *G. m. centralis* and *G. m. submorsitans* (Diptera: Glossinidae). *Canadian Journal of Zoology* 63: 2694-2702.
- Lakovaara, S. and A. Saura. 1982. Evolution and speciation in the *Drosophila obscura* group. Chapt. 11, pp 23-59 in M. Ashburner, H.L. Carson and J.N. Thompson, Jr. The Genetics and Biology of *Drosophila*. Vol. 3b. Academic Press, N.Y. xiv + 428pp + xxxix.
- Rawlings, P. and I. Maudlin. 1984. Sex ratio distortion in *Glossina morsitans submorsitans* Newstead (Diptera: Glossinidae). *Bulletin of Entomological Research* 74: 311-315.
- Sokal, R.R. and F.J. Rohlf. 1981. Biometry. The principles and practice of statistics in biological research. Second Edition. W.H. Freeman and Company. San Francisco. xviii + 859 pp.
- Smith, J. Maynard. 1978. The evolution of sex. Cambridge University Press. Cambridge, x + 222 pp.

Table 1. Sex ratio distortion in *Glossina morsitans submorsitans* from Burkina Fasu.¹

	Colony	Second Generation Males	
	Gms(BF)	Gms(BF)-D-F ₂	Gms(BF)-N-F ₂
	0.00 (15/16)	0.00 (14/15)	0.00 (14/14)
	0.00 (14/14)	0.00 (15/17)	0.00 (15/16)
	0.00 (14/16)	0.00 (15/15)	0.00 (13/15)
	0.00 (12/16)	0.00 (18/18)	0.38 (13/15)
	0.07 (15/16) ²	0.00 (17/17)	0.43 (14/15)
	0.31 (13/16)	0.00 (19/20)	0.46 (13/14)
	0.33 (15/18)	0.06 (17/19)	0.58 (12/12)
	0.33 (18/18)	0.19 (16/16)	0.62 (13/15)
	0.33 (12/16)	0.29 (17/17)	0.64 (14/17)
	0.38 (16/18)	0.31 (13/17)	
	0.40 (15/18)	0.40 (15/15)	
	0.50 (12/16)	0.53 (19/20)	
	0.53 (15/17)	0.54 (13/15)	
	0.54 (13/13)	0.65 (20/20)	
	0.55 (11/11)		
	0.63 (16/17)		
Number	16	14	9
Average	0.31	0.21	0.35

¹Numbers in table are the sex ratio (expressed as proportion of males in the sample) followed, in parentheses, by no. adults/no. puparia in sample.

²Females from this family were not used.

Table 2. Sex ratio distortion in *Glossina morsitans submorsitans* from Nigeria.¹

	Colony	Second Generation Males	
	Gms(N)	Gms(N)-D-F ₂	Gms(N)-N-F ₂
	0.00 (18/20)	0.00 (17/17)	0.00 (17/17)
	0.00 (13/16)	0.00 (18/19)	0.00 (18/18)
	0.00 (15/15)	0.00 (13/15)	0.00 (13/13)
	0.00 (17/17)	0.00 (20/21)	0.23 (15/16)
	0.00 (14/15)	0.00 (14/15)	0.38 (16/16)
	0.08 (12/15) ²	0.00 (14/14)	0.42 (12/16)
	0.20 (20/21)	0.00 (15/16)	0.43 (14/16)
	0.27 (15/15)	0.00 (17/18)	0.44 (18/18)
	0.38 (13/15)	0.28 (18/18)	0.47 (17/18)
	0.40 (15/18)	0.40 (15/16)	0.50 (16/16)
	0.41 (17/17)	0.44 (16/18)	0.53 (17/18)
	0.43 (14/15)	0.73 (15/15)	0.63 (16/19)
	0.44 (16/17)		0.69 (13/15)
	0.44 (16/17)		0.72 (25/25)
	0.47 (15/19)		0.73 (15/17)
	0.47 (17/18)		
	0.50 (20/20)		
	0.50 (16/17)		
	0.50 (18/18)		
	0.59 (17/17)		
	0.64 (14/15)		
	0.68 (19/19)		
number	22	12	15
average	0.36	0.15	0.41

¹Numbers in table are the sex ratio (expressed as proportion of males in the sample) followed, in parentheses, by no. adults/no. puparia in sample.

²Females from this family were not used.

Table 3. Statistical comparison of sex ratios in the groups of *G. m. submorsitans* families.¹

Groups being compared		U _s	t _s	p
Gms(BF)	Gms(N)	193.0	0.4989	>0.05
Gms(BF)	Gms(BF)-D-F ₂	140.5	1.1627	>0.05
Gms(BF)	Gms(BF)-N-F ₂	84.0	0.6717	>0.05
Gms(BF)-D-F ₂	Gms(BF)-N-F ₂	80.5	1.0709	>0.05
Gms(N)	Gms(N)-D-F ₂	191.5	2.0856	0.05 > p > 0.02
Gms(N)	Gms(N)-N-F ₂	197.0	0.9842	> 0.05
Gms(N)-D-F ₂	Gms(N)-N-F ₂	138.0	2.2673	0.05 > p > 0.02
Gms(BF)-D-F ₂	Gms(BF)-N-F ₂			
+	+	441.5	2.4379	0.02 > p > 0.01
Gms(N)-D-F ₂	Gms(N)-N-F ₂			

¹ Statistical analyses done by Wilcoxon two-sample test (Sokal and Rohlf 1981). In all comparisons, except the first listed, a one-tailed test was used to calculate the value of p.

Table 4. Tests of three genetic models to explain sex ratio distortion in *Glossina morsitans submorsitans*.¹

Model and Parameter	Data Set Tested							
	Gms(BF)-D-F ₂		Gms(BF)-N-F ₂		Gms(N)-D-F ₂		Gms(N)-N-F ₂	
	No. Obs.	No. Exp.	No. Obs.	No. Exp.	No. Obs.	No. Exp.	No. Obs.	No. Exp.
X chromosome								
distorters	7	9.19	3	1.41	8	7.64	3	2.05
normal	7	4.81	6	7.59	4	4.36	12	12.95
χ^2	1.38		1.42		0.17		0.26	
Autosomal recessive								
distorters	7	3.91	3	1.33	8	3.13	3	2.38
normal	7	10.09	6	7.67	4	8.87	12	12.62
χ^2	2.99		1.93		9.35**		0.11	
Autosomal dominant								
distorters	7	5.02	3	0.77	8	4.10	3	1.10
normal	7	8.98	6	8.23	4	7.90	12	13.90
χ^2	1.12		4.79*		5.27*		2.20	

¹ Data for tests are from Tables 1 and 2. Sample calculations are given in Appendix I.

* p < 0.05, ** p < 0.005

APPENDIX I

For each genetic model tested it is assumed that the tendency towards sex ratio distortion is only expressed in males, that the “distorter gene” has no effect on fitness, that the “distorter gene” is not associated with meiotic drive, and that each colony is in Hardy-Weinberg equilibrium for the “distorter gene”. In each model a distorter male is considered to be one which sires zero or one male offspring; normal males sire two or more offspring. The following examples show the calculation of the number of “distorter males” and “normal males” expected among the 14 males tested in group Gms(BF)-D-F₂.

X chromosome model

Frequency of distorter X chromosomes, $d = 5/16 = 0.3125$.

Frequency of normal X chromosomes, $+ = 1 - 0.3125 = 0.6875$.

Gms(BF)-D-F₁ females will be sired by d/Y males and will be +/d (0.6875) and d/d (0.3125). (The numbers in parentheses are the portion of the population made up by these genotypes.)

+/d females contribute +/Y (0.34375) and d/Y (0.34375) and d/d females contribute d/Y (0.3125) to the composition of the Gms(BF)-D-F₂ males.

Thus expected number of distorters, $d/Y = (14)(0.65625) = 9.19$,

and expected number of normals, $+/Y = (14)(0.34375) = 4.81$.

For autosomal recessive model

Frequency of distorter males, $d/d = 5/16 = 0.3125$.

Frequency of distorter gene, $d = (0.3125)^{0.5} = 0.5590$,

and frequency of non-distorter gene, $+ = 1 - 0.5590 = 0.4410$

Gms(BF)-F₁ females will be d/d (0.5590) and +/d (0.4410).

Gms(BF)-F₁ females which mate with non-distorter colony males [(i.e. +/+ (0.2829) and +/d (0.7171), (numbers in parentheses are the portions of males which sire sons)] will give rise to Gms(BF)-F₂ males.

Gametes produced by Gms(BF)-F₁ females are d (0.7795) and + (0.2205), whilst gametes produced by normal colony males are d (0.35855) and + (0.64145).

Thus among the 14 Gms(BF)-F₂ males the expected number of distorter males will be = $(14)(0.7795)(0.35855) = 3.91$,

and the expected number of normal males will be = $14 - 3.91 = 10.09$.

Autosomal dominant model

The frequency of normal males, $+/+ = 11/16 = 0.6875$.

Therefore the frequency of the non-distorter gene, $+ = (0.6875)^{0.5} = 0.8292$,

and frequency of the distorter gene, $D = 1 - 0.8292 = 0.1708$.

To produce Gms(BF)-D-F₁ females, the colony females must have mated with D/D (0.0935) or D/+ (0.9095) males. (Numbers in parentheses are the proportion of each genotype among the distorter males.)

The gametes produced by colony females are + (0.8292) and D (0.1708) and gametes produced by distorter males are + (0.4532) and D (0.5467).

Thus the Gms(BF)-F₁ females are D/D (0.0934), +/D (0.4533), and +/+ (0.3758), and the gametes they produce will be + (0.6412) and D (0.3588).

For Gms(BF)-D-F₁ females to produce sons they must have mated with +/+ males, thus the Gms(BF)-D-F₂ males will be +/+ (0.6412) and +/D (0.3588).
The expected number of distorter Gms(BF)-D-F₂ males will be = (14)(0.3588) = 5.02,
and the expected number of non-distorter Gms(BF)-D-F₂ males will be = (14)(0.6412) = 8.98.