Trophic niche segregation between the sexes in two species of livebearing fishes (Poeciliidae)

Geschlechtsunterschiede in den trophischen Nischen zweier lebendgebärender Zahnkarpfen (Poeciliidae)

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Summary: Fishes of the genus *Poecilia* are highly sexually dimorphic. In the two species investigated here (*P. latipinna* and *P. mexicana*) males are, on average, of smaller body size and more colorful than females. Males also differ from females in time allocated to feeding as they engage in mating behavior almost day-round. We hypothesized that, due to different time allocations and energy requirements, the sexes might forage on different food items and thus could occupy different trophic niches. We investigated gut content compositions, intestinal tract length and gut fullness in multiple populations of *P. latipinna* and *P. mexicana*. Our finding of females having fuller guts than males corroborated sex differences in time allocation for foraging. A major difference between sexes was also found in intestinal tract length, with males consistently having shorter guts, likely reflecting spatial constraints due to sexually dimorphic traits (like a more anterior anal porus). Contrary to prediction, however, gut content composition indicated no clear-cut pattern of sex-specific trophic niches across study sites. Niche widths, on the other hand, differed between sexes with males having narrower trophic niches than females. Overall, we found sex-specific differences in some aspects of feeding ecology, but no clear trophic niche segregation was detected.

Keywords: trophic niche segregation, sexual dimorphism, gut content analysis, Poeciliidae, sexual segregation

Zusammenfassung: Fische der Gattung *Poecilia* weisen einen deutlichen Sexualdimorphismus auf. Die Männchen der beiden hier untersuchten Arten (*P. latipinna* und *P. mexicana*) sind zumeist kleiner und bunter gefärbt als die Weibchen. Sie unterscheiden sich weiterhin darin, dass sie weniger Zeit mit der Nahrungs-aufnahme zubringen, da sie viel Zeit für das Fortpflanzungsverhalten verwenden. Wir vermuteten, dass die Geschlechter aufgrund dieser Unterschiede nach unterschiedlichem Futter suchen und somit unter-schiedliche trophische Nischen einnehmen. Aus diesem Grund untersuchten wir den Darminhalt und die Darmlänge von Individuen aus verschiedenen Populationen von *P. latipinna* und *P. mexicana*. Weibchen wiesen einen höheren Darmfüllungsgrad auf; dies untermauert die These, dass Weibchen mehr Zeit für das Fressen aufwenden. Einen erheblichen Unterschied zwischen den Geschlechtern fanden wir hinsichtlich der Darmlänge; die Männchen zeigten kürzere Därme, was sich jedoch weitgehend durch Besonderheiten der männlichen Anatomie (eine nach vorne verlagerte Analöffnung) erklären lässt. Entgegen unserer Prognose konnten wir keine klaren geschlechterspezifischen Unterschiede in den Darminhalten an verschiedenen Untersuchungsstandorten feststellen. Die Nischenweite unterschied sich jedoch zwischen den Geschlech-tern, Männchen zeigten eine geringere trophische Nischenweite als Weibchen. Zusammenfassend haben wir geschlechterspezifische Unterschiede in einigen Aspekten der Nahrungsökologie gefunden, jedoch ließ sich keine eindeutige Nischentrennung feststellen.

Schlüsselwörter: Trophische Nischensegregation, Sexualdimorphismus, Darminhaltsanalysen, Poeciliidae, sexuelle Segregation

1. Introduction

Sexual selection is a major evolutionary force leading to sexual dimorphism in traits like color patterns and body size (ANDERSSON 1994). In many fishes, females prefer males exhibiting conspicuous ornaments (REYNOLD & GROSS 1992, SEEHAUSEN & VAN ALPHEN 1998, SCHLUPP et al. 2010). Livebearing fishes (Poeciliidae) are particularly well studied in this context. They are characterized by internal fertilization and vivipary (GREVEN 2011), and males use their modified anal fin, the gonopodium, as a copulatory organ (ROSEN & BAILEY 1963, GREVEN 2005, 2011). Most species of poeciliid fishes exhibit distinct sexual dimorphism in morphology, body size and coloration (BISAZZA 1993). Despite pronounced differences in numerous traits relating to reproduction and sexual selection, surprisingly little is known about potential sex differences in ecological characteristics.

In both species investigated herein, the Atlantic molly *Poecilia mexicana* Steindachner, 1863 and the sailfin molly *P. latipinna* (Lesueur, 1821), males are more brightly colored compared to the cryptically colored females (PARZEFALL 1969, MILLER et al. 2005, THOMAS et al. 2007). Also, *P. latipinna* males are characterized by an enlarged dorsal fin (HUBBS 1933, PARZEFALL 1969). Males occur in several size classes, but females are typically of larger body size (MARLER & RYAN 1997). Females favor copulations with males of larger body size, and male size classes embark on different mating tactics (PARZEFALL 1969, PTACEK 2002, MAC LAREN & ROWLAND 2006, PLATH et al. 2007). Larger males defend females (PARZEFALL 1969) and in *P. latipinna* they also exhibit courtship behavior using their sail-like dorsal fin in a visual display (PARZEFALL 1969, WOODHEAD & ARMSTRONG 1985, FARR et al. 1986). In contrast, smaller males rely on sneaky mating tactics and forced copulations (SCHLUPP et al. 2001, PLATH et al. 2007). To avoid the costs of forced mating, including reduced feeding opportunities (SCHLUPP et al. 2001) or potential physical damage to the gonopore (CONSTANTZ 1984, R. DEATON et al. pers. comm.), females are expected to adopt counterstrategies (ARNQVIST

& ROWE 2005). Female guppies (*P. reticulata* Peters, 1859), for example, reside in the deeper portions of streams despite an increased piscine predation risk to avoid male sexual harassment (DARDEN & CROFT 2008). Therefore, sexes in *P. reticulata* show a different spatial distribution and use different physical environments as part of their home ranges (CROFT et al. 2003, DARDEN & CROFT 2008, JONES et al. 2010). This pattern that emerges is known as 'habitat segregation', a special form of sexual segregation (CLUTTON-BROCK et al. 1982). In another poeciliid, the eastern mosquitofish *Gambusia holbrooki* GIRARD, 1859, females form denser schools when a male is visible and females harassed by a male spend more time associating with larger groups (DADDA et al. 2005, AGRILLO et al. 2006). Sexual harassment could lead to a certain degree of habitat segregation in *P. latipinna* and *P. mexicana* as well, possibly translating into sex differences in trophic resource use.

It is also possible that the sexual size dimorphism affects trophic niche segregation between the sexes. The larger (female) sex has greater absolute metabolic requirements and is also able to retain food longer and therefore digests food items more efficiently, assuming that gut capacity is a constant proportion of body mass (GROSS 1998). Consequently, the larger-bodied sex could prefer habitats with abundant but low quality food, whereas small-bodied individuals might be forced to compensate for their digestive inferiority and hence, could be constrained to sites where they can obtain a high quality diet (forage-selection or gastrocentric hypothesis: BEIER 1987, BARBOZA & BOWYER 2000). Recently, feeding rates of *P. mexicana* males were found to be four-fold lower than in females (KÖHLER et al. 2011), probably due to males' high mating activity. Hence, it seems reasonable to hypothesize that males have to forage on more energy-rich and nutritious food items to cover their energy demands.

To detect potential trophic niche segregation between sexes in *P. mexicana* and *P. latipinna* we analyzed four different aspects of their feeding ecology. (1) We conducted a gut content analysis of wild caught fish to test whether the sexes feed on different items. (2) We measured the trophic

niche widths in females and males, as differences in niche widths could be an indicator for trophic differentiation. (3) We compared intestinal tract length as one trait that frequently reflects dietary types in fishes, with shorter guts being indicative of a more insectivorous diet (WINEMILLER et al. 1995, HORSTKOTTE & STRECKER 2005, TOBLER 2008), and (4) included an analysis of gut fullness to estimate sex-specific differences in feeding activities.

2. Methods

2.1. Study populations and general sampling procedure

Data on female trophic ecology were reanalyzed from a previous study investigating patterns of trophic niche segregation between female *P. latipinna* and *P. mexicana* and the co-occurring asexual species *P. formosa* (Girard, 1859) (SCHARNWEBER et al. 2011). Here, we additionally investigated males for both sexual species. We examined three populations of *P. latipinna* from Texas, USA, and three populations of *P. mexicana* from Tamaulipas and Nuevo León, Mexico (see tab. 1 for collection sites). The population of *P. latipinna* in Central Texas represents an introduced population of Floridian origin (BROWN 1953). Fishes were caught between April and August 2009 using a seine (length 4 m; mesh-width 4 mm), euthanized with MS222 (Tricaine Methanesulfonate) immediately after capture and fixed in a 1:9 formaldehyde solution.

2.2. Gut content analysis

Fish were measured for standard length (SL) to the nearest mm and weighed to the closest 0.01 g (blotted wet weight). Fish were then dissected and entire intestinal tracts removed from the body cavity. We measured the length of the digestive tract, which is tubular and without a discrete stomach in *Poecilia*. Volume of intestinal contents was determined by calculating the water displacement in a graded cylinder filled with tap water after introduction of (1) the full and (2) carefully emptied intestine. Methodologies for gut content analysis were adapted from HELLAWELL & ABEL (1971), HYSLOP (1980), WINEMILLER (1990) and TOBLER (2008). We investigated gut contents of the first quarter of the intestine under a stereomicroscope. Items too small for identification were placed on a glass slide for examination under a compound microscope. We sampled five different areas on the slide at random and the proportion of dietary items in each area was estimated. Diet categories were adapted from WINEMILLER (1990) and the following categories were considered in this study: fine detritus, diatoms, desmids and unicellular green algae, filamentous algae, parts of vascular plants, protozoa, rotifers, and sand. All items with an overall occurrence

Tab. 1: Field sites sampled for this study.
Tab. 1: Untersuchungsstandorte der vorliegenden Studie.

Study site	River basin	Latitude	Longitude
Sites of *Poecilia latipinna*			
Central Texas	Guadalupe river	29.857	-97.868
Lincoln Park	Rio Grande (Bravo)	25.900	-97.479
Weslaco	Rio Grande (Bravo)	26.121	-97.962
Sites of *Poecilia mexicana*			
Río Mante	Río Guayalejo	22.705	-99.001
Barretal	Río Soto La Marina	24.079	-99.123
Río Juanillo	Río San Fernando	24.608	-98.299

of less than 5% in the gut content (including protozoa, rotifers, plant parts, and filamentous algae) were merged into a group of "rare items" for data analysis.

2.3. Statistical analyses

2.3.1. Differential resource use

To test for sex-specific variation in resource use, we excluded fish with empty intestines from the analysis. Proportions of dietary items were arcsine(square-root)-transformed to normalize distributions, subjected to Principal Component Analyses (PCA) based on a covariance matrix, and principal components with an Eigenvalue over 1 (three principle components accounting for 76.78 % of variance, see tab. 2 for axis loadings) were used as dependent variables in a Multivariate Analysis of Covariance (MANCOVA) with sex, species, study site (nested within species), and their interactions as factors, as well as SL as covariate. We approximated F-ratios using Wilks' lambda and effect sizes using partial eta squared (η_p^2). The assumptions of normal distribution and homogeneities of variances and covariances were met for all analyses.

2.3.2. Trophic niche width

The dietary niche width of each individual was calculated using the inverse of Simpson's (1949) diversity measure $\beta = (\sum p_i^2)^{-1}$, where p is the proportional utilization of each dietary item i (Pianka 1973, 1986). Niche width values were subjected to Analysis of Covariance (ANCOVA) using sex, species, study site (nested within species), and their interactions as independent variables and SL as covariate.

2.3.3. Intestinal tract length

We compared gut length as a morphological indicator for potential niche segregation. In this ANCOVA model, we also included data from fish with empty intestines. Intestinal tract length was used as dependent variable and sex, species, species nested within study site and their interactions as independent variables. Kramer & Bryant (1995a, b) suggested using individuals' body mass rather than size as a covariate in comparisons of intestinal tract length; thus a mass-based covariate ($10*mass^{1/3}$) adapted from the Zihler index was included (Zihler 1982). Interactions were not significant ($F_{1,271} \leq 2.180$, $P \geq 0.071$, $\eta_p^2 \leq 0.031$), therefore only main effects were analyzed.

2.3.4. Gut fullness

Individuals' gut fullness was estimated by square-root-transforming the volume of gut content and using the transformed data as the dependent variable in an ANCOVA, while including sex,

Tab. 2: Component matrix of the PCA on the proportion of food items ingested by male and female *Poecilia* spp. Axis loadings for the first three principal components are shown (including the percent variation explained by each).
Tab. 2: Matrix der Hauptkomponentenanalyse zu den prozentualen Nahrungsbestandteilen männlicher und weiblicher *Poecilia* sp. Aufgezeigt sind die Achsenladungen der ersten drei Hauptkomponenten, sowie der relative Anteil der von ihnen erklärten Varianz.

	% variation explained	Fine detritus	Sand	Diatoms	Desmids/ green algae	Rare items
PCA 1	28.4	0.466	0.681	-0.845	0.155	0.047
PCA 2	27.2	-0.727	0.325	0.024	0.817	0.237
PCA 3	21.2	0.079	-0.389	-0.226	-0.036	0.922

Tab. 3: Proportion of dietary items averaged across individuals of different species and sex of each sampling site (including the sample size, N).

Tab. 3: Relative Anteile verschiedener Nahrungsbestandteile von Individuen beider Geschlechter bzw. verschiedener Arten an jedem besammelten Untersuchungsstandort (sowie deren jeweilige Stichprobenzahl, N).

	Lincoln Park		Central Texas		Weslaco		Río Juanillo		Río Mante		Río Purification (Barretal)	
	P. latipinna male	*P. latipinna* female	*P. latipinna* male	*P. latipinna* female	*P. latipinna* male	*P. latipinna* female	*P. mexicana* male	*P. mexicana* female	*P. mexicana* male	*P. mexicana* female	*P. mexicana* male	*P. mexicana* female
N	10	30	26	38	23	32	15	16	24	30	24	21
Niche width	0.87 ± 0.03	0.86 ± 0.04	0.77 ± 0.01	0.77 ± 0.07	0.86 ±0.00	0.84 ± 0.04	0.80 ± 0.09	0.83 ± 0.04	0.80 ± 0.06	0.80 ± 0.07	0.82 ± 0.05	0.78 ±0.07
Fine detritus	0.45 ± 0.12	0.46 ± 0.14	0.62 ± 0.25	0.70 ± 0.10	0.51 ± 0.09	0.52 ± 0.17	0.55 ± 0.23	0.58 ± 0.10	0.64 ± 0.12	0.64 ± 0.12	0.32 ± 0.28	0.46 ± 0.32
Sand	0.08 ± 0.04	0.11 ± 0.05	0.12 ± 0.12	0.09 ± 0.06	0.10 ± 0.08	0.10 ± 0.10	0.05 ± 0.07	0.11 ± 0.07	0.16 ± 0.08	0.14 ± 0.05	0.00 ± 0.01	0.02 ± 0.02
Diatoms	0.11 ± 0.09	0.12 ± 0.10	0.05 ± 0.04	0.06 ± 0.04	0.19 ± 0.08	0.16 ± 0.07	0.24 ± 0.17	0.15 ± 0.10	0.12 ± 0.06	0.11 ± 0.05	0.24 ± 0.22	0.21 ± 0.17
Desmids / green algae	0.28 ± 0.11	0.25 ± 0.09	0.06 ± 0.05	0.09 ± 0.05	0.16 ± 0.08	0.14 ± 0.10	0.07 ± 0.06	0.12 ± 0.07	0.05 ± 0.04	0.08 ± 0.04	0.00 ± 0.01	0.01 ± 0.01
Rare items	0.08 ± 0.06	0.06 ± 0.04	0.06 ± 0.05	0.07 ± 0.06	0.03 ± 0.04	0.01 ± 0.01	0.02 ± 0.03	0.03 ± 0.04	0.03 ± 0.04	0.04 ± 0.04	0.06 ± 0.10	0.04 ± 0.04

species, species nested within study site, and their interactions as independent variables. Standard length was used as a covariate. As interactions were not significant ($F_{1,270} \leq 2.836$, $P \geq 0.093$, $\eta_p^2 \leq 0.010$), only main effects were analyzed. All analyses were conducted using SPSS 16.0.

3. Results

In total, we investigated gut contents of 289 individuals, 159 of *P. latipinna* (100 females and 59 males) and 130 of *P. mexicana* (67 females and 63 males). Fishes with empty intestines were only found at two sites, Weslaco (a single *P. latipinna* female) and Barretal (6 out of the 21 examined *P. mexicana* females, compared to 9 out of 24 males). At the latter site, the frequency of individuals with empty intestines did not differ significantly between females and males ($\chi^2_{1,15}$=0.60, P=0.44). Mollies mainly fed on detritus, and sand represented the second most common food category, which is typical for deposit feeders (tab. 3).

The comparison of dietary items between males and females revealed no significant effect of 'sex' as a main effect, but in interactions with the factor 'species' and the factor 'study site' (tab. 4, fig. 1). Differences in gut content composition between males and females could only be found in Barretal and the Río Juanillo (*P. mexicana* at both sites), which was reflected by a significant interaction effect of 'sex by study site' (tab. 4). The analysis showed a high spatial variation and general differences between *P. mexicana* and *P. latipinna* sites, as the main factors 'study site' and 'study site nested within species' had significant effects.

This finding is supported by the results from the comparison of niche widths between males and females, where a significant effect of 'study site nested within species' was detected (tab. 4). Also, SL was a significant predictor of niche widths: on average, larger fish had narrower niche widths than smaller individuals, indicating an ontogenetic niche shift. In this analysis, a significant effect of the factor 'sex' was detected (tab. 4), and males showed narrower trophic niches than females.

Tab. 4: Results of multivariate analysis and analysis of covariance examining differences in gut content, niche width, gut length and gut fullness of female and male poeciliids.

Tab 4: Ergebnisse der Multivariaten Varianzanalysen sowie Kovarianzanalysen zur Untersuchung von Unterschieden im Darminhalt, der Nischenweite, der Darmlänge und der Darmfüllung von männlichen und weiblichen Poeciliiden.

Effect	F	df	P	η^2_P
(*a*) Gut content				
SL	3.506	3,252	**0.016**	0.04
Sex	0.857	3,252	0.464	0.010
Species	3.541	3,252	**0.015**	0.040
Study site (species)	6.057	12,667.021	**<0.0001**	0.087
SL × Sex	0.807	3,252	0.491	0.010
SL × species	0.856	3,252	0.465	0.010
SL × study site (species)	4.113	12,667.021	**<0.0001**	0.061
Sex × species	4.770	3,252	**0.003**	0.054
Sex × study site (species)	2.483	12,667.021	**0.003**	0.038
(*b*) Niche width				
SL	5.571	1,251	**0.019**	0.022
Sex	4.228	1,251	**0.041**	0.017
Species	2.369	1,251	0.125	0.009
Study site (species)	2.916	4,251	**0.022**	0.044
SL × Sex	3.895	1,251	**0.050**	0.015
SL ×species	0.960	1,251	0.328	0.004
SL× study site (species)	2.306	4,251	0.059	0.035
Sex × species	0.003	1,251	0.960	0.000
Sex × study site (species)	1.478	4,251	0.209	0.023
(*c*) Gut length				
10*mass $^{1/3}$	326.609	1,282	**<0.0001**	0.537
Sex	38.626	1,282	**<0.0001**	0.120
Species	2.262	1,282	0.134	0.008
Study site (species)	12.583	4,282	**<0.0001**	0.151
(*d*) Gut fullness				
SL	60.147	1,281	**<0.0001**	0.176
Sex	17.131	1,281	**<0.0001**	0.057
Species	13.821	1,281	**<0.0001**	0.047
Study site (species)	15.594	4,281	**<0.0001**	0.182
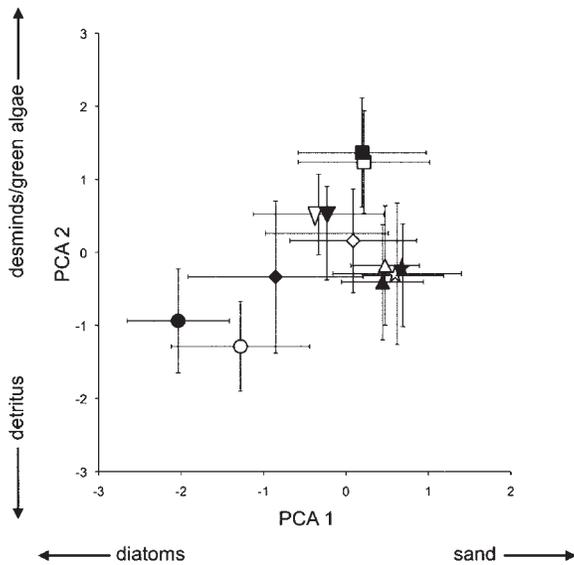
Fig. 1: Comparison between males and females of *P. latipinna* and *P. mexicana*. Discriminant function plots for the PCA scores 1 and 2. The mean ± SD discriminant function scores for each site are illustrated. ■ Lincoln Park; ★ Central Texas; ▼ Weslaco; ● Barretal; ◆ Río Juanillo; ▲ Mante. Closed symbols represent males, open symbols females.

Abb. 1: Vergleich von männlichen und weiblichen *P. latipinna* und *P. mexicana*. Gezeigt sind die Mittelwerte der ersten beiden Hauptkomponenten (± Standardabweichung) für jeden Untersuchungsstandort. ■ Lincoln Park; ★ Central Texas; ▼ Weslaco; ● Barretal; ◆ Río Juanillo; ▲ Mante. Ausgefüllte Symbole = Männchen, leere Symbole = Weibchen.
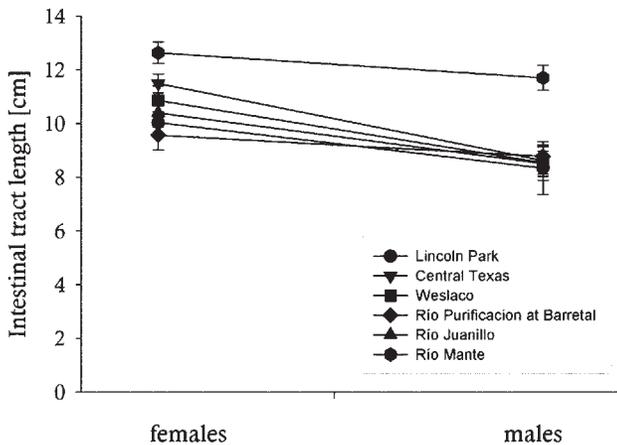
Fig. 2: Intestinal tract length of *P. latipinna* and *P. mexicana* females and males at each study site. Depicted are estimated marginal means (±SE).

Abb. 2: Darmlänge von Weibchen und Männchen bei *P. latipinna* und *P. mexicana* von den unterschiedlichen Untersuchungsstandorten. Aufgezeigt sind geschätzte Randmittelwerte (± Standardfehler).
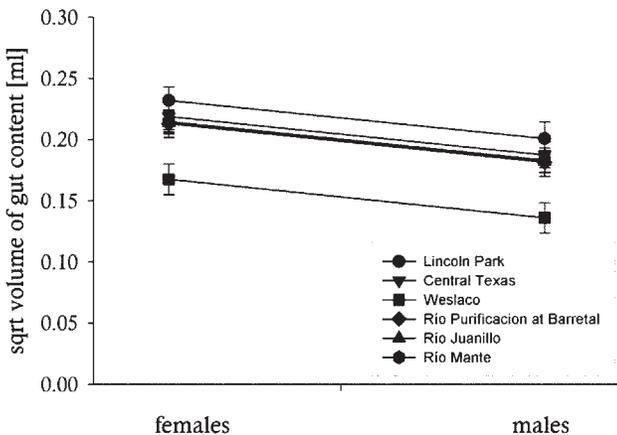
Fig. 3: Square-root-transformed volume of gut content (gut fullness) of *P. latipinna* and *P. mexicana* females and males at each study site. Depicted are estimated marginal means (±SE).

Abb. 3: Wurzeltransformiertes Darminhaltsvolumen (Darmfüllung) von Weibchen und Männchen der Arten *P. latipinna* und *P. mexicana* aus den unterschiedlichen Untersuchungsstandorten. Aufgezeigt sind geschätzte Randmittelwerte (± Standardfehler).

Finally, males generally had shorter intestines than females (tab. 4, fig. 2) and lower gut fullness (tab. 4, fig. 3). Most variation in gut fullness, however, was explained by 'study site nested within species' (η_p^2=0.182).

4. Discussion

We found significantly narrower trophic niches in males than females for both *Poecilia latipinna* and *P. mexicana*, along with site-specific sex differences in diet composition, particularly in Barretal and the Río Juanillo. However, most variation in gut content compositions and niche widths was explained by differences across collection sites, which is probably related to general differences in geophysical properties of the water bodies (e.g. substrate conditions, physiography, etc.). Caution is required when trying to interpret these findings as evidence for habitat segregation between the sexes at some sites. Little is known about the general ecological differences between study sites; for example, it remains unknown whether some sites have a higher predation pressure than others. According to the predation risk hypothesis (Main et al. 1996), sexual segregation could occur at sites of high predation pressure, as the brightly colored males with a high risk of predation are forced to use safer habitats compared to the cryptically colored females (Main et al. 1996, Croft et al. 2004, Croft et al. 2006).

At all sites, mollies of both sexes mainly fed on detritus, a food source of poor quality. High quality food (such as invertebrate larvae) was completely missing in the spectrum of food sources. Thus, a segregation of the sexes due to sex-specific, different food requirements (forage-selection or gastrocentric hypothesis; Beier 1987, Barboza & Bowyer 2000) seems to play a minor role in the species examined here.

Differences in gut length between males and females were pronounced throughout sites. For the most part, they are probably not a consequence of differential resource use: in poeciliids, males have a modified anal fin that serves as a copulatory organ and is located much more anterior than the females' anal fin (Rosen & Bailey 1963, Tobler et al. 2008). This shift in anal fin/gonopore location constrains the position of the anus, and especially in herbivorous species with very long intestines, male gut length may be limited by the reduced size of the abdominal cavity (Tobler 2008).

Furthermore, males were generally found to have lower gut fullness than females. These findings coincide with recent findings by Köhler et al. (2011), who reported on *P. mexicana* males spending far less time feeding and allocating more time in mating than females. As we also found lower niche widths in males, this might just be an indirect effect of the overall lower food uptake. Given these findings, it remains unclear how males can cover the energy demands for mating and the development of costly ornaments and enlarged dorsal fins in *P. latipinna*.

Overall, we could not detect a clear trophic niche segregation between females and males in *P. mexicana* and *P. latipinna*. However, we found differences between the sexes in gut content composition at the sites Barretal and Río Juanillo. These two sites differed in structure and abiotic characteristics from the other study sites. While the other habitats investigated herein were dominated by muddy substrates and turbid water, Barretal and Río Juanillo were characterized by rocky substrates and clearer water. In addition, Barretal is the only study site where intestinal tract lengths did not significantly differ between sexes. The reasons for the outstanding position of this particular site remain unclear to this point. Also, we found smaller (younger) fishes of both species feeding on different items than larger (older) fishes. Future studies, especially on sex- and size-specific microhabitat utilization need to be conducted to place these findings in a wider ecological context, but our present study represents a first step towards an understanding of the multiple pathways by which sex-specific selection affects the evolutionary trajectories of males and females in natural *P. latipinna* and *P. mexicana* populations.

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