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Ornamentation and Characteristics of the Tail in the Male Guppy

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Submission date: June 2014

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ACKNOWLEDGEMENTS

Several people have contributed to the work of this master project and to them I am very grateful. First, I would like to thank my supervisor, the most positive and genius man I have ever met, Christophe Pélabon. You served me an interesting theme for my master, and it turned out to be much more engaging than I initially thought. This master was supposed to equal a half year of work, not only for me but also for you, and I know it must have felt like working double shifts at least a couple of times, so thank you for all the time you have put into this work, the constructive guidance and for including me in the academic environment at the department. I am also grateful to my other supervisor, Gunilla Rosenquist, who always is in good mood, has helped me on the lab and been supportive while I was ill for a long while. I am also very grateful for the help I have received from Cyril Firmat, for his earlier experiment and access to the guppy pedigree. You have showed me everything I needed to know on the lab and how to handle my data set, in addition to contribute to important discussions. Thanks to Geir Hysing Bolstad who also has contributed with fruitful ideas and for lending me books. I also have to thank Henriette Vaagland, Cyril, Gunilla and the other people who have taken care of the guppies, making this whole experiment possible. I thank my boyfriend, Alexander, for making every day incredible, helping me on the lab and bearing out with my long nerdy monologs about the disturbing findings of my master. Thanks to my friends who have forced me to live a social life while writing my master, especially Ingrid Bruvoll, Kristin Johnsen, Inger Ane Hole and Elida Skøien, who also have been good company these 5 years at LUR. And finally, thank God for my parents and family who doesn't care about guppies but always have faith in me.

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ABSTRACT

Male guppies (*Poecilia reticulata*) show great variation in both shape and coloration of the caudal fin. In some males, an elongation of the caudal fin is present, referred to as a *sword*. This thesis will mainly focus on the sword and how it is related to other properties in the male guppy. Here, the first part is a description of the sword. Then we analyze allometric relationship of different sexual traits, including the sword, and their correlations. We then test whether “sworded” and “non-sworded” males differ in terms of their characteristics and the ones of their offspring. Finally, we estimate the heritability of the different traits. Our results show that the caudal fin length (excluding the sword) and the gonopodium length both present negative allometry and are correlated. On the other hand, sword length and the length of the color length of the caudal fin do not show any relationship to standard length. However, the sword is always associated with a color band. Sworded males differ from non-sworded males in that they have a smaller body size but a larger total tail length, and they also sire offspring with different characteristics of their caudal fin. Furthermore, while we generally found substantially genetic variation in the studied sexual traits, the sword length did not seem to harbor any genetic variation.

NORWEGIAN ABSTRACT

I arten guppy (*Poecilia reticulata*) finnes det stor variasjon i både form og farge på halefinnen til hannene. Noen av disse hannene har en forlengelse av halefinnen, som kalles et *sverd*. Denne masteroppgaven vil hovedsakelig fokusere på sverdet og hvordan sverdet er relatert til andre egenskaper hos guppy-hannen. Første delen er en beskrivelse av sverdet. Deretter vil vi analysere de allometriske forholdene til ulike seksuelle trekkene, inkludert sverdet, og korrelasjoner mellom disse. Deretter tester vi om hannene med sverd skiller seg fra hannene uten sverd når det gjelder disse trekkene, men også trekkene i deres avkom. Til slutt vil vi gi et estimat av den genetiske variasjonen som finnes i trekkene. Våre resultat viser at halefinnen (ekskludert sverd) og gonopodium har en negativ allometri og er sterkt korrelerte. Derimot er det ingen forhold mellom lengden av sverdet eller lengden av farge på halen og standard lengde. Sverd er imidlertid alltid assosiert med farge. Hanner med sverd skiller seg fra hanner uten sverd da de viste seg å ha en kortere standard lengde, men en lengre total halefinne, og de fikk også avkom med ulike egenskaper. Videre, fant vi betydelig additive genetisk variasjon i flere av trekkene som ble studert, men det var derimot ingen additiv genetisk variasjon for sverdet.

INTRODUCTION

Trait, whose function is to affect the attractiveness towards the opposite sex, is often exaggerated or enlarged, as in the long tailed widowbird *Euplectes progne* (Andersson, 1982), the peacock *Pavo cristatus* (Petrie, Halliday & Sanders, 1991) or the barn swallow *Hirundo rustica* (Møller, 1994). Such elaborated traits are generally assumed to be costly in terms of survival, but can still increase fitness as a result of female preferences (Zahavi, 1975; Partridge & Endler, 1987; Halliday, 1994; Basolo & Wagner, 2004).

Several models have been suggested to explain the evolution of female preferences and the elaboration of male ornaments, such as the Fisherian and the good-gene models. These models make different predictions regarding the relationship between the expression of the trait and the overall condition of the bearer, and the correlation between the trait expression and offspring fitness.

Fisher (1958) suggests that exaggerated traits, which affect the survival negatively, can evolve if there is a strong female preference for these exaggerated traits, because of the genetic correlation that arises between the preference and the trait. The Fisherian model predicts that there is *no* relationship between the development of the ornament and the male vigor or fitness (Heisler *et al.*, 1987; Kirkpatrick, 1982). Thus, a trait preferred by females that is not correlated with male quality, is likely to have evolved through a Fisherian process (Grafen, 1990).

On the other hand, the good-gene model suggests that elaborated traits can be genetically correlated with traits that increases viability, and in that sense function as signals of high “genetic quality” (Grafen, 1990). Thus, females may indirectly benefit by mating with these males, given that the traits are heritable (Zahavi, 1975; Andersson, 1994). Because condition is often linked to size, several authors have further suggested that secondary sexual traits should be proportionally larger in larger individuals, and therefore present positive allometric relationship (slope > 1) (Kodric-Brown & Brown, 1984; Petrie, 1988, 1992; Green, 1992). However, Bonduriansky & Day (2003) suggests that positive allometry will *only* evolve if larger individuals have a greater relative

advantage of increased trait size than smaller ones, in terms of sexual and viability selection.

An important refinement of the good-gene model was provided by Rowe and Houle (1996), who suggested that the condition dependence of secondary sexual traits allowed these traits to capture the genetic variation linked to condition and therefore harbor some genetic variation despite the continuous directional selection due to female preference. Indeed, directional selection by female preference is expected to erode the genetic variation in sexually selected traits (Taylor & Williams, 1982). This has been proved to be incorrect and sexual selected traits were found to exhibit a much greater additive genetic variance than first expected (Pomiankowski & Møller, 1995). The capture of genetic variance suggested by Rowe and Houle (1996) therefore explained the presence of high genetic variation in the expression of sexual selected trait. Note that also other mechanisms may allow genetic variation in sexual selected traits to persist in populations. For example, females may differ in their preference (Brooks & Endler, 2001a), use multiple cues when choosing mate partners (Møller & Pomiankowski, 1993), or males can use different mating strategies depending on their morph (Karino & Kamada, 2009; Hurtando-Gonzales & Uy, 2009). Female may also show preference toward males with rare (Farr, 1977) or novel (Hughes, Du, Rodd & Reznick, 1999) color patterns.

There has been done an extensive work on sexual traits and sexual selection in the guppy (*Poecilia reticulata*), and it has been one of the key species to understand the interplay between sexual and natural selection the last fifty years (Haskins, Haskins, McLaughlin & Hewitt, 1961; Houde, 1997). This success is partly due to the ease of breeding guppies in lab and their suitability for both behavioral and morphological studies.

The guppy is a freshwater fish native to rivers and streams of Trinidad and northeastern South America, known for their pronounced sexual dimorphism (Houde, 1997). Male exhibits great variation in color patterns and an eye-catching courtship display. They have also a proportionally larger caudal fin than the female (Endler, 1995). Furthermore, some males develop an elongation of the caudal fin, generally referred to

as a sword (Nicoletto, 1991; Houde, 1997), even though it may not be homologous to the sword observed in other species like the green swordtail, *Xiphophorus helleri* (Basolo, 1995), where *all* males in the species develops a sword (Basolo, 2002). Female preferences for male secondary sexual traits vary among and within guppy populations (Endler & Houde, 1995), and also show plasticity due to experiences (Kodric-Brown & Nicoletto, 2001, Rosenquist & Houde, 1997). In general, orange coloration (Endler, 1983; Endler & Houde 1995), body size (Reinolds & Gross, 1992), caudal fin size (Bischoff, Gould & Rubenstein, 1985; Endler & Houde 1995), total length (Karino & Matsunaga, 2002) and display rate (Farr, 1980) has been found to be positively associated with the attractiveness in males.

Considering the caudal fin, Bischoff *et al.* (1985) found that the female guppies display a direct preference for long tails in males. However, Karino and Matsunaga (2002) have criticized these results and pointed out that Bischoff *et al.* (1985) used males with different tail lengths, but similar body length, leading the long tailed males to be generally longer than the short tail males, therefore confounding preference for tail length and preference for total length. Karino and Matsunaga (2002) further showed that female preference was for male total length, and that tail length only acted as a contributor. They also suggested that elongated tails may have evolved as a male deceptive tactic to appear larger and attract females with fewer growth costs. Because of all the embellishment of the caudal fin in male guppies, the exact target of female preferences may be difficult to study and the resulting selection may be more complex than initially thought.

Furthermore, Karino, Kobayashi & Orita (2005) found that long tailed males got fewer numbers of offspring, where the daughters tended to be smaller and had a lower reproductive output compared to offspring from males with short tail. Moreover, they found that the sons of the long tailed males had a greater total length due to their long tails, which may contribute to a higher reproductive output in these male individuals. Karino, Kobayashi & Orita (2006) also showed that the sex-ratio of the offspring from long tailed males were male biased. Although Karino and Matsunaga (2002), Karino *et al.* (2005) and Karino Kobayashi & Orita (2006) recognized the presence of an

elongation on the caudal fin, these authors did not consequently distinguish between sworded and non-sworded males in their experiments.

In general, very little is known about the elongation of the caudal fin in guppy, the *sword*. These swords is developed only by some males and Egset (2011) found that the proportion of males developing a sword differ among populations. Egset (2011) also showed that the elongation continues to grow, even after males were fully grown.

In other species were swords have been studied such as in the green swordtail, *Xiphophorus helleri*, all males possess a sword consisting of colored elongated ventral caudal fin rays (Basolo, 2002). In this species it has been suggested that females may harbor a preexisting preference for elongated tail (Endler & Basolo, 1998; Rosenthal & Evans, 1998). Such pre-existing receiver bias favoring the evolution of caudal fin elongation has also been demonstrated for the *Xiphophorus maculatus*, where female prefer males with sword, though sword is normally absent in the species (Basolo, 1990a,b).

Generally, sexual selection that favors exaggerated secondary sexual traits is often counterbalanced by natural selection if the traits incur cost to the bearer (Fisher, 1930; Partridge & Endler, 1987; Andersson, 1994). Karino, Orita & Sato (2006) showed that long tails hamper the swimming performance in male guppies and therefore lead to costs in terms of increased predation risk (Godin, 1997; Basolo & Wagner, 2004). Thus, considering the potentially reduced probability of survival, it is plausible that the males pay a cost by having longer tails (Karino Orita & Sato, 2006). However, Nicoletto (1991) compared guppy males with sword, rounded and flag shaped tails in his study, and found that the caudal fin shape did not affect the swimming performance.

The goal of this thesis is to get a deeper knowledge about the ornamentation of the caudal fin in the guppy. This thesis consists of four parts. The first part is a description of the ornamentation of the caudal fin, focusing on the sword. In the second part we analyze phenotypic variation of both primary and secondary sexual traits and their correlations. In the third part we test whether or not there are differences between

sworded and non-sworded males. Finally, we estimate the heritability of the various traits from parent-offspring regressions.

Based on the assumption that larger males are in better condition and that exaggerated traits are costly to produce, we expect larger males to develop larger ornaments. However, if a trait is deceptive and cheap to obtain, the trait will not be restricted to only large individuals, therefore we do not expect such traits to increase with body size. Moreover, traits that are made out of similar structures may be determined by the same genes and are therefore expected to be correlated. Based on Karino *et al.* (2005), we also expect to find differences in the offspring of sworded and non-sworded males. Finally, a lot of factors have the potential to maintain high additive genetic variation in sexual selected traits. We therefore expect the studied traits to harbor additive genetic variance.

METHODS

Study population and lab condition

The males used in this study are descendant from a wild population of Trinidad. The lab population was founded with approximately 500 individuals sampled at a downstream locality of the river Quare (10°39'N, 61°12'W). This is a high predation site where the predator pike cichlid (*Crenicichla alta*) is common. After the fish were transported to the lab in Trondheim (Norway), the population was always maintained with more than 200 individuals. The fish were kept under standardized conditions in 200-500-L aquariums with a 12L: 12D cycle and a water temperature of 24° ± 2°C. They were fed daily alternating commercial dried flakes and newly hatched brine shrimp (*Artemia nauplii*).

In this study we took advantage of a selection experiment where newborn fish were placed in individual aquariums max. 5 days after birth and grown in isolation. Overall we measured 287 individuals, belonging to two successive generations: 115 from the first generation, and 172 from the second generation. With knowledge about the pedigree of the father and sons, we estimated the heritability. However, not all males from the first

generation sired offspring, therefore the sample size were reduced to 70 sires and 172 offspring in this part of the study.

Measurements

All photographs were taken using a digital camera (Canon E 300D) with remote control, two mounted lights on each side, and a petri dish with moistened white plastic background. Before each photograph session, we photographed a standard scale (Ted Pella, Inc. micrometer scale, 10 mm). The fish were immobilized in cold water (8-10 °C) and placed on the moistened white plastic sheet before shooting. Anesthetic was not used because it alters the color patterns (Reynolds *et al.*, 1993). After the fish were photographed they were placed in an aquarium at room temperature where they rapidly recovered. From these photos landmarks were recorded using tpsDig2 and various length measurements were calculated. Males from the first generation were photographed at an age between 365 and 401 days, and males from the second generation were photographed between 157-190 days of age. All fish were photographed on the right side, with the body lying in a straight position, the gonopodium pointing out and the caudal fin in a spread posture. The recorded landmarks are presented in figure 1.

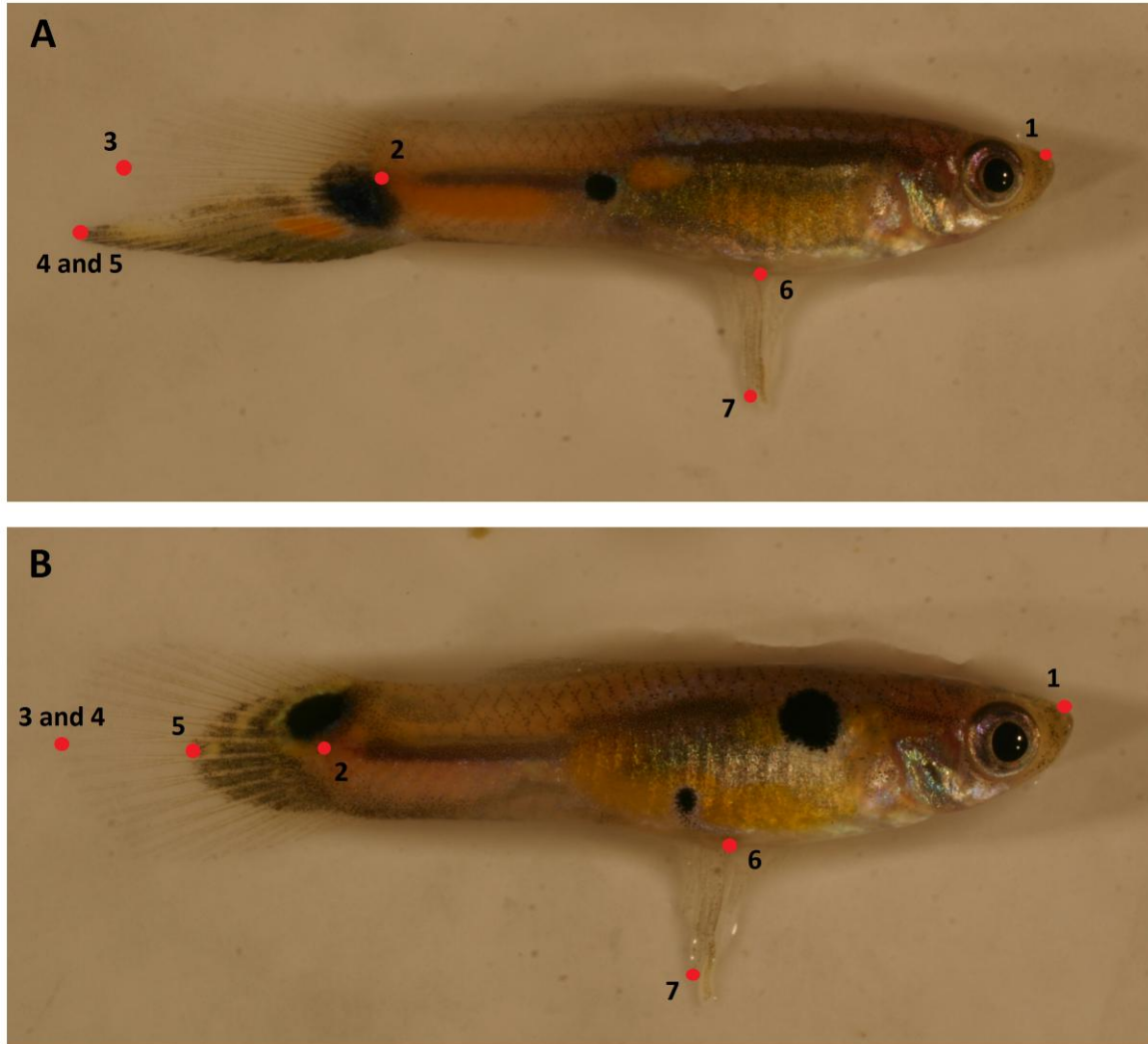


FIG. 1 Positions of the landmarks on male with sword (A) and male without sword (B). The end of the upper jaw (1); The central back part of the body, where the shells end (2); The end of the central part of the rounded caudal fin (3); The tip of the sword, if no sword, same as landmark 3 (4); The outermost point of the continuous color on the tail (5); Where the front part of the hood connects to the body (6); The tip of the hook (7).

The traits measured were: Standard length, total length, caudal fin length, total tail length (caudal fin including the sword), sword, tail color length and gonopodium length. Note that two different measurements of the tail length were obtained; one *with* and one *without* including the sword. These measurements are summarized in table 1.

The *standard length* was measured as the length between the upper jaw (landmark 1) and the central back part of the fish, where the shells end (landmark 2). The end of the

upper jaw was used as a measurement point instead of the lower jaw, to avoid measurement errors due to the lower jaw being a movable part.

The *total length* was measured as the length between the upper jaw (landmark 1) and the tip of the sword (landmark 4). If sword was absent, landmark 4 was placed on the end of the central part of the rounded caudal fin.

The *caudal fin length* was measured as the distance between the central back part of the body (landmark 2) and the end of the central part of the rounded caudal fin (landmark 3).

The *total tail length* was measured as the distance between the central back part of the body (landmark 2) and the tip of the sword (landmark 4). On non-sworded males, landmark 4 was placed on the end of the central part of the rounded caudal fin.

To obtain a measure of the elongation of the caudal fin, the *sword length*, we subtracted the caudal fin length from the total tail length. For the males without sword, landmark 3 and 4 were placed at the same point, giving these males a sword length of zero mm (Fig. 1B and Fig. 2.1 and 2.2). Some males had an asymmetrical shape of the caudal fin, with what looked like a start of extension on the upper or lower part of the caudal fin (Fig. 2.3). For these males the landmark 4 was placed on the tip of this extension even if the position was more proximal than landmark 3. This resulted in a negative value for the measure of the sword length. Figure 2 shows also other examples of different phenotypes and placing of the landmarks.

The *tail color length* was estimated as the distance between the central back part of the body (landmark 2) and the outermost part of the continuous color (landmark 5).

The *gonopodium length* was estimated by the distance between the tip of the hook (landmark 7) and where the front part of the hood connected to the body (landmark 6). This was done to reduce measurement errors due to difficulties in obtaining a correct point where the hook connected to the body.

TABLE 1 Definition of the traits and how they were measured.

Trait	Landmark	
	number	Definition
Standard length	1-2	From the upper jaw to the central back part of the body where the fish shells ends.
Total length	1-4	From the upper jaw to the tip of the sword. If no sword: the end of the central part of the rounded caudal fin.
Caudal fin length	2-3	From the central back part of the body to the end of the central part of the rounded caudal fin.
Total tail length	2-4	From the central back part of the body to the tip of the sword. If no sword: the central part of the rounded caudal fin.
Sword length	(2-4) - (2-3)	The difference between the total tail length and the caudal fin length.
Tail color length	2-5	From the central back part of the body to the outermost point of the continuous color on the tail.
Gonopodium length	6-7	From the front part of the hood elongated from the body to the outermost point on the hook.

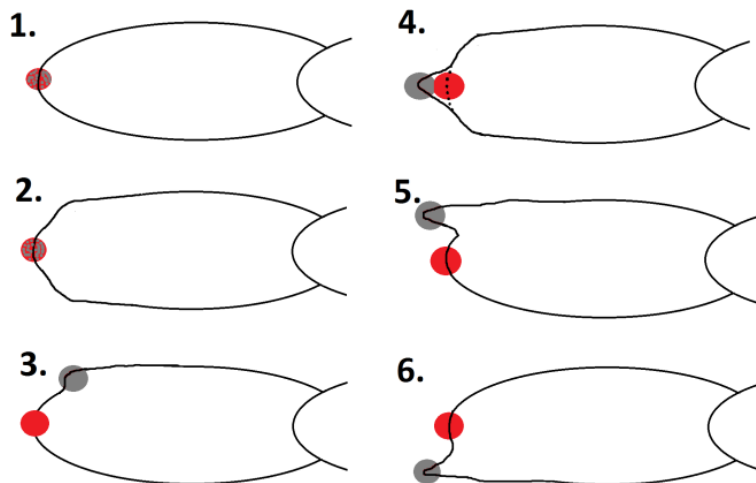


FIG: 2 Illustration of different possible positions of landmarks. The end of the central part of the rounded caudal fin (red); The end of the sword (grey). In example 1 and 2 the landmarks are positioned at the same location.

Statistical analysis

For 66 individuals (31 from the first generation and 35 from the second generation) we took a second picture in order to estimate measurement errors, i.e. the proportion of variance within individual compared to among individual variance. The measurement error is estimated as in Yezerinac, Loughheed & Handford (1992) and is reported in Appendix 1. The measurement errors ranged from 0.36 - 2.62 % for all the traits, except for the gonopodium, which had a measurement error of 26 %. All the males were photographed and measured by the same person.

Data were analyzed in R Core Team (2013). Differences in the relationship between the total tail length and the tail color length among positive, negative and non-sworded males were investigated by performing a regression between the two traits on original scale. Here, we did not control for body size, because this would disturb the relationship we wanted to investigate. Allometry concerns the relative growth of traits and it is therefore customary to use log scale to analyze this type of relationship. In our data set, however, some of the recorded sword lengths could be zero or negative. Therefore we mean scaled the variables instead of using log-transformation in order to obtain the allometric relationship on a proportional scale without facing the problem of non-defined values. First, static allometries of the different traits were analyzed using ANCOVA, with the mean-standardized trait as response variable, the mean-standardized standard length as predictor variable and generation as factor. Second, the correlations between the different traits were then investigated by using the residuals of the allometric relationships. Third, we separated the positive and negative sworded from the non-sworded males to test whether the two groups were different or not. Here we used an ANOVA with both generation and morph (sworded/ non-sworded) as predictor variable. When testing whether the sworded and non-sworded differed in terms of their offspring, we used an ANOVA, with offspring trait as response variable and father morph as predictor variable. Standard length was controlled for by using residuals in both models.

Finally, heritabilities were estimated using the residuals of the allometric relationships in linear mixed models, where the offspring value was the response variable, the father

value the predictor variable and the father identity was used as a random factor to account for the non-independence between siblings. Additionally to estimate the heritability of the sword length, we also performed a t-test to see if sworded males got larger proportion of sworded offspring than non-sworded males.

RESULTS

1. Description of the ornamentation of the caudal fin

Morphology

Generation means for the different traits are reported in Appendix 2. The caudal fin of the male guppies exhibits a wide variation of shape and color. Some males have a symmetrical round caudal fin similar to the female guppy (Fig. 3.1 - 3.3), while others have an elongation stretching beyond the rounded curvature of the caudal fin, referred to as a *sword* (Fig. 3.5 - 3.11). The sword consists of a few elongated fin rays that can be found either in the central part, the upper part, the lower part or in both upper and lower parts of the caudal fin. The sword can be of varying lengths, and sometimes some elongated fin rays can be observed either on the upper or lower part, but without stretching beyond the rounded part of the caudal fin. This results in an asymmetrical shape of the caudal fin. In these cases, it is difficult to say whether a real sword is present or if the fin is just asymmetrical (Fig. 3.4).

Coloration

We observed great variation in the amount and patterns of color among both the non-sworded and the sworded males. In non-sworded males the color can cover everything from the whole caudal fin to only a small part of it, or color can be nearly absent (Fig. 3.1- 3.3). This variation result in an absence of relationship between color length and tail length in these males (Fig. 4A). The color area could also be restricted to the lower or the upper part of the fin, or in the center of the fin. For the males with a positive sword, the sword is always present together with a continuous color band, stretching from the body along the caudal fin up to the tip of the sword. This generates a perfect correlation between the total color length and the total tail length (Fig. 4B). The five points that does

not follow the strict line in figure 4B is due to fading color on the sword tip, where the measurer had to decide a limit for what could be regarded as color.

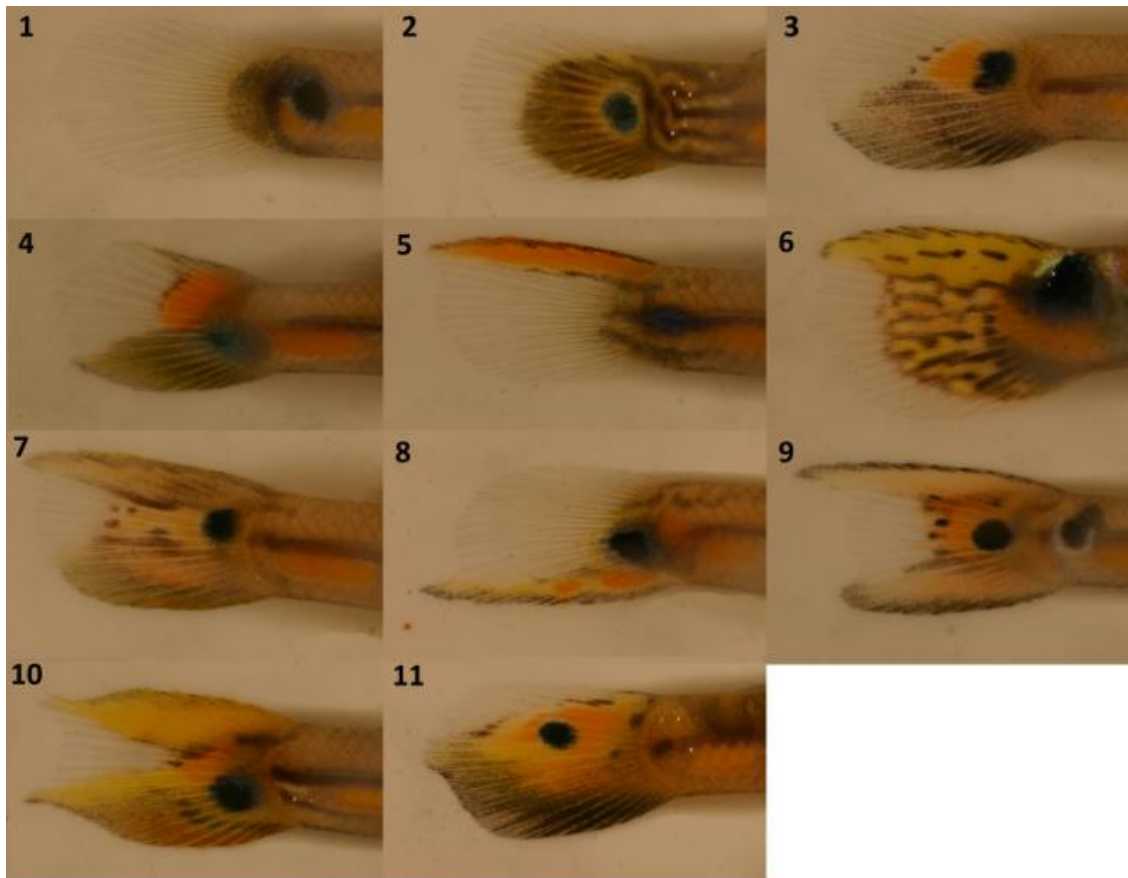


FIG. 3 Variation in morphology and color of the caudal fin. Symmetrical and modest color (1); Symmetrical and medium color (2); Symmetrical and color on the lower part (3); Asymmetrical and color on the lower part (4); Sword with color band on the upper part (5); Sword with color band and medium color on caudal fin (6); Sword with color band on upper part, and great coloration on lower part (7); Sword with color band on lower part (8); Asymmetrical fin with sword and color band on both upper and lower part (9); Symmetrical fin with sword and color band on upper and lower part (10); Sword and color band on central part (11).

It is important to note that the positive sworded males also showed varying color and color pattern placed in different area of the caudal fin, like for the non-sworded, but in contrast, there were no males with nearly absence of color on the tail. Surprisingly, some males with the negative elongation value also had a color band stretching across the asymmetrical part of the fin, as for the ones with positive sword. However, as shown in figure 4C, this was not true for everyone. These males were difficult to measure, and

many of them had a clearly asymmetrical shape, but without the shape really resembling a sword.

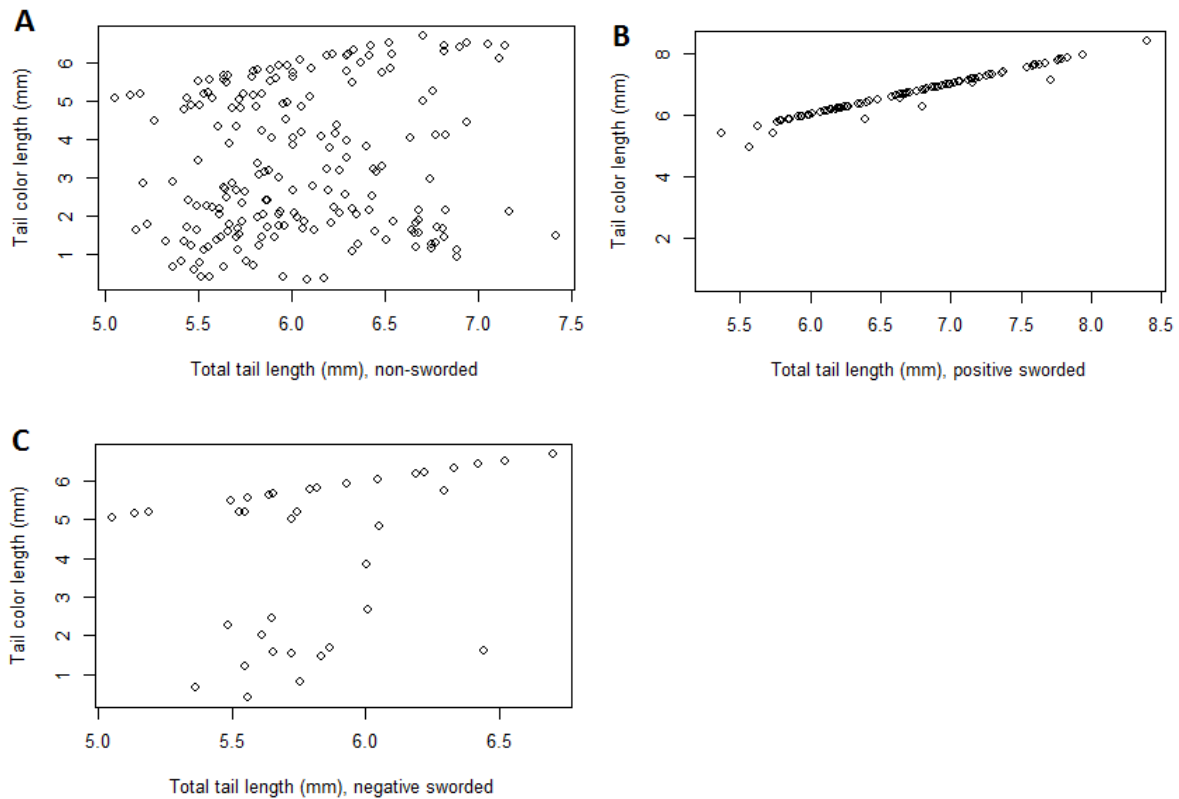


FIG. 4 A-C Tail color length in respect to total tail length. Non-sworded males (A); Positive sworded males (B); Negative sworded males (C).

2. Allometric relationships

For all traits there was no difference in slope between generations, as the interaction term between generation and the covariate being always statistical non-significant ($P > 0.39$) in the different ANCOVA. Allometric slopes for all traits are reported in table 2 and illustrated in figure 5.

The caudal fin length displayed a negative allometry with standard length ($\beta = 0.60 \pm 0.05$), but the males in the first generation had on average a larger caudal fin length relative to the body size than those in the second generation (elevated intercept = 0.04 ± 0.01). The allometric slope for the total tail length including the sword was slightly lower than for caudal fin length ($\beta = 0.58 \pm 0.09$), but most importantly the r-squared was really lower indicating a less tight relationship between total caudal fin length and

standard length. This was due to the sword itself, which showed no relationship with standard length ($\beta = -0.15 \pm 2.58$). In addition, there was no difference among generations in sword length (elevated intercept = 0.31 ± 0.46). No relationship was found between the tail color length and standard length ($\beta = 0.60 \pm 0.59$), but males from the first generation had a relatively longer stretch of color on their caudal fin than males from the second generation (elevated intercept = 0.31 ± 0.11).

The gonopodium length displayed a negative allometry ($\beta = 0.34 \pm 0.07$), and the relative length of the gonopodium was similar in both generations (elevated intercept = 0.01 ± 0.01).

TABLE 2 The slopes \pm SE and p-value from the static allometry performed on the different traits. In addition, the generation effects \pm SE, p-values of the generation effects and R-squared from the different traits.

Trait	Slope \pm SE	P-value	Generation		R-squared
			effect \pm SE	effect, p-value	
Caudal fin length	0.60 ± 0.05	< 0.01	0.04 ± 0.01	< 0.01	0.75
Total tail length	0.58 ± 0.09	< 0.01	0.04 ± 0.02	< 0.01	0.49
Sword length	-0.15 ± 2.58	0.95	0.31 ± 0.46	0.51	0.00
Tail color length	-0.60 ± 0.59	0.31	0.31 ± 0.11	< 0.01	0.05
Gonopodium length	0.34 ± 0.07	< 0.01	0.01 ± 0.01	0.42	0.24

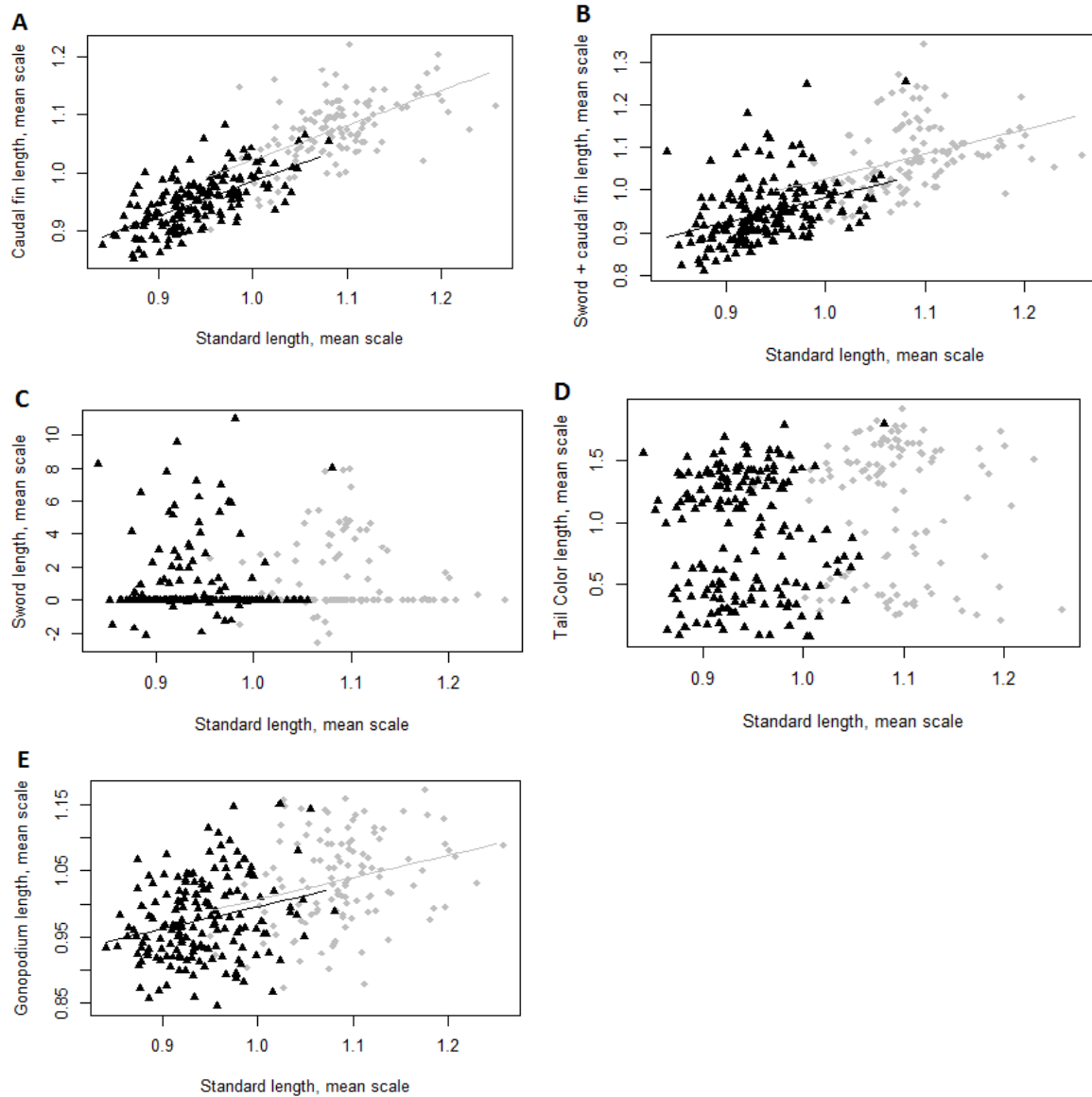


FIG. 5A-E Static allometry of traits in male guppy. Caudal fin length (A); Total tail length (caudal fin length + sword length) (B); Sword length (C); Tail color length (D); Gonopodium length (E).

3. Correlation between traits

According to our results caudal fin length and the gonopodium length are correlated, even after controlling for the body size effect. However, we found no correlation between the sword and the gonopodium, nor between the sword and the caudal fin. The correlations are reported in table 3.

TABLE 3 Correlation in lengths among traits, corrected for body size. Caudal fin length and gonopodium length; Sword length and gonopodium length; Sword length and caudal fin length.

Traits	Correlation	95% confidence interval	p-value
Caudal fin and gonopodium	0.32	[0.21, 0.42]	< 0.01
Sword and gonopodium	-0.05	[-0.17, 0.06]	0.38
Sword and caudal fin	-0.07	[-0.18, 0.05]	0.26

4. Differences between sworded and non sworded males

The differences and similarities of sworded and non-sworded males are presented in table 4. By comparing (positive and negative) sworded with non-sworded males, we found that sworded males had a larger total tail length and a longer part of their tail covered with color. The sworded males are also likely to be shorter in standard length than the non-sworded males, as shown by the p-value = 0.074. However, the two groups did not differ in overall total length, nor in gonopodium length.

TABLE 4 Differences between non-sworded and sworded males regarding their traits, accounted for generation effect. Both positive and negative sworded males are considered sworded. All traits except for standard length and total length are controlled for body size by using residuals.

Trait	Effect of sword	SE	P-value
Standard length	-0.011	0.006	0.074
Relative total tail length	0.058	0.008	< 0.01
Total length	0.010	0.128	0.938
Relative tail color length	0.609	0.047	< 0.01
Relative gonopodium length	-0.007	0.007	0.35

We also tested whether or not the offspring of the sworded and non-sworded males differed in terms of the same traits. Our results are presented in table 5. Considering both positive and negative sworded males as sworded, our results suggest that sworded males sire offspring with larger sword, larger total tail length and longer tail color. In addition, the sworded males seems to sire offspring with a larger total length (p-value = 0.14). However, there were no differences in standard length, caudal fin length or gonopodium length.

TABLE 5 Differences between non-sworded and sworded males in their offspring traits. Both positive and negative sworded males are considered sworded. All traits except for standard length and total length are controlled for body size by using residuals.

Trait	Effect of sworded		
	father	SE	P-value
Offspring total length	0.231	0.154	0.136
Offspring standard length	0.048	0.111	0.664
Offspring relative sword length	1.051	0.334	< 0.01
Offspring relative caudal fin length	-0.001	0.005	0.786
Offspring relative total tail length	0.029	0.010	< 0.01
Offspring relative tail color length	0.241	0.073	< 0.01
Offspring relative gonopodium length	0.005	0.009	0.566

5. Heritability

Estimates of the heritability are presented in table 6 and graphical in figure 7. There is a substantial genetic variation for standard length, caudal fin length, tail color length and gonopodium length. In contrast, the estimate of the genetic variation of the sword length was very low and statistically not significant. Because of the sword being one of the components contributing to the total tail length, this also explains the low genetic variance in total tail length (table 6). There were no differences in the proportion of sworded males between the sworded and non-sworded males, the difference in mean \pm SE being 0.122 ± 0.229 and non-significant (p -value = 0.287).

TABLE 6 Estimated additive genetic variation (h_2), standard error and t-value from parent-offspring regression for each trait.

Trait	h_2	SE	t-value
Standard length	0.332	0.075	4.44
Relative caudal fin length	0.309	0.067	4.58
Relative tail sword length	0.071	0.095	0.75
Relative sword length	0.082	0.090	0.91
Relative tail color length	0.430	0.113	3.80
Relative gonopodium length	0.211	0.093	2.27

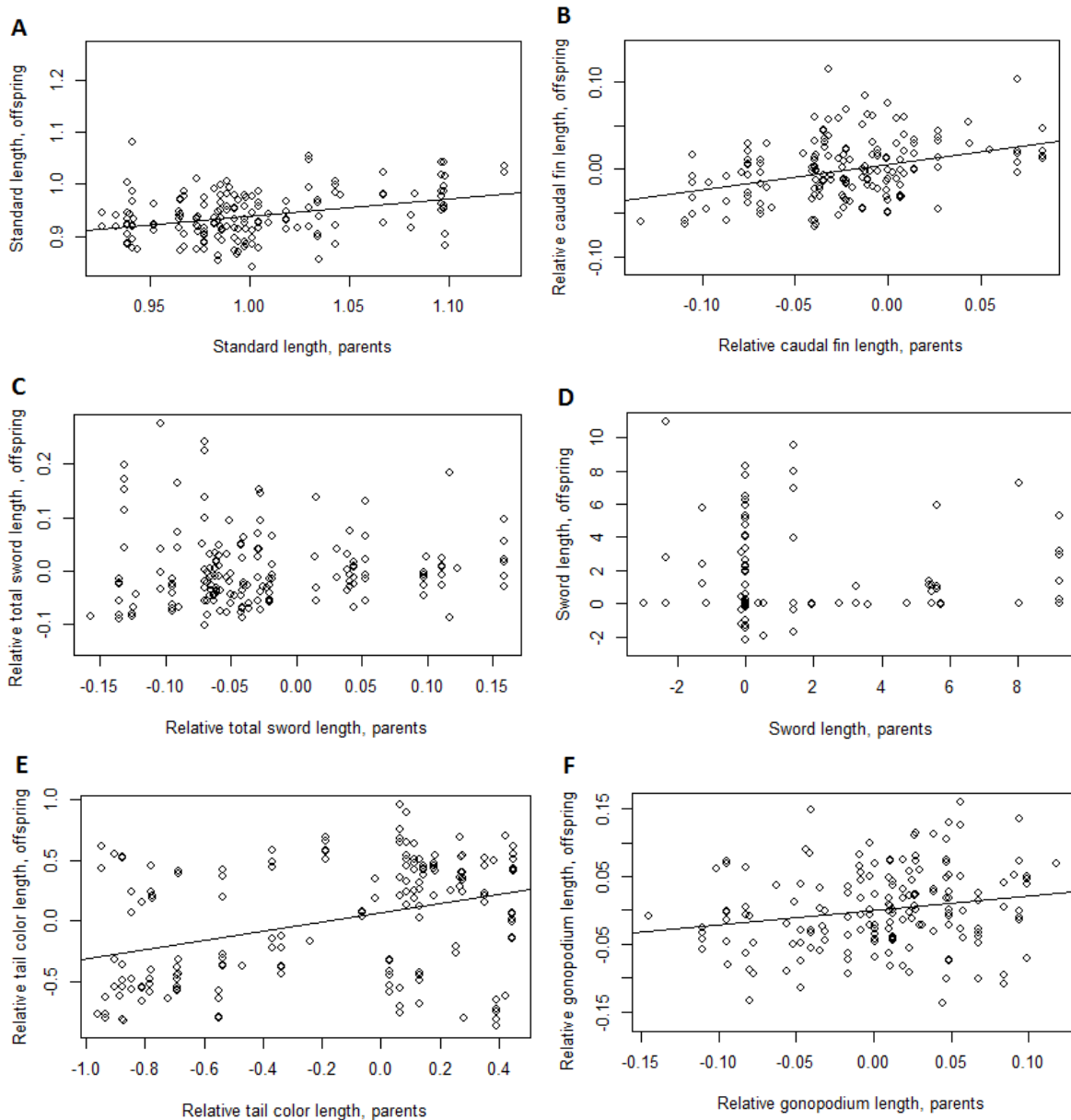
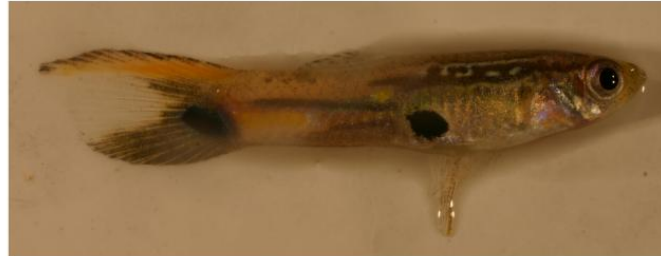


FIG. 7A-F Parent-offspring regression for the different traits. Standard length (A); caudal fin length (B); total sword length (C); sword length (D); tail color length (E); gonopodium length (F). To better illustrate the presence and absence of sword in (D), residuals were not used for sword length.

The tail color length showed great additive genetic variation, which is supported by a visual inspection of the color pattern in father and offspring. This inspection suggests that offspring tend to have very similar color patterns as their father. However, in some clutches some of the offspring develop a sword while others don't, and different degree of sword elongation can be observed among offspring from the same clutch. Note also

that the sword in the offspring does not necessary develop at the same position where the sword has developed in the father (Fig. 8).

Father:



Sons:

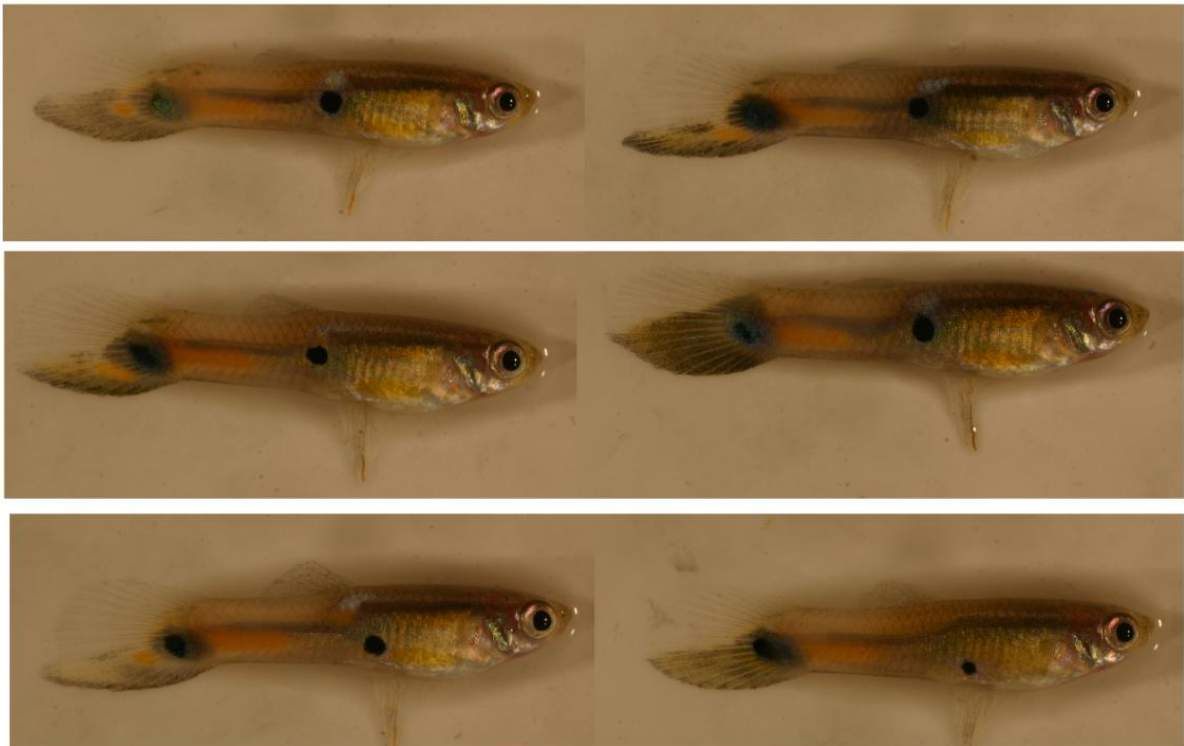


FIG. 8 Sword and color variation in a sworded father with six of his offspring; Some of them sworded and others non-sworded.

DISCUSSION

This study presents a description of the variation in ornamentation of the caudal fin in male guppies from the Quare population, together with some interesting findings. By decomposing the tail into three traits (caudal fin, sword and color), and distinguish between sworded and non-sworded males, we discovered very different properties of both the traits and the males. The caudal fin length displayed a negative allometry, in contrast to sword and tail color length, where neither showed any relationship to standard length. The caudal fin length and gonopodium length were highly correlated, even after the effect of body size was removed, but the sword length was independent of these traits. Moreover, estimates of the heritability, h^2 , suggest that there is additive genetic variation in both caudal fin length and tail color length. However, there were no additive genetic variation in sword length, nor did the sworded males get a larger proportion of sworded offspring. This seems to contradict the fact that sworded males tended to sire offspring with greater swords than non-sworded males. In addition, sworded males differed from non-sworded males by having a shorter standard length, but a greater total tail length, always followed by a color band stretching along the sworded part of the caudal fin.

Bonduriansky and Day (2003) suggested that larger individuals must have a greater advantage of relative larger traits in terms of sexual and viability selection, for positive allometry to evolve. The absence of positive allometry (slope > 1) in the caudal fin length, but also in the total tail length, may be due to two reasons, based on the statement of Bonduriansky and Day (2003). Because long tails hamper the swimming performance in male guppies (Karino, Orita & Sato, 2006) this may reduce viability in terms of predation risk (Godin, 1997; Basolo & Wagner, 2004). Alternatively, the female preference may be for total length rather than tail length, as proposed by Karino and Matsunaga (2002). Consequently, sexual selection is not directly favoring a large tail, which makes the benefits of a larger tail less pronounced.

Consistent with earlier findings, the gonopodium display a negative allometry (Eberhard, Huber, Rodriguez, Briceno, Salas, & Rodriguez, 1998; Eberhard 2009; Bernstein & Bernstein, 2002; Jennions & Kelly, 2002; Voje, Hansen, Egset, Bolstand &

Pelabon, 2014). The gonopodium length was also highly correlated with the caudal fin length. Since these are homologous characters (both are fin rays), their development may be determined by the same genes/ growth hormones (Brooks, 2002). Due to the high correlation, selection working on one of these traits may affect the appearance of the other. It is possible that natural selection working on tail length also indirectly limits the gonopodium length. Because long tail reduces swimming performance (Karino, Orita & Sato, 2006) it would be a disadvantage to have long tails in such habitat. However, natural selection working on long tails in terms of sword would in contrast have no impact on the gonopodium, because these two traits are not correlated. However, the presence of additive genetic variation in the caudal fin length makes it prone to evolve through both sexual and natural selection. Due to sexual selection which favors indirectly a larger caudal fin, and natural selection which favors the opposite, we may expect different populations to exhibit differences in the average of the caudal fin length. However, behavioral adaptations can limit the selection against tail length. Karino, Orita and Sato (2006) found that long tailed males often were located in microhabitats with low water flow velocity, where they could swim more easily.

By multiplying the heritability of caudal fin length by 2, accounting for both the father and the mother, our estimated h^2 (0.618 ± 0.067) is not much different from the findings of Brooks and Endler (2001b) on the heritability of tail area in the guppies (0.823 ± 0.31).

There were no relationship between sword length and standard length, which also caused there to be no relationship between the total tail length and standard length. The lack of allometry suggests that the costs of producing a sword may be small and that it is unlikely to be used as an honest signal of condition. According to Wallace (1987), positive allometry would be favored in traits used as honest advertisement of body size, because it would make assessment easier by amplifying the differences between large and small individuals. According to Wallace's statement, the sword length will not act as an honest advertisement, but rather the other way around; making it more difficult for the female to decide the "true" size (body size) of the male.

The lack of allometry also applies to the tail color length. However, the great complexity of the color expression on the guppy tail is difficult to describe and even more difficult to measure. The measurement that has been done for color length in this study will therefore be of limited use; it tells us nothing about the area of color, color pattern or strength in color. Clearly, there are two different groupings with different means (Fig. 5D), which make it hard to detect any allometry in this trait. Even when separating the sworded and non-sworded into two groups, there were still not detected any allometric relationship. However, the generation effect was clear, consistent with Egset (2011) findings; color is something that comes with age.

The results from the parent-offspring regression show that there is no additive genetic variation in sword length. Neither did sworded males get larger proportions of sworded offspring, compared to non-sworded males. These findings were surprising, because we were expecting the offspring to resemble their fathers, based on Karino *et al.* (2005) findings; long-tailed males get larger male offspring, due to their greater tail length. However, other findings in this study suggest that the heredity of the sword may be much more complex. When studying differences among sworded and non-sworded males, we found that both positive and negative sworded males tend to get offspring with on average larger swords and thus larger total lengths (p-value 0.14) compared to the sworded offspring of the non-sworded males.

Likely, there are different factors determining the presence, length and position of the sword, and that their interactions results in the great complexity of the sword which has emerged from this and other studies. So far we haven't discussed the position of the sword, which we didn't account for in the present study. However, figure 8 illustrates that the position of the sword in the offspring, may be independent of the position of the sword in the father.

In contrast to the sword, the color length proved to have a significant amount of additive genetic variance. Though our way to measure the color may be a great oversimplification of the true complexity of the color in the male guppy, study by a handful of random clutches together with their sire (Fig. 8), witness of a strong and consistent pattern of color, which also correspond to early findings by Winge (1922a, b, 1927, 1937) and Winge and Ditlevsen (1947), which states that color pattern are highly

heritable. Many factors have the potential to contribute to the presence of additive genetic variation, among other things females may differ in their preferences (Endler & Houde, 1995), they may prefer males with rare color pattern (Farr, 1977) and even unattractive males gets the opportunity to mate through sneak copulation, (Karino & Kamada, 2009; Hurtando-Gonzales & Uy, 2009). In addition, the color expression of the tail may possibly be condition dependent.

One of our main goals in this study was to identify potential differences among the sworded and non-sworded males regarding the studied traits. In our search for differences, we found that sworded males are on average shorter in body length than the non-sworded males, but have on the other hand a greater total tail length. As a consequence of the opposite properties, the males groups do not differ in overall total length. However, our results suggest that the offspring of sworded males are likely to have a greater total length than offspring from non-sworded males. This is very similar to Karino *et al.* (2005) findings for long-tailed males, and due to the female preference for total length Karino *et al.* (2002) and this may contribute to increase their reproductive outcome. However, Karino *et al.* (2005) found that long tailed males tend to sire fewer offspring, where daughters had a lower reproductive output than daughters from short-tailed males. This may indicate that the sworded and non-sworded males are using different reproductive strategies to increase their fitness.

The complexity in the properties of the sword make it difficult to say whether the tail fulfill the predictions of the Fisherian or the good-gene model model. From this study we cannot say whether or not there are any relationships between the female choice of sworded or non-sworded males and the offspring fitness or vigor, only that the offspring will differ. It may depend on the environmental factors such as predation risk whether the differences in offspring will affect their vigor and fitness or not.

Moreover, Nicoletto (1991) found that the caudal fin shape didn't affect the swimming performance in male guppy, which doesn't match the predictions in the Fisherian model, where the trait are predicted to show cost in terms of survivorship (Heisler *et al.*, 1987; Kirkpatrick, 1982). However, as complex as the tail characteristics are, we have to account for the different relationships and correlations that exist in order to reach an

overall understanding. Accounting for the color band linked to the sword, we may assume the sword to increase the conspicuousness towards predators, thus result in a cost for the bearer. This may indeed support that the tail elongation has evolved through a Fisherian process, by being both arbitrary and assumingly having a cost of predation due to the color band, although our study do not qualify to end the “Fisherian vs. good-gene” discussion.

Karino and Matsunaga (2002) found that female preference is for male total length and not tail length. However, the presence of sword may not always contribute to total length. From our study we see that the presence of a sword, which is an elongation of some few fin rays, doesn't necessary contribute to an elongated tail, like in the negative sworded males. Both the length and position will determine if this will result in a true elongation, which it indeed does in the positive sworded males. Even though not all the sworded males increase that much in true length, they may gain more in visual length due to the presence of color on the sword. One important question when doing measurement is “What should we measure in order to capture the properties of the traits that we are interested in?” In this particular case, the physical sword may not be the character of interest for the female, but rather the properties related to the sword. We have no basis for stating that the sworded males are more colorful, or that they are more attractive towards females. However, it may be possible that these males may appear larger due to the additional length and color of the sword. Indeed females may not look at the presence of sword at all, only the length, or the color. However, the sword has the potential to influence both of these qualities, and thus may be a trait that is *only* indirectly selected.

In our study, there were challenges regarding the measurements of the sword. At first it seemed rather easy to divide the males into two groups; sworded and non-sworded. This turned out to be rather difficult as it became clear that some males exhibit an elongation that did not reach beyond the longest part of the main caudal fin. However, based on the visual inspection of sword-like structures by the measurer, males with sword-like structures were always given a sword length value different from zero. Because the sword length may not be greater than the caudal fin length, we categorized the positive and negative sworded males in the same group. However, from figure, 4C

we see that not all the negative sworded males possess the color band which we assume is a characteristic of a “true” sword. Grouping these males together with the sworded males may be an important source of errors in our estimates. It is important to note that these males did not have a typical sword, but with the measurer been very objective, even a tiny asymmetry in the caudal fin was categorized as a sword.

The way we estimated the sword length may not prove to be the best. Subtracting the caudal fin length from the total tail length will not give a real representation of the appearance of the sword. Neither will it describe the true elongation of the tail. From our measurement we cannot directly state that the presence of a sword on average increases the tail length. We only know that it is longer than the caudal fin from the central back part of the fish, and will therefore only be an estimate of the contribution in tail length. However, even though our way to group the males was not completely flawless, differences among the group were found, indicating that we, at least partly, have managed to separate two groups with different properties.

However, it is important to note that the negative sworded males have an artificially negative impact on the average tail length due to the way they were measured in this study. By using the sword length in negative sworded males as an estimate of their tail length, which indeed is shorter than their real tail length (Fig. 2.3), gives us a underestimate of the group`s overall tail length. Therefore the sworded group may have a larger total tail length and consequently a larger total length than estimated in this study.

CONCLUSION

There is no doubt that the caudal fin in the male guppy is extremely complex both in terms of color, morphology and the interaction between these. As complex as the tail characteristics are, we have to account for the different relationships and correlations that exist in order to reach an overall understanding of the evolution of the ornamentation in the caudal fin. In addition this will prove challenging because of the difficulty to properly quantify the traits under specific selection. This study contributes

with some interesting finding on the morphology and heritability of the sword, but we encourage others to learn from our mistakes and to continue the study of the mysterious properties of the ornamentation in the male guppy.

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APPENDIX

Appendix 1 Measurement error in the different traits.

Trait	Measurement error, %
Standard length	0.46
Caudal fin length	2.62
Total tail length	1.22
Tail color length	0.36
Gonopodium length	26.00

Appendix 2 Mean lengths of the different traits among first and second generation .

Trait	First generation		Second generation		Generation effect (Trait~Generation)
	Mean, cm	SE, cm	Mean, cm	SE, cm	P-value
Standard length	17,53	0,083	15,14	0,056	<0.01
Caudal fin length	6,52	0,032	5,76	0,021	<0.01
Total sword length	6,74	0,047	5,92	0,035	<0.01
Sword length	0,21	0,036	0,16	0,030	0.278
Tail color length	4,95	0,213	4,00	0,160	<0.01
Gonopodium length	3,20	0,020	3,01	0,014	<0.01