

Male size polymorphism and testis weight in two species of mollies (*Poecilia latipinna*, *P. mexicana*, Poeciliidae, Teleostei)

Größenpolymorphismus und Hodengewichte bei zwei *Poecilia*-Arten (*Poecilia latipinna* und *P. mexicana*, Poeciliidae, Teleostei)

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Summary: We investigated the relationship between testis weight and male body weight in two species of mollies (*Poecilia latipinna*, *P. mexicana*), which show a pronounced size-polymorphism in the male sex. In both species, large males are favored in sexual selection by female choice and male competition, and small males engage in forced copulations apparently to compensate for this. We asked whether this conflict is reflected by higher investment in testis-development in small males. We found the absolute gonad weight of males to strongly increase with increasing body size in both species, but the relative gonad weight to slightly decrease with increasing body weight. The hypo-allometric relationship between gonad weight and body weight suggests higher relative investment in gonad-development in small males.

Key words: alternative mating behavior, gonadosomatic index, Poeciliidae, mating preference, sexual selection

Zusammenfassung: Wir haben die Beziehung zwischen Hodengewicht und Körpergewicht bei zwei *Poecilia*-Arten untersucht (*Poecilia latipinna* und *P. mexicana*). Beide Arten zeigen einen deutlichen Polymorphismus bezüglich ihrer Körpergröße. Bei beiden Arten haben große Männchen bei der sexuellen Selektion einen Vorteil, weil sie sich gegen kleine Männchen bei aggressiven Auseinandersetzungen besser durchsetzen können und weil sie von Weibchen bei der Partnerwahl bevorzugt werden. Kleine Männchen versuchen diesen Nachteil zu kompensieren, indem sie Weibchen zur Paarung zwingen. Wir haben untersucht, ob dieser Konflikt bei kleinen Männchen zu einer stärkeren Investition in die Hodenentwicklung führt. Wir fanden eine deutliche Beziehung zwischen absolutem Hodengewicht und absolutem Körpergewicht. Das relative Hodengewicht nahm mit der Größe ab. Diese Beziehung deutet auf stärkere Investition in die Hoden bei kleineren Männchen hin.

Schlüsselwörter: alternative Paarungsstrategien, gonosomatischer Index, Poeciliidae, Paarungspräferenzen, sexuelle Selektion

1. Introduction

Sperm competition occurs when sperm from different males compete for fertilizations. It has been suggested to lead to adaptations ranging from the gamete to the whole organism (PARKER 1970, BIRKHEAD & MÖLLER 1998). Across-species comparisons revealed a positive correlation between relative testis size and the level

of sperm competition (PARKER et al. 1997). Testis size often directly relates to the amount of sperm produced (BILLARD 1986) and, although fertilization success is influenced by a wide range of spatial and/ or temporal factors arising from the behavior of males and/ or females (BIRKHEAD & MÖLLER 1998), greater numbers of sperm essentially enable males to gain more fertilizations (MARTIN et al. 1974, PARKER

1982). Hence, high relative gonad weight of males is likely to be an adaptation to polygamy, multiple mating of the females and ultimately sperm competition (BIRKHEAD & MØLLER 1998). Beside pronounced differences between species, differences in testes-sizes have also been found among populations of the same species such as in selection lines of yellow dung flies (HOSKEN & WARD 2001) or meal moths raised in different population densities (GAGE 1995).

On a within-species level, differences in relative testis size between individual males would be expected in species where different male types embark on different mating strategies. Theoretical models predict that male types mating in unfavorable roles, such as males that loose in male-male competition and/or are avoided by females, should compensate by investing more in spermatogenesis (PARKER 1990, GAGE ET AL. 1995). This prediction was confirmed in various fish species with external fertilization (GAGE ET AL. 1995, TABORSKY 1994).

Poeciliid fishes are unique models to study the relation between testes size and alternative mating tactics. Fertilization is internal, and females store sperm (CONSTANZ 1989). Furthermore, multiple mating is frequent, copulation rates are usually high, and males cannot monopolize females in most species (FARR 1989). Thus, sperm competition should be pronounced in these species.

The sailfin molly, *Poecilia latipinna*, has been used to study male body size polymorphism and the associated morphological and behavioral variation like size-dependent “alternative” male mating behavior. Males of both species almost cease growth at maturation (TRAVIS et al. 1989, SCHLUPP unpublished data), whereby small males mature in less than one third of the time required by large males (TRAVIS 1989). Large males may have more than three times the length of small ones (PTACEK & TRAVIS 1997), and the body dry weight has been reported to vary by the factor of 27 between different sized males (TRAVIS 1989). There are no distinct size classes, but a continuous range of male sizes (FARR et al. 1986). Large males possess an enlarged sail-like dorsal fin (PARZEFALL

1969, PTACEK 2002), may court females using their dorsal fin for visual displays (PARZEFALL 1969, FARR 1980, 1989) and are favored by female choice (SCHLUPP et al. 1991, PTACEK & TRAVIS 1997). In contrast, small males do not court (PARZEFALL 1969, FARR 1980, TRAVIS & WOODWARD 1989) and rely on forced copulations (TRAVIS & WOODWARD 1989). Such sexual harassment has been shown to impose costs on females: When small males have exclusive access to a female, they show high frequencies of sexual behavior, and female feeding rates decline in the presence of small males (WOODHEAD & ARMSTRONG 1985, SCHLUPP et al. 2001).

A comparable polymorphism in male size is found in the Atlantic molly, *P. mexicana* (PARZEFALL 1969, MENZEL & DARNELL 1973, PLATH et al. 2003), where male body size ranges from 18 to more than 70 mm SL (MENZEL & DARNELL 1973, PLATH unpublished data). However, the two species differ in at least one important aspect of their mating system: Even large Atlantic molly males do not court (PARZEFALL 1969, PTACEK 2002). Under natural conditions as well as in large aquaria, however, large males aggressively defend territories comprising all-female shoals from intruding smaller males. Small males often attempt to mate by coercive copulations at the margins of territories and whenever females are not defended by large males (PARZEFALL 1969). Like in the sailfin molly, male body size and male sexual activity are negatively correlated (i.e., small males exhibit higher frequencies of sexual behavior, PLATH et al. 2003, HEUBEL & PLATH unpublished data), indicating size-dependent alternative male mating behavior. *P. mexicana* females show a mating preference for larger males (PLATH et al. 2004).

In this study we asked which relationship male absolute testis weight and male body weight show in two species of mollies (*P. latipinna* and *P. mexicana*). Furthermore, we asked if small males compensate for their mating disadvantage by investing relatively more into gonad development. In addition, we asked how a frequent parasite of these species (TOBLER et al. 2005, TOBLER unpublished data) interacts

with the development of male testes. We hypothesized that fish infected with the trematode *Uvulifer* sp. (“black spot disease”) would have reduced gonads, both in terms of absolute and relative weight.

2. Methods

Poecilia latipinna is widespread in fresh and brackish water habitats at the coast of the Gulf of Mexico from the Rio Tuxpan, Mexico, north to North Carolina, USA (SCHLUPP et al. 2002). Furthermore, *P. latipinna* was introduced to the San Marcos river system in central Texas (BROWN 1953, SCHLUPP et al. 2002). *P. mexicana* occurs from the Rio San Fernando drainage in Mexico, where both species live in syntopy (DARNELL & ABRAMOFF 1968), south through Central America into northern Costa Rica (BUSSING 1998). In all populations used, *P. latipinna* and *P. mexicana* coexist with the gynogenetic Amazon molly (*P. formosa*), which uses the two species as sperm donor (reviewed by SCHLUPP 2005).

We used wild caught males from several years and populations that were fixed in 70% ethanol immediately after capture. Fixation in ethanol results in shrinkage of tissues, but since all tissues were treated similarly, comparisons between the samples are possible. Measurements were carried out in 1998 in the Biozentrum Grindel in Hamburg. Fish were stored in water for 24 h before the measurements to avoid weight losses by evaporating alcohol. They were dried on paper for several seconds, and the total weight and standard length were determined for each individual. We recorded the presence of black spots, i.e. externally visible encysted metacercariae of *Uvulifer* sp. (BASSLEER 1983). Among the 82 *P. mexicana* males examined, 36 males (43.9%) had black spots. By contrast, only 7 of 86 *P. latipinna* males (8.1%) had black spots. Prior to measuring testis weight, the total body weight was determined. The body cavity of the fish was then opened, the gonads were carefully removed and their weight was determined. The gonadosomatic index (GSI) was calculated as: gonad weight [g]*100/total weight [g] (CRIM & GLEBE 1990).

To test for an effect of male body size on male testis weight we used ANCOVA, where ‘species’ was the between factor and ‘BSD’ (black spots present/not present) was the within factor. Body weight was used as covariate instead of body size so that the covariate had the same unit as the dependent variable. To test for size-dependent differences in the relative investment in testis development, we repeated our analysis using the gonosomatic index (GSI) as dependent variable. To *post hoc* analyze an influence of BSD on the testis weight, absolute as well as relative testis weight (GSI) was compared between BSD-infected and non-infected males using two-sample *t*-tests. To control for an increased prevalence of parasites (BSD) in larger (i.e., heavier) males, a logistic regression was used (log likelihood: -93.79, intercept log likelihood: -95.56, $R^2 = 0.018$), where BSD-prevalence was the dependent (categorical) variable, and male body weight was the independent variable.

Relative testis weight (GSI) may be influenced by male body condition. To avoid an influence of male condition, we intended to include the condition factor as another covariate in the ANCOVA. We calculated the condition factor as: total weight [g]/(standard length [mm])³. However, male body weight and condition factor were negatively correlated (Pearson product moment correlation: $r = -0.18$, $P = 0.021$, $n = 168$). Hence, the condition factor was not included in the analyses. To analyze an influence of the condition factor on the GSI, condition factors were compared between BSD-infected and non-infected *P. mexicana* males using two-sample *t*-tests.

3. Results

3.1. Body size and gonad weight

Since the interaction term ‘species’ x ‘BSD’ x ‘body weight’ had no significant influence on the testis weight ($F_{1,160} = 1.05$, $P = 0.31$), only interactions up to the depth of 2 were analyzed (tab. 1). Mean testis weight (\pm SD) was 1.69 ± 1.25 mg in *P. latipinna* and 1.49 ± 1.05 mg

	<i>df</i>	<i>F</i>	<i>P</i>
species	1,164	0.035	0.86
BSD	1,164	0.06	0.81
body weight	1,164	271.52	<0.0001
species x BSD	1,161	6.12	0.014
species x body weight	1,161	0.45	0.50
BSD x body weight	1,161	0.05	0.83

Tab. 1: Testis weight in *P. latipinna* and *P. mexicana* males. ANCOVA with male body weight as covariate. Significant effects are in bold typeface.

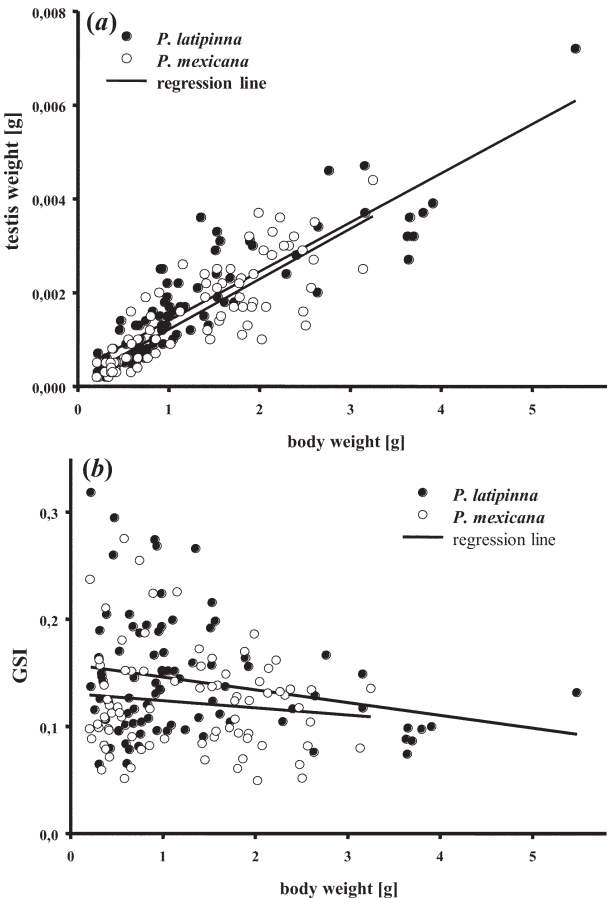
Tab. 1: Hodengewicht von *P. latipinna* und *P. mexicana*. ANCOVA mit dem Körpergewicht der Männchen als Kovariante. Signifikanzen fett.

in *P. mexicana* males. The two species did not differ significantly (tab. 1: factor ‘species’). ‘Body weight’ had a significant effect on male testis weight, and larger (i.e. heavier) males had heavier gonads (fig. 1 a). The slope of the linear regressions describing the relationship between

male body weight and testis weight did not differ between the two species (tab. 1: interaction term ‘species’ x ‘body weight’).

3.2. Body size and GSI

The interaction term ‘species’ x ‘BSD’ x ‘body weight’ had no significant influence on the GSI ($F_{1,160} = 0.07, P = 0.80$), and only interactions up to the depth of 2 were analyzed (tab. 2). The covariate ‘body weight’ had a significant effect on the GSI, because the GSI decreased with increasing body weight (fig. 1 b). Again, the slopes of the linear regressions describing the relationship between male body weight and testis weight did not differ between the two species (tab. 2: interaction term ‘species’ x ‘body weight’).



Figs. 1 a-b: (a) Scattergram showing the correlation between male body weight [g] and testis weight [g] in *P. latipinna* and *P. mexicana* males. Linear regression lines are shown (*P. latipinna*: $y = 0.000357 + 0.00105 x$; *P. mexicana*: $y = 0.000142 + 0.00107 x$). (b) Correlation between male body weight and the GSI (*P. latipinna*: $y = 0.158 - 0.0119 x$; *P. mexicana*: $y = 0.131 - 0.00668 x$).

Abb. 1 a-b: (a) Beziehungen zwischen Körpergewicht (g) und Hodengewicht (g) der Männchen von *P. latipinna* und *P. mexicana*. Lineare Regressionen $y = 0,000357 + 0,00105 x$ (*P. latipinna*) und $y = 0,000142 + 0,00107 x$ (*P. mexicana*). (b) Beziehungen zwischen dem Körpergewicht der Männchen und dem gonadosomatischen Index (*P. latipinna*: $y = 0,158 - 0,0119 x$; *P. mexicana*: $y = 0,131 - 0,00668 x$).

	df	F	P
species	1,164	0.53	0.47
BSD	1,164	0.51	0.48
body weight	1,164	6.84	0.0097
species x BSD	1,161	3.86	0.051
species x body weight	1,161	0.01	0.98
BSD x body weight	1,161	0.13	0.72

Tab. 2: GSI in *P. latipinna* und *P. mexicanana* males. ANCOVA with male body weight as covariate. Significant effects are in bold typeface.

Tab. 2: Gonadosomatischer Index (GSI) der Männchen von *P. latipinna* und *P. mexicanana*. ANCOVA mit dem Körpergewicht der Männchen als Kovariate. Signifikanz fett.

3.3. BSD and testis weight

The interaction term ‘species’ x ‘BSD’ had a significant influence on the absolute testis weight and a marginally non-significant effect

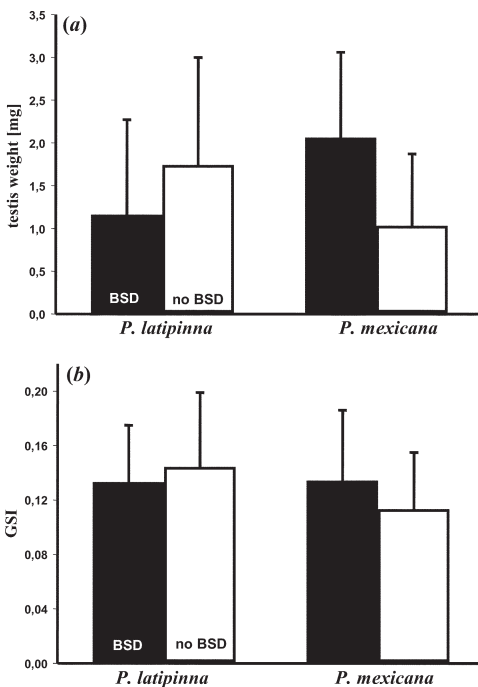


Fig. 2: (a) Testis weight (mean±SD) and (b) GSI of BSD infected males (black bars) and non-infected males (open bars) in *P. latipinna* and *P. mexicanana*.

Abb. 2: (a) Hodengewicht (Mittelwert und Standardabweichung) und (b) gonadosomatischer Index von BSD infizierten (schwarze Balken) und nicht infizierten Männchen (helle Balken) von *P. latipinna* und *P. mexicanana*.

on the GSI (tab. 1, 2). This reflects that the testis weight was higher in infected *P. mexicanana* males, whereas testis weight was lower in infected *P. latipinna* males (fig. 2). Since only seven *P. latipinna* males in our sample were infected the effect of BSD was further examined only in *P. mexicanana* males. Infected *P. mexicanana* males had heavier testes than non-infected ones (two-sample *t*-test: $t_{80} = 5.06$, $P < 0.0001$, fig. 2 a). We controlled whether this difference was due to higher parasite prevalence in larger males. A logistic regression revealed that male body weight and infection with BSD were slightly, however not significantly, positively correlated (coefficient: 0.034, $c^2 = 3.56$, $P = 0.059$). Even when we controlled for this by comparing the relative testis weight (GSI), infected *P. mexicanana* males still had significantly heavier testes than non-infected males (two-sample *t*-test: $t_{80} = -2.08$, $P = 0.041$, fig. 2 b). We controlled whether this was due to lower body condition of infected males. However, infected males had a higher condition factor ($2.66 \pm 1.17 \cdot 10^{-8}$, $n = 36$) than non-infected males ($2.14 \pm 0.86 \cdot 10^{-8}$, $n = 46$, two-sample *t*-test: $t_{80} = -2.31$, $P = 0.023$).

4. Discussion

Overall, our data do not indicate significant differences between the two species examined, although *P. latipinna* had slightly heavier gonads (absolute gonad weight). Male body size had a strong effect on both the absolute gonad weight and on the relative gonad weight (GSI), but the direction of the respective body weight-regressions were different: While the absolute testis weight increased with increasing body weight, the relative gonad weight decreased, indicating a higher relative investment into the gonads by smaller males. There was considerable variance in the GSI data, especially for small males. This is likely to reflect the naturally high variance in body weight and -condition. High variance of the relative abdominal distension and condition factor has been reported for *P. mexicanana* males of various populations (PLATH et al. 2005, PLATH unpublished data).

Recent studies have shown that large *P. latipinna* and *P. mexicana* males produce more sperm (ASPBURY & GABOR 2004, SCHLUPP & PLATH 2005), so that absolute gonad weight appears to predict the absolute sperm production in this species. This may be one of the direct benefits large males offer to females: they provide sufficient amounts of sperm more quickly. Together with other factors like the absence of sexual harassment in large males (SCHLUPP et al. 2001), this may contribute to the evolution and maintenance of the female preference for large male body size in *P. latipinna* (SCHLUPP et al. 1991) and *P. mexicana* (PLATH et al. 2004).

In contrast to the absolute gonad weight, the relative gonad weight (GSI) slightly but significantly decreased with increasing male body size. Small males apparently invest relatively more into gonad development. Possibly, large territorial males cannot afford such a high investment due to the costs of growth, ornaments, and defending a territory (TABORSKY 1994). This idea is supported by the negative correlation between male size and body condition. Furthermore, small males may try to compensate for the disadvantages of both being rejected by females and being inferior in male competition. Increased relative testis size may be adaptive for them, because small males may have to transfer as much sperm as possible quickly upon finding a mate. It is unclear for the mating systems investigated here, if the fitness return for smaller and larger males is comparable.

Contrary to our predictions, the GSI increased in BSD-infected *P. mexicana* males. Impaired body condition of infected males (i.e. body weight losses) might have had an influence on the GSI. However, this was not the case in our study, because infected males did not have a lower condition factor. On the one hand, higher body condition and increased GSI in infected males could be explained by parasite-induced growth enhancement (ARNOTT et al. 2000) or a final investment of individuals facing immediate death due to parasite infection. Alternatively, only individuals with above average body condition may survive an infection with BSD. Without controlled laboratory experiments,

however, the interpretation of these correlative field data remains problematic, since pre-infection conditions of the hosts are unknown.

Future studies will have to answer how male body size and the presence of competitive males relate to the amount of sperm transferred per copulation in the species examined. For example, mosquitofish (*Gambusia holbrooki*) can adjust the amount of sperm they transfer in response to actual risk of sperm competition (assessed by the presence of another male, EVANS et al. 2003). Furthermore, future studies will need to examine how plastic the relative investment in gonad development is in these species, for example, maturing males may respond to higher perceived risk of sperm competition by investing more in gonad development.

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