

Geographical variation in allometry in the guppy (*Poecilia reticulata*)

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Abstract

Variation in static allometry, the power relationship between character size and body size among individuals at similar developmental stages, remains poorly understood. We tested whether predation or other ecological factors could affect static allometry by comparing the allometry between the caudal fin length and the body length in adult male guppies (*Poecilia reticulata*) among populations from different geographical areas, exposed to different predation pressures. Neither the allometric slopes nor the allometric elevations (intercept at constant slope) changed with predation pressure. However, populations from the Northern Range in Trinidad showed allometry with similar slopes but lower intercepts than populations from the Caroni and the Oropouche drainages. Because most of these populations are exposed to predation by the prawn *Macrobrachium crenulatum*, we speculated that the specific selection pressures exerted by this predator generated this change in relative caudal fin size, although effects of other environmental factors could not be ruled out. This study further suggests that the allometric elevation is more variable than the allometric slope.

Introduction

Static allometry describes the change in the relative size of a trait compared to the rest of the body for individuals of the same species, measured at similar developmental stage (Gould, 1966). It is classically described by a power relationship: $y = ax^b$, where y is the size of the trait of interest, and x is the body size (Huxley, 1932). When both x and y are expressed on log scale, this relationship becomes linear: $\log(y) = \log(a) + b \log(x)$. Positive and negative allometries occur when $b > 1$ or < 1 , respectively, and refer to situations where trait size changes either faster or slower than body size. Isometry occurs when $b = 1$ and refers to a situation where the trait size and the body size change at similar rate across individuals. In this latter case, the shape of the organisms does not change with size (Huxley, 1932; Gould, 1966).

The allometric exponent b was initially assumed to have little or even no possibility to vary adaptively

(Huxley, 1932). This idea was first challenged by Newell (1949) who argued that natural selection can generate changes in b . More recently, several authors endorsed this viewpoint by suggesting that secondary sexual traits under directional selection should display positive allometry (Petrie, 1988, 1992; Green, 1992), whereas traits under stabilizing selection should display negative allometry (Eberhard *et al.*, 1998; Eberhard, 2009). Theoretical models challenged these hypotheses and suggested that directional selection may lead to various types of allometry depending on the relative strength and shape of selection on both trait size and body size (Bonduriansky & Day, 2003).

The biological and evolutionary significance of the allometric constant a has been the subject of even more controversy (Gayon, 2000). Because a is scale dependent, Huxley (1924) tended to deny any biological meaning to this parameter. Based on the inter- and intra-specific variation in a reported by Teissier (1936) and others, Newell (1949) suggested that a can change because of natural selection, supporting the idea of a biological and evolutionary meaning of the allometric constant. As noticed by Gould (1966), part of the confusion was generated by the strong correlation between the slope

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and the intercept when different allometric relationships cross each other at a point different from $x = 1$. However, if the allometric slope is constant, differences in the intercept reflect differences in relative trait size compared to the body size at the population mean (Teissier, 1936; White & Gould, 1965; Cock, 1966; Gould, 1966, 1971). For clarity, we decided here to define the intercept when the allometric slope is constant as the *allometric elevation*, because this parameter describes the elevation of parallel lines along the y axis. When allometric slopes are different, elevation can still be estimated as the intercept calculated on population-mean-centred data (Enders & Tofghi, 2007). Surprisingly, the recent discussion on the effects of directional and stabilizing selection on allometry has devoted little attention to changes in allometric elevation, although Bonduriansky (2007) in his review on allometry and sexual selection noticed that the effects of sexual selection were more often observed on the allometric intercept than on the allometric slope.

Empirical tests of the adaptive evolution of allometry have been conducted either by comparing allometry across traits under presumably different selection regimes (stabilizing vs. directional selection; Eberhard *et al.*, 1998; Bonduriansky, 2007; Eberhard, 2009) or by artificial selection aiming at altering the allometric relationship (Wilkinson, 1993; Frankino *et al.*, 2005, 2007; see review in Frankino *et al.*, 2009). While evidence reported by comparative studies remains inconclusive (Bonduriansky, 2007), selection studies have suffered from methodological problems (e.g. selection on arithmetic and not geometric scale), rendering their interpretation difficult (Houle *et al.*, 2011). Few studies have reported differences in allometry across populations (but see Kelly *et al.*, 2000; Bernstein & Bernstein, 2002), and to our knowledge, only one (Jennions & Kelly, 2002) has tested the effect of an ecological factors on allometry. Here, we analyse natural variation in the allometric relationship between the caudal fin size and the body size among male guppies (*Poecilia reticulata*) from populations belonging to different river systems and exposed to different levels of predation, to test whether ecological factors can affect allometry.

The guppy (*P. reticulata*) is a freshwater fish native to rivers and streams in Trinidad and the north-eastern part of South America. The species presents a pronounced sexual dimorphism, including an enlarged caudal fin in males (Houde, 1997), and several studies suggest that, in some populations, females show mating preference for males with a larger caudal fin (Bischoff *et al.*, 1985; Endler & Houde, 1995). On the other hand, Karino *et al.* (2006) showed that a large caudal fin negatively affects swimming performances. Furthermore, Basolo & Wagner (2004) showed that predation can negatively affect the relative caudal fin size in *Xiphophorus helleri* (Poeciliidae). In their natural environment, guppy populations experience different predation pressures due to natural barriers creating patchy distribution of predators (Endler,

1978; Magurran, 2005). This has profound consequences on the relative importance of sexual vs. natural selection in shaping male secondary sexual characters (Endler & Houde, 1995; for review in Endler, 1995).

We hypothesized that variation in predation pressures in interaction with female mating preference can affect both the allometric intercept and/or the allometric slope of the caudal fin. The allometric intercept can evolve if the optimal relative caudal fin size for escaping predators varies with the type of predators encountered by the guppy populations. Bonduriansky & Day (2003) suggested that the allometric slope will evolve according to the relationship between body size and the fitness advantage of an increase in trait size relative to the fitness advantage of an increase in body size (equation 4 in Bonduriansky & Day, 2003). Under the premise that females prefer males with large caudal fins, but that a large caudal fin hampers the ability to escape predators, the relative caudal fin size of male guppies exposed to large predators may experience the same selection (i.e. same optimum value) for males of different body size. However, in populations exposed to gape-limited predators such as *Rivulus hartii*, large males above the size threshold will not experience the predation cost associated with enlarge caudal fin. Consequently, in these populations, enlarged caudal fin size should be more beneficial for large males, and we expect steeper allometry in these populations, compared to populations exposed to large, gape-unlimited predators.

In the present study, we compared the allometric relationship between the caudal fin size and the body size among 21 populations of guppy from three different drainages in Trinidad to test for natural variation in allometry. We further compared the caudal fin allometry across 14 populations exposed to fish predators of different size to test whether variation in the selection pressures generated by predation could affect allometry.

Material and methods

Sampling and measurements

We studied the allometric relationship between caudal fin length and standard length in 21 guppy populations from Trinidad. Standard length (from the tip of snout to the insertion of the caudal fin) and caudal fin length (from the beginning to the edge of the caudal fin) were measured on photographs of male guppies taken by J. A. Endler in Trinidad during the period 1975–1988 in three different drainage systems: the Northern Range (independent rivers not connected to the other two drainages), the Caroni Drainage and the Oropouche Drainage (map in Endler, 1978 and Magurran, 2005). There are marked genetic differences between drainages, and also between populations within rivers due to natural barriers that limit dispersion (Carvalho *et al.*, 1991; Crispo *et al.*, 2006; Suk & Neff, 2009; Willing *et al.*, 2010). These

barriers also reduce upstream dispersal of predators and generate differences in the predation pressures encountered by guppy populations in the same river (Endler, 1995). Following part of Endler's (1983) classification, we made use of two predation categories referred to as low and high predation. Low-predation populations (LP) only hold a small predator species, the killifish *R. hartii* (Rivulidae), that preys upon juvenile and small adult guppies (Liley & Seghers, 1975; Endler, 1983). High-predation populations (HP) comprise large predators like cichlids or characins that prey on guppies of all size classes. These two predation categories therefore represent variation not only in predation intensity but also in the size-specific mortality associated with predation. Some populations were classified as low-macro-predation populations (LMP, Table 1). These populations comprise similar fish predators as the low-predation populations, but include an additional predator, the freshwater prawn *Macrobrachium crenulatum* (Palaemonidae). This prawn can be more dangerous than *R. hartii* because it attacks guppies of all sizes with a similar frequency (Endler, 1983). However, these populations ($N = 6$) are mainly located in the Northern Range, therefore confounding this predation level with the geographical area. Consequently, these populations were

not included in the analyses testing for the effect of predation on allometry.

Photographs analysed in this study were originally taken to test for variation in colour patterns with predation (Endler, 1978, 1983, 1991). Therefore, these photographs only included mature males with developed colour patterns, but the sampling was random regarding the size of the fish. Each picture contained a varying number of males, approximately 10–30, and a ruler for size measurements (see Endler, 1978). The photographs were scanned to be analysed using *АДОВЕ РНОТОНОР* CS3 Extended, version 10.0.1. In each of the drainage systems, we sampled all possible populations that contained at least 25 fish that could be measured (i.e. with sufficient contrast for the full outline of the caudal fin to be visible). In total, we estimated the allometric relationship in 21 populations, with a minimum of six populations per predation level (see Table 1 for details).

The fish were measured by a single person (CKE). Repeatability of the measurements (Lessells & Boag, 1987) was estimated by measuring twice both traits on 22 individuals in three different populations (66 fish in total) using photographs with differing contrast. The repeatability was higher for standard length (0.93–0.98) than for caudal fin length (0.61–0.83), probably because

Table 1 Means, standard deviations (SD) and sample size (N) for standard length and caudal fin length in male guppies from the different populations. The predation level for each population is reported (LP, low-predation: *Rivulus hartii* also including *Hemigrammus* (*); LMP, low-macro-predation: *R. hartii* and *Macrobrachium crenulatum*; HP, high-predation: several species from the genera *Crenicichla*, *Aequidens*, *Astyanax*, *Agonostomus*, *Awous*, *Rivulus*, *Dormitator* and *Hemibrycon*). We also report the estimates (\pm SE) and correlation coefficient, r^2 , of the allometric relationship between caudal fin length and body length on log-transformed data for each population.

Drainage	Population	Predation	Standard length (mm)			Caudal fin length (mm)			Population allometry			
			Mean	SD	N	Mean	SD	N	Slope \pm SE	Intercept \pm SE log (mm)	r^2	Elevation log (mm)
Northern Range	Yarra	LMP	18.22	1.36	44	5.51	0.71	35	0.80 \pm 0.27	-0.62 \pm 0.78	0.21	1.63
Northern Range	Marianne	LMP	16.94	1.13	70	5.23	0.59	55	0.67 \pm 0.22	-0.25 \pm 0.61	0.15	1.63
Northern Range	Brasso Seco	LMP	16.78	1.01	52	5.00	0.62	49	0.79 \pm 0.30	-0.63 \pm 0.84	0.13	1.59
Northern Range	Paria	LMP	16.45	0.86	78	4.94	0.61	64	0.72 \pm 0.27	-0.42 \pm 0.75	0.10	1.59
Northern Range	Tompire 1	HP	15.45	0.72	81	4.93	0.49	80	0.78 \pm 0.20	-0.55 \pm 0.54	0.17	1.64
Northern Range	Tompire 2	LMP	15.25	0.75	99	4.56	0.44	97	0.95 \pm 0.23	-1.01 \pm 0.62	0.15	1.57
Northern Range	Balandra	LMP	15.37	0.55	27	4.91	0.41	27	1.25 \pm 0.40	-1.83 \pm 1.10	0.28	1.64
Caroni	Tacarigua	HP	16.21	1.12	34	5.19	0.49	32	0.98 \pm 0.19	-1.09 \pm 0.52	0.48	1.65
Caroni	Lopinot	LMP	16.84	0.54	31	5.79	0.37	29	0.72 \pm 0.37	-0.28 \pm 1.06	0.12	1.74
Caroni	Arima	LP	17.09	1.03	57	4.91	0.41	52	0.56 \pm 0.27	0.04 \pm 0.75	0.08	1.61
Caroni	El Cedro 1	HP	15.54	1.02	48	5.08	0.47	42	0.87 \pm 0.22	-0.75 \pm 0.60	0.28	1.67
Caroni	El Cedro 2	LP	15.80	0.92	35	5.11	0.49	34	0.92 \pm 0.24	-0.91 \pm 0.67	0.31	1.66
Caroni	Guanapo 1	HP	20.05	1.06	52	6.29	0.46	39	0.43 \pm 0.21	-0.55 \pm 0.63	0.10	1.68
Caroni	Guanapo 2	LP	19.25	1.16	49	6.08	0.44	38	0.65 \pm 0.16	-0.12 \pm 0.47	0.32	1.69
Caroni	Aripo 1	HP	15.25	0.70	47	5.02	0.65	42	0.84 \pm 0.37	-0.68 \pm 1.02	0.11	1.67
Caroni	Aripo 2	LP	17.08	1.33	36	5.43	0.55	28	0.88 \pm 0.16	-0.79 \pm 0.45	0.53	1.67
Caroni	Ceniza	HP	16.78	0.96	110	5.00	0.62	107	0.74 \pm 0.16	-0.41 \pm 0.46	0.17	1.68
Oropouche	Rio Barro	LP	15.35	0.85	35	4.99	0.49	33	0.42 \pm 0.30	0.46 \pm 0.83	0.06	1.66
Oropouche	Quare	LP*	17.10	1.75	55	4.93	0.49	53	0.90 \pm 0.12	-0.81 \pm 0.34	0.53	1.72
Oropouche	Oropouche	HP	15.28	0.88	42	5.23	0.59	40	0.87 \pm 0.23	-0.81 \pm 0.64	0.28	1.68
Oropouche	Rio Grande	HP	14.51	0.74	31	4.78	0.55	24	0.65 \pm 0.44	-0.19 \pm 1.18	0.09	1.65
Total					1113			1000				

of the low contrast of the edge of the fin in some photographs. Note that measurement error inherent from the positioning of the fish during the photographic session could not be estimated. In total, we obtained data on standard length and caudal fin length for 1000 fish (Table 1).

Statistics

We first tested for variation in fish size and caudal fin size among the three drainage systems and predation categories using mixed-effects models on untransformed data where drainage or predation category were entered as fixed factor and population as random factor. Populations from the Northern Range were excluded from the second set of analyses because the two factors, *Macrobrachium* predation and drainage, were confounded.

We subsequently analysed the effect of drainage and predation on the allometric relationship between caudal fin length and standard length on log-transformed data. We first tested whether allometry differed among populations using an analysis of covariance (ANCOVA) with caudal fin length as response variable, population as factor and standard length as predictor variable. Variation in allometry among drainage systems and predation categories was tested using contextual models (Heisler & Damuth, 1987). Contextual models are multiple regressions where group predictors are included as well as individual predictors. These models can estimate the contrast between within-group and among-group relationships and test their difference. In our case, these models allow us to estimate the allometric relationship between caudal fin length and body length within and among populations. Failure to do so would confound the within-population (static) allometry with the among-population (evolutionary) allometry. We therefore performed mixed-effects models with standard length as predictor variable both at the individual level (individual trait values) and at the population level (population mean trait values), and caudal fin length as response variable. Drainage or predation categories were included as fixed factor and population identity as random factor. River was not included as random factor because river and population were almost completely confounded. We performed model selection using the Akaike information criteria (AIC) between different models fitted with maximum likelihood (ML), whereas parameter estimates were obtained from models fitted with restricted maximum likelihood (REML, Zuur *et al.*, 2009). In the following, AIC values are reported for the different models with K , the number of parameters estimated in the model. To reduce the correlation between the allometric slope and intercept, we centred the standard length on the grand mean (across all populations and predation levels/drainage levels) before the analyses.

We tested for nonlinear allometry (Knell, 2009) by including a quadratic term for standard length both at the

within- and among-population levels. This quadratic term did not improve the fit of the models (global model in Table 3 with quadratic term: AIC = -1053.1, $K = 11$; without quadratic term: AIC = -1056.5, $K = 9$) and therefore was not included in further investigations.

Major-axis regression has often been recommended in allometry studies (Warton *et al.*, 2006). However, neither major axis nor reduced major axis provides good estimates of the allometric slope when biological error is included in the model (Hansen & Bartoszek, 2011). Therefore, we used ordinary regression in our analyses. All the statistical analyses were performed in R, version 2.10.0 (R Development Core Team, 2010), using the lme4 package (Bates, 2010).

Results

Effects of the drainage systems

Across all populations, male guppies ranged from 13.2 to 22.9 mm in standard length. We found no difference in mean standard length among the three drainage systems (model with drainage AIC = 3274.5, $K = 5$; without drainage AIC = 3273.4, $K = 3$; Table 2). The caudal fin length was, however, shorter in the Northern Range (model with drainage AIC = 1702.6, $K = 5$; without drainage AIC = 1705.1, $K = 3$; Table 2).

Considering the allometric relationship, we observed a negative allometry between caudal fin length and standard length (average \pm SE slope = 0.79 ± 0.05) with no statistically significant differences among populations (ANCOVA interaction effect: $F_{20,958} = 0.42$, $P = 0.99$, $r^2 = 0.49$). Populations, however, differed in allometric elevation (population effect: $F_{20,978} = 10.04$, $P < 0.01$; Table 1). Similarly, there was no difference in allometric slope among drainage systems, but the allometric elevation varied, populations from the Northern Range showing a lower allometric elevation than in the two other drainages (Fig. 1, Table 3). The allometric slope among populations (evolutionary allometry) was slightly steeper than the average within-population slope, although the difference was not statistically significant (Table 3).

Table 2 Estimated means and standard error for standard length and caudal fin length from mixed-effects models including either drainage or predation category as fixed factor.

Factor	Level	Standard length (mm)		Caudal fin length (mm)	
		Mean \pm SE	N	Mean \pm SE	N
Drainage	Caroni	16.99 \pm 0.43	499	5.56 \pm 0.12	433
	Oropouche	15.79 \pm 0.64	162	5.29 \pm 0.23	105
	Northern Range	16.18 \pm 0.45	451	4.98 \pm 0.14	407
Predation	Low	16.95 \pm 0.67	267	5.42 \pm 0.19	238
	High	16.25 \pm 0.64	364	5.35 \pm 0.26	326

Table 3 Results of the contextual models testing for variation in static allometry between caudal fin length and standard length among drainage systems. K , number of parameters in the model; AIC, Akaike information criterion value; Δ AIC, difference in AIC units from the best model; w_i , Akaike weights. Estimates (\pm SE) are presented for each model. The estimates of the intercepts and within-population slopes are presented for the Caroni Drainage (CD), the following columns give the contrasts for the Oropouche Drainage (OD) and the Northern Range (NR). The last column provides the estimate of the slope for the among-population allometry as a contrast from the within-population allometry (of CD). The first model allows for different slopes among drainages. The second model gives the same slope for the different drainages but allows for different intercepts. The final model gives the same slope and same intercept across all drainages.

Models*	K	AIC	Δ AIC	w_i	Intercept log (mm)			Within-population slope			Among-populations slope
					CD	OD	NR	CD	OD	NR	
$D_s + SL_L + D_s \times SL_L + SL_p$	11	-1828.0	3.2	0.17	1.667 (\pm 0.011)	0.022 (\pm 0.022)	-0.052 (\pm 0.016)	0.769 (\pm 0.073)	0.096 (\pm 0.128)	-0.007 (\pm 0.102)	0.069 (\pm 0.111)
$D_s + SL_L + SL_p$	9	-1831.2	0	0.82	1.678 (\pm 0.011)	0.018 (\pm 0.022)	-0.051 (\pm 0.016)	0.786 (\pm 0.051)	-	-	0.056 (\pm 0.110)
$SL_L + SL_p$	7	-1822.2	9.0	0.01	1.651 (\pm 0.009)	-	-	0.786 (\pm 0.051)	-	-	0.118 (\pm 0.131)

*Notation in the different models: D_s : factor drainage, SL_L : grand mean-centred log (individual standard length), SL_p : grand mean-centred log (population standard length).

Effects of predation

Including only populations from the Caroni and Oropouche drainages, guppies from LP tended to be longer than guppies from HP, although statistical evidence for this difference was weak (model with predation AIC = 1879.5, $K = 4$; without predation AIC = 1878.1, $K = 3$; Table 2). Similarly, we found no clear decrease in caudal fin length under high predation (model with predation AIC = 931.8, $K = 4$; without predation AIC = 929.7, $K = 3$; Table 2). Finally, neither the slope nor the elevation of the allometric relationship between caudal fin length and body length differed between predation categories (Table 4).

Discussion

By comparing static allometry between caudal fin length and body length in guppy populations from different drainage systems and exposed to different predation pressures, we aimed at testing whether allometry can be affected by ecological variables and whether both allometric parameters, the slope and the elevation, were equally variable. Under the premise that the relative costs and benefits of enlarged caudal fin in male guppies were influenced by both predation and sexual selection, we predicted that differences in selection pressures among populations could affect the caudal fin allometry. In general, the allometric slope appeared invariant among populations, across drainage systems and between the two categories of predation. In contrast, the allometric elevation was more labile and differed among drainage systems, the populations from the Northern Range showing lower allometric elevation than the populations in both the Caroni and the Oropouche drainages. However, contrary to our predictions, allometry was not affected by differences in the predator fauna.

We found only limited support for earlier findings that predation negatively affects absolute fish size in guppies (Liley & Seghers, 1975; Endler, 1980, 1995; Reznick *et al.*, 1996; Johansson *et al.*, 2004). Indeed, male guppies in our sample were only 4% smaller in populations exposed to large predators. Furthermore, the similar allometry between caudal fin length and body length under different predation pressures showed that predation did not affect the relative caudal fin length, a result in contrast with the one observed by Basolo & Wagner (2004). However, the relative caudal fin length varied among geographical areas, the populations living in the Northern Range displaying a relatively shorter caudal fin than populations in the two other drainages. Phylogenetic inertia cannot explain this pattern, because rivers from the Northern Range are a collection of independent rivers with no recent shared history. Consequently, populations in this area are distantly related compared to the rivers within the Caroni and the Oropouche drainages (Suk & Neff, 2009). This suggests that the

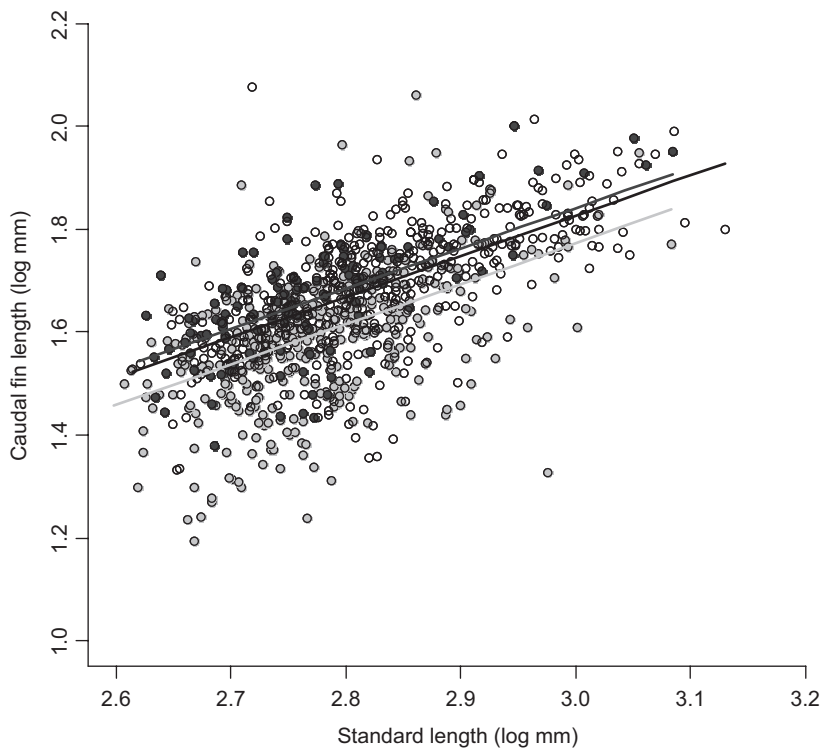


Fig. 1 Allometric relationship between caudal fin length and standard length in male guppies in populations from three drainage systems in Trinidad. The parameter estimates from the model with similar slope and different intercepts among drainages are slope = 0.79 ± 0.05 , intercept for the Caroni drainage (black line and open circles) = -0.53 , the Northern Range (light grey line and light grey circles) = -0.59 , and the Oropouche Drainage (dark grey line and dark grey circles) = -0.52 (these estimates of the intercept differ slightly from the ones presented in Table 3 because they are not calculated on mean-centred data).

Table 4 Results of the contextual models testing for variation in static allometry between caudal fin length and standard length among predation categories. Estimates (\pm SE) are presented for each model. The within-population estimates of the intercepts and slopes are presented for the high-predation populations (HP), the following columns give the contrasts for the low-predation (LP) populations. The last column provides the estimate of the slope for the among-population allometry as a contrast from the within-population allometry for the HP populations. The first model allows for different slopes depending on predation category. The second model gives the same slope for the different predation intensities but allows for different intercepts. The final model gives the same slope and same intercept for the two predation levels.

Models*	K	AIC	Δ AIC	w_i	Intercept log (mm)		Within-population slope		Among-populations slope
					HP	LP	HP	LP	
$P_i + SL_i + P_i \times SL_i + SL_p$	9	-1056.5	3.5	0.29	1.689 (± 0.013)	-0.011 (± 0.018)	0.780 (± 0.097)	-0.036 (± 0.127)	0.122 (± 0.123)
$P_i + SL_i + SL_p$	8	-1058.5	1.5	0.11	1.687 (± 0.012)	-0.008 (± 0.015)	0.763 (± 0.066)	-	0.122 (± 0.121)
$SL_i + SL_p$	7	-1060.0	0	0.61	1.683 (± 0.009)	-	0.763 (± 0.067)	-	0.103 (± 0.115)

*Notation in the different models: P_i : factor predation, SL_i : grand mean-centred log (individual standard length), SL_p : grand mean-centred log (population standard length).

difference in allometric elevation observed in these rivers is generated by some ecological factors. One possible agent responsible for lower allometric elevation in the Northern Range is the predator prawn *M. crenulatum*. Indeed, most populations exposed to this specific predator are located in the Northern Range (Table 1). One can speculate that this predator generates different selection pressures on fish morphology compared to the ones exerted by fish predators. Note that predation by the prawn, together with sexual selection, has been shown to influence male colouration in guppies (Endler, 1980,

1983; Rodd & Reznick, 1991). Whereas fish predators typically use a lunge and chase tactic, prawns use a sit and wait tactic before suddenly lunging out with pincers. Therefore, although high burst speed increases the probability of surviving a fish attack in guppies (Walker *et al.*, 2005), it is possible that attacks by prawn predator create an even stronger selection on this swimming performance at the expense of other swimming performances such as maximum swimming speed or critical speed (but see Oufiero & Garland, 2009). Although several studies analysed the relationship between body

shape and swimming performances (Blake, 2004; reviewed in Langerhans, 2008), it remains difficult to understand the contribution of the size and the shape of the caudal fin on different swimming performances, and Nicoletto (1991) did not find any differences in swimming performances among three types of caudal fin shape in male guppies. However, the meta-analysis by Langerhans (2008) suggests that both the rigidity and the length of the caudal fin affect swimming performances. Because rigidity of the body and the caudal fin may be crucial for achieving high burst speed, longer caudal fins with lower rigidity may be disadvantageous for fish exposed primarily to prawn predation. A better understanding of the relationships between absolute and relative caudal fin length and swimming performances is clearly needed to link the selection pressures exerted by different types of predator with differences in allometric elevation observed in this study.

Nevertheless, because low-macro populations are almost solely found in the Northern Range in our data set, environmental factors specific to this range, such as water velocity or the chemical composition of the water (Haskins *et al.*, 1961), could also be responsible for the change in allometric elevation (e.g. faster running water in the Northern Range could favour relatively small caudal fin). Unfortunately, the limited information on flow rates and other abiotic characteristics of the rivers prevented us from extending this analysis.

This study further suggests that the allometric slope is relatively invariant among populations and environments, whereas the allometric elevation can vary with ecological factors (see also Bonduriansky, 2007). It remains an open question whether the observed differences reflect evolutionary changes or the effects of selective mortality. Nevertheless, we believe that such a comparative approach testing the effects of ecological factors on the allometry of single traits or highly homologous traits can prove particularly powerful to study the evolutionary dynamics of allometry. First, it allows controlling for trait dimensionality and complexity, which often obscure the results of the studies analysing co-variational patterns among different characters (Hansen *et al.*, 2007; Pélabon *et al.*, 2011). Furthermore, it should help understanding what type of selection affects allometry, and whether both allometric parameters can respond to such selection.

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