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Lack of functional link in the tadpole morphology induced by predators

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Abstract

Most studies of predator-induced plasticity have focused on documenting how prey species respond to predators by modifying phenotypic traits and how traits correlate with fitness. We have previously shown that *Pleurodema thaul* tadpoles exposed to the dragonfly *Rhionaeschna variegata* responded strongly by showing morphological changes, less activity, and better survival than non-exposed tadpoles. Here, we tested whether there is a functional link between morphological plasticity and increased survival in the presence of predators. Tadpoles that experienced predation risk were smaller, less developed, and much less active than tadpoles without this experience. Burst speed did not correlate significantly with morphological changes and predator-induced deeper tails did not act as a lure to divert predator strikes away from the head. Although we have previously found that tadpoles with predator-induced morphology survive better under a direct predator threat, our results on the functional link between morphology and fitness are not conclusive. Our results suggest that in *P. thaul* tadpoles (1) burst speed is not important to evade predators, (2) those exposed to predators reduce their activity, and (3) morphological changes do not divert predator attacks away from areas that compromise tadpole survivalEE. Our results show that morphological changes in *P. thaul* tadpoles do not explain burst speed or lure attraction, although there was a clear reduction of activity, which itself reduces predation. We propose that changes in tadpole activity could be further analyzed from another perspective, with morphological change as an indirect product of behavior mediated by physiological mechanisms.

Key words: induced morphology, lure effect, predator exposure, swimming performance, tadpoles.

Inducible morphological defenses have served as model systems to test the evolution and maintenance of phenotypic plasticity as an important source of natural variation (Agrawal 2001). Most studies of predator-induced plasticity have focused on documenting how prey species respond to predators by modifying several traits and how traits correlate with fitness. Many studies have focused on Arnolds̆ (1983) paradigm, "Morphology, performance and fitness," by analyzing the effect of trait variation on performance and fitness (Kingsolver and Schemske 1991; Scheiner et al. 2000; Johnson et al. 2008; Calsbeek and Kuchta 2011). When exposed to predators, larval amphibians develop inducible defenses as changes in morphology (e.g., deeper or colored tails) and/or changes in behavior (e.g., decreased activity or increased refuge use) (Morin 1986; Skelly and Werner 1990; Skelly 1996; Van Buskirk et al. 1997; Van Buskirk and McCollum 1999; Relyea 2001; Kishida and Nishimura 2004; Laurila et al. 2004). These induced defenses (Tollrain and Harvell 1999) can be effective but are sometimes associated with costs, and tadpoles exposed to predators are usually smaller and/or less developed than non-exposed tadpoles (Werner 1992; Storfer et al. 1999; LaFiandra and Babbitt 2004; Steiner 2007; Steiner and Van Buskirk 2008; Touchon and Warkentin 2008). Some studies have correlated swimming responses (in acceleration or speed) in tadpoles with induced morphological characters, such as wider, longer, and deeper tails (Dayton et al. 2005; Teplisky et al. 2005). Additionally, changes in morphology may also act as predator distracters, as proposed in the "lure effect" hypothesis, which proposes that larger tails may distract the predator from attacking vulnerable regions of the body (Van Buskirk et al. 2003; Johnson et al. 2008). Recent studies have shown that survival of tadpoles is enhanced through changes in body and tail shape that either affect swimming performance or serve as a "lure" to attract predators (Johnson et al. 2008; Calsbeek and Kutcha 2011). We know from previous studies that tadpoles of *Pleurodema thaul* (Schneider 1799) (Anura: Leptodactylidae) exposed to non-lethal risk of predation by the dragonfly *Rhionaeschna variegata* (Fabricius 1775) reduce their activity and change their morphology (deep tails and small sizes) (Jara 2010; Jara and Perotti 2010).

Based on this information, we performed a series of experiments to test whether the morphological changes induced in *P. thaul* tadpoles pre-exposed to predators correlate with functional response components (burst speed and lure effect), which ultimately enhance tadpole fitness (survival). We have previously determined that tadpoles with previous exposure to predators have better survival than tadpoles without this experience (Jara 2010). We predicted that the morphological changes induced by predators result in better burst swimming performance to evade predation and/or that the distractive effect (lure effect) should direct predator strikes more often on tails rather than on vital body parts. Thus, we expected (1) that morphological changes correlate with swimming performance in tadpoles pre-exposed to predators, implying an adaptive response, and/or (2) that tadpoles developing morphological changes attract predator attacks to body parts that result in enhanced survival (i.e., inducing non-lethal attacks).

Materials and Methods

Study system

We studied a common predator–prey system that occurs in temporary and semipermanent wetlands in Northwestern Patagonia (Argentina) composed of tadpoles of *P. thaul* (prey) and larvae of *R. variegata* (Anysoptera: Aeshnidae) (predator) (Jara and Perotti 2010). Both tadpoles and larvae were collected from the same site (Fantasma lagoon, 41°05′S, 71°27′W, 794 m.a.s.l.; Río Negro province, Argentina) in October 2011 and October 2012. Specimens collected in 2011 were used to study the morphological responses of tadpoles exposed to *R. variegata* larvae and the relationship between morphology and burst speed, whereas specimens collected in 2012 were used to test whether morphological changes apply to the hypothesis of "lure effect." All procedures were authorized by the corresponding authorities of Nahuel Huapi National Park and Subsecretaria de Medio Ambiente of San Carlos de Bariloche, Río Negro, Argentina.

Effect of predator exposure on morphology and burst swimming performance

The 8 clutches of *P. thaul* (Gosner stages 11–13; Gosner 1960) collected in October 2011 were reared outdoors in eight 500-L containers under natural photoperiod and temperature conditions. After hatching, tadpoles of all 8 clutches were mixed and reared to reach developmental stages 25–26 (total length average: 13.7 ± 0.11 mm; free swimming tadpoles, 2 weeks old; Gosner 1960) to avoid confounding genetic effects when setting the experiment.

Next, we conducted a completely randomized experimental design, in which tadpoles were reared under 2 predation conditions (treatments): presence and absence of caged predator larvae of *R. variegata*. Treatments were replicated in 60 plastic containers (15 L) filled with tap water (30 replicates for each treatment). The bottom of each container was covered with 500 g of fine sediment and each tank was inoculated with 500 mL of an algal culture mixture (*Chlamydomonas* sp. + *Scenedesmus* sp.) as food. Each replicate consisted of a plastic cage (5 cm × 10 cm) with six tadpoles selected at random from the rearing containers. The 30 replicates of the predator treatment contained 1 caged larva of *R. variegata* (average size 28.99 mm ± 1.94 mm) whereas the other 30 replicates of the non-predator treatment consisted of empty cages. The water volume in the containers was kept constant, checked and cleaned daily, and re-filled when necessary. The larvae of *Rhionaeschna* in the predator treatment were fed every other day with one *P. thaul* tadpole. Therefore, tadpoles in the predator treatment were provided with a combination of chemical cues from the predator (kairomones) and chemical cues derived from the damage (alarm cues) and digestion of conspecifics (Schoeppner and Relyea 2009). Cages with predators were checked daily and those with dead larvae or predators that had stopped feeding were replaced by a new larva of similar size.

The experiment finished 50 days later, before forelimbs emerged (around stage 39, Gosner 1960). At this stage, tadpoles from all treatments were photographed for later measurement of morphological features. Each tadpole was photographed in its lateral view with a digital camera (Canon PowerShot IF S5). Photographs were taken from the same distance and under the same light conditions (Figure 1), and then analyzed using the ImageJ software (version 1.47). The following morphological measurements were obtained from the digital images: tail length (TL), body length (BL), body depth (BD), tail muscle depth (MD), tail fin depth (TD), and total tadpole length (TTL) (Figure 1). These measurements were considered as important for swimming trials (Smith and Van Buskirk 1995; Relyea 2001). Tadpole measurements from each replicate were averaged to analyze morphological features in each treatment. In addition, size and developmental stage of each tadpole were measured 30 days after the beginning of the experiment in the 2 treatments and the average of each replicate was used for the analysis (exposure and non-exposure to predator risk).

We used a racetrack (1 m long × 0.08 m wide × 0.12 m high) with 7 LED sensors and beams (spaced every 0.10 m) connected to an electronic circuit and hooked up to a computer to measure burst speed (maximum speed in m/s) of tadpoles from the 2 treatments; the maximum velocity measured was considered analogous to burst speed. Measurements were performed on a same day for all tadpoles. The racetrack was placed in an indoor experimental room provided by 2 fluorescent lamps (Philips daylight, TLT 40 W/54RS) and filled with tap water at 15°C until 0.10 m depth. Sixty tadpoles (30 per treatment) at stages 40–41 were used to measure burst swimming performance. These 60 tadpoles were obtained by randomly selecting 1 tadpole from each replicate (total length of tadpoles in the predator treatment was 21.52 ± 0.62 whereas that in the non-predator treatment was 24.42 ± 0.54). Tadpoles were allowed to habituate for a couple of minutes and a predator attack was simulated by touching the tail with a stick. Each tadpole performed 3 races, with 1-min rest between races. Water was changed between

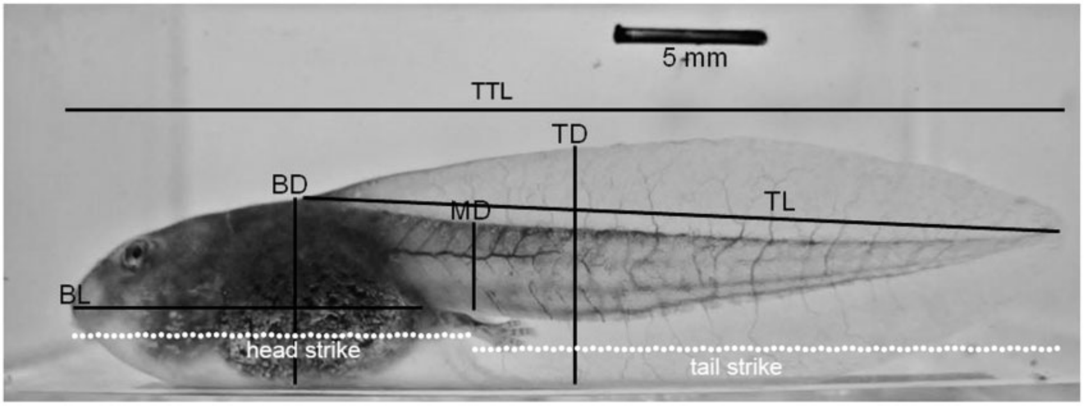

Figure 1. Digital photograph showing tadpole morphological measurements and sections considered for predator attacks (white dotted lines). Total tadpole length (TTL); Tail length (TL); Body length (BL); Body depth (BD); Tail muscle depth (MD); and Tail fin depth (TD).

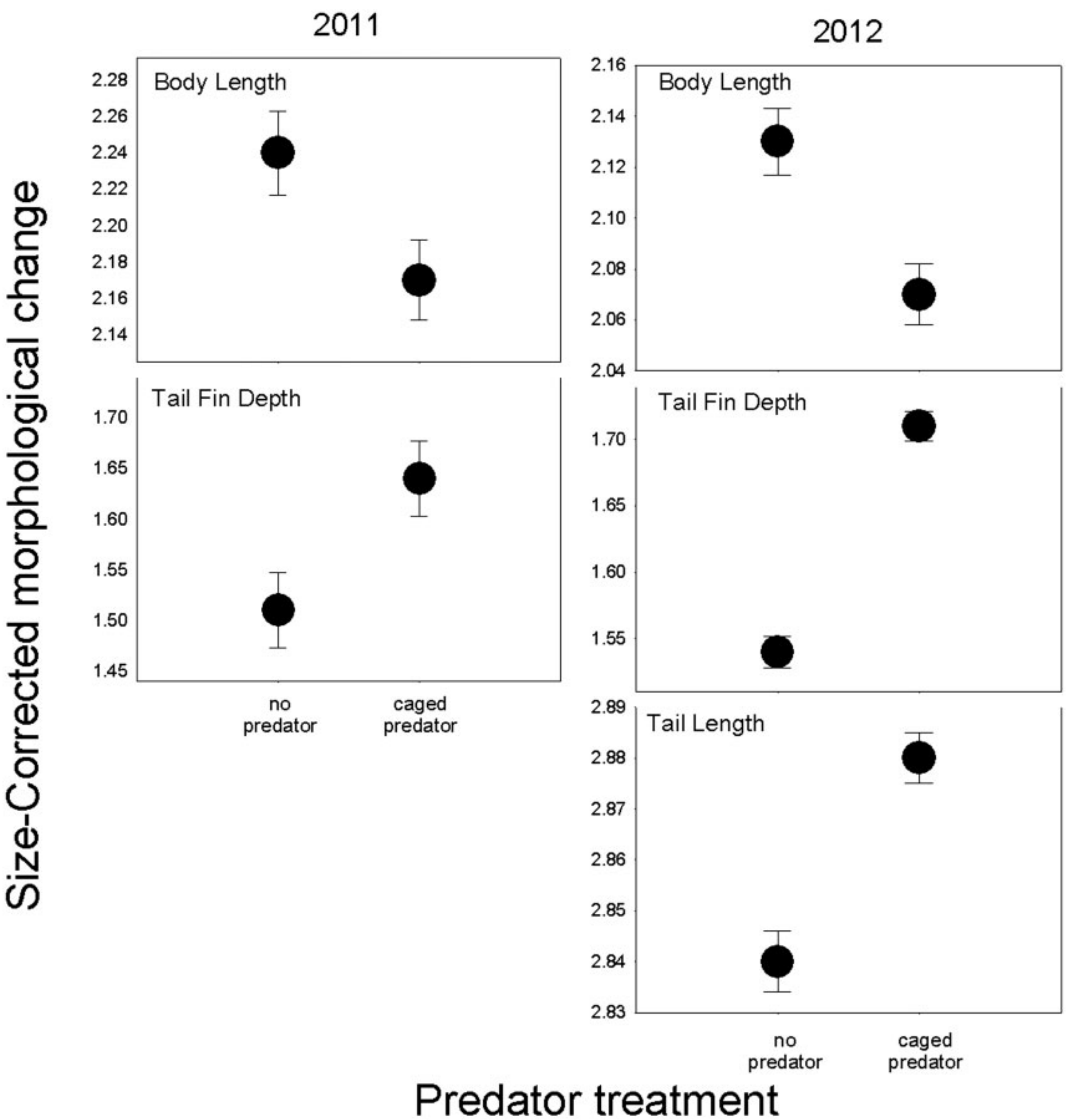

Figure 2. Body and tail changes of *P. thaul* after experimental switch of predator setting in 2 different years.

Table 1. Univariate GLMs with TTL as covariate testing for mean differences in morphological traits between predator treatments in 2011 and 2012

Source	Season-2011		Season-2012	
	F	*P*-value	*F*	*P*-value
Body length				
Predator	4.499	**0.038**	7.789	**0.011**
TTL	106.511	**0.000**	73.304	**0.000**
*Predator x TTL	4.586	**0.036**	-	-
Body depth				
Predator	1.295	0.259	1.339	0.261
TTL	66.542	**0.000**	80.036	**0.000**
Tail muscle depth				
Predator	2.269	0.137	0.088	0.769
TTL	23.352	**0.000**	107.688	**0.000**
Tail fin depth				
Predator	5.321	**0.025**	68.209	**0.000**
TTL	47.718	**0.000**	230.234	**0.000**
Tail fin length				
Predator	2.139	0.149	17.198	**0.000**
TTL	133.431	**0.000**	514.989	**0.000**

Significance is highlighted in boldface. *Only significant interaction.

trials. Only the best of the 3 runs was considered at the "burst speed" run for each specimen. Usually, the first run after simulating the attack was the one computed as the best run.

Effect of predator exposure on morphology and lure effect

To study predator strikes, we conducted a second experiment with the clutches collected in October 2012. To induce morphological changes by the presence of the predator, we followed the same protocol as in 2011 but varying the number of replicates (12 replicates for the predator treatment and 11 replicates for the non-predator treatment), and recorded the same morphological measurements (TL, BL, BD, MD, TD, and TTL).

To record the predator attacks, we took into account the different vulnerability of 2 sections of a tadpole body (as described by Van Buskirk et al. 2003, Figure 2): (1) head/body plus one-third of the tail section (from now on "head") and (2) the last two-thirds of the tail section (from now on "tail") (Figure 1). Each replicate consisted of groups of 5 tadpoles from the same rearing container exposed to 1 free *Rhionaeschna* larva in 1-L plastic containers. Before the experiment, tadpoles were allowed to acclimate for 3 min and after acclimation a larva was placed on a perch. We recorded predator attacks in 17 experimental units (6 experimental units were discarded because they did not complete the minimal of 5 tadpoles per replicate): nine with tadpoles from the predator treatment and eight from the non-predator treatment. Predators were starved for 48 hours prior to the start of the experiment to increase hunger level and standardize motivation. We used a digital video camera (Sony HDR-XR200V; 30 frames s-1) placed 0.70 m above the container to record both the predator and prey for 30 min. Between each test, the containers were cleaned and the water replaced. Testing all the individuals took 2 days.

Video recordings were evaluated using VLC media player 2.0.1, which allows the observer to reduce the playback speed to 0.02 x and thus accurately determine strike location (head or tail of tadpoles). A larval labium contacting a tadpole was considered a strike. We analyzed only the first strike in each container and did not record subsequent attacks because we considered that predator strikes on scared tadpoles were not comparable to those on unaware tadpoles. Additionally, we quantified the proportion of active tadpoles (the number of tadpoles moving in each cage). Activity was recorded for each replicate and expressed as the proportion of active tadpoles over total observations (30) per container (Jara and Perotti 2010). A tadpole was considered active if it was either swimming or moving the tail. All tadpoles were weighed at the end of the evaluation. Weight was calculated as the mean value per replicate.

Statistical analysis

For analyses of tadpole morphology, we performed a univariate GLM for each ln-transformed trait with predator treatment as a factor. To evaluate the effect of the predator on morphological traits, we performed ANCOVAs. We controlled for differences in size by including size (centered TTL measure) as a covariate in the model (Berner 2011; El Balaa and Blouin-Demers 2013; Touchon and Wojdak 2014). In general, we ran reduced models (without interaction), because interactions between TTL and treatment were not significant; the only exception was BL in 2011 for which we ran the full model. TTL and developmental stage were compared between predator treatments by a *t*-test in both experiments (2011 and 2012).

To explore the effect of morphology on performance gradients (effects of size and morphological traits on swimming speed), we ran generalized least squares (GLS) models considering every treatment separately. GLS models were performed considering all possible models with morphological predictor variables (BL, TL, BD, MD, TD, and TTL), and burst speed as dependent variable. All the analyses were performed using the 'dredge' function of the 'MuMIn' package (Multi-Model Inference. R package version 1.12.1; Barton 2014), which performs automated model selection. To ensure that the regression model provided the best fit among the candidate models (Angilletta 2006), we used the Akaike information criterion (AIC). Because of the limited number of samples, we used the AIC for small sample sizes and Akaike weights (Wi), which indicates the probability that a given model is the best among a series of candidate models (Burnham and Anderson 2004). Model averaging (typified by AIC) was calculated to estimate the effect size of every predictor variable on the response variable (burst swimming), considering the subset of models where the target variable appeared (Burnham et al. 2011).

We analyzed predator strikes, activity and body mass of tadpoles as a function of predator treatments. Scores of predator strikes were analyzed by Chi-square test. Tadpole activity and tadpole size were analyzed by parametric *t*-tests for independent samples. To explore the relationship between tadpole activity and tadpole size, we performed Pearson correlation between the total proportion of active tadpoles and the mean body weight of the tadpoles in each container.

Results

Morphology in *P. thaul* tadpoles covaried with tadpole size and some specific traits were affected by the predator treatment (Table 1). Body length and tail fin depth were affected by the predator treatment in the two seasons evaluated; during 2012, tail fin length was also affected. Tadpoles exposed to caged predators showed shorter body length, greater tail fin depth, and longer tail fin length than non-exposed tadpoles (Figure 2). The analysis of body length in 2011 showed an interaction between the predator treatment and tadpole size, indicating that body length increased with

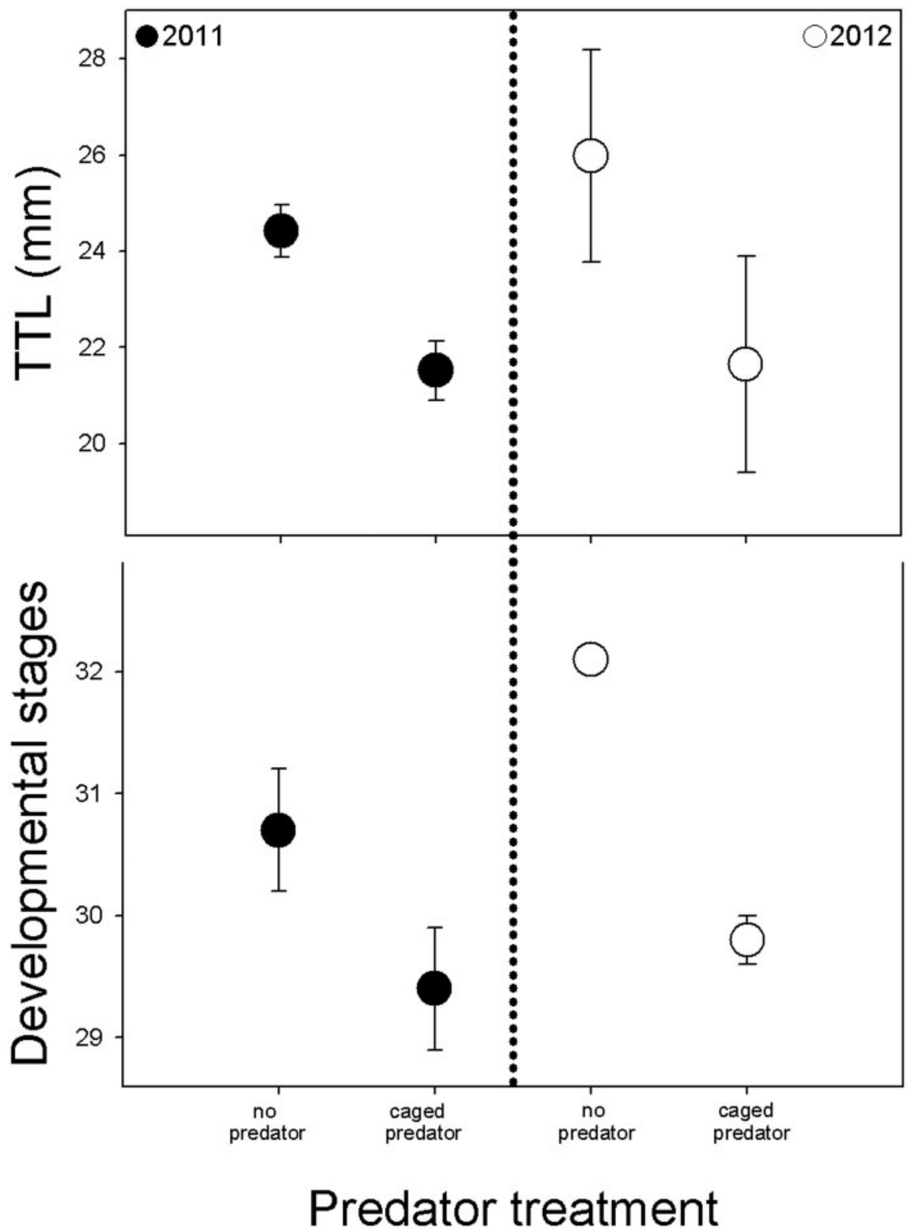

Figure 3. Average changes in tadpole size (mm) and developmental stage (Gosner 1960) after 30 days of exposure and non-exposure of predator risk (black circles = experiment 2011, white circles = experiment 2012). Total tadpole length (TTL).

tadpole total length. No differences were observed in body depth or tail muscle depth between treatments in either experiment (2011–2012) (Figure 2).

Tadpole size (total length) and developmental stage were affected by the presence of the predator in the same way. After 30 days, tadpoles exposed to caged predators were smaller and less developed than non-exposed tadpoles (2011 *t*-test; size $t = 2.0$, $df = 58$, $P < 0.001$, developmental stage, $t = 2.2$, $df = 58$, $P < 0.05$; 2012 *t*-test; size $t = 2.07$, $df = 15$, $P < 0.001$, developmental stage, $t = 7.74$, $df = 15$, $P < 0.001$; Figure 3).

Swimming speed did not differ significantly between treatments (predator treatment: 0.150 m/s ± 0.004; non-predator treatment: 0.165 m/s ± 0.009; *t*-test, $t = 1.67$, $df = 58$, $P = 0.49$). However, since we observed morphological changes, we used GLS models to test the effect of morphological traits (after predator treatment) on swimming. In the predator treatment, the swimming of tadpoles showed that the model including tail fin depth presented the lowest AICc value, although the regression coefficient value was low (see Appendix; VELOC~TD, $R^2 = 0.029$, AICc = −72.454, $W_i = 0.082$). In the non-predator treatment, the lowest AICc was observed in the model including body depth (BD) (Appendix; VELOC~BL, $R^2 = 0.023$, AICc = −50.969, $W_i = 0.082$). Parameter estimates after model averaging in the predator treatment showed that no variable contributed significantly to the models evaluated and that body length was the only variable with positive effect on tadpole swimming. In contrast, in the non-predator treatment, tail fin depth and tail length showed a negative effect on tadpole swimming while all the other traits showed a positive effect (Table 2). The analysis of strikes on the head and tail of tadpoles was not significant ($\chi^2 = 0.055$, $P > 0.8$).

Table 2. Model averaged parameter estimates from the model selection explaining the effect of predator-induced morphological variables on burst swimming

	Estimate	*SE*	*z* value	Pr(> |z|)
Predator				
Intercept	0.201	0.260	0.748	0.454
TD	−0.077	0.101	0.731	0.465
TL	−0.138	0.211	0.632	0.527
TTL	−0.003	0.011	0.271	0.786
BD	−0.032	0.116	0.269	0.788
BL	0.162	0.196	0.800	0.424
MD	−0.007	0.083	0.078	0.938
No Predator				
Intercept	0.333	0.805	0.404	0.686
BD	0.109	0.209	0.496	0.620
BL	0.150	0.305	0.471	0.638
TTL	0.013	0.022	0.558	0.577
MD	0.077	0.262	0.284	0.776
TD	−0.042	0.278	0.144	0.886
TL	−0.335	0.391	0.829	0.407

Predictor variables correspond to: Total tadpole length (TTL), Tail length (TL), Body length (BL), Body depth (BD), Tail muscle depth (MD), and Tail fin depth (TD). Shown are: Averaged coefficient (estimate), unconditional standard error, *z*-test statistic, and associated *P*-value.

We also found significant differences in the activity of tadpoles ($t = -2.18$; $df = 15$, $P < 0.05$): tadpoles exposed to the predator were less active than non-exposed tadpoles (predator treatment: 0.18 ± 0.02, $n = 9$; non-predator treatment: 0.23 ± 0.01, $n = 8$). Tadpole weight was also significantly affected by the predator treatment ($t = -4.39$; $df = 15$, $P < 0.00005$), with larger tadpoles in the non-predator treatment (predator treatment: 0.30 ± 0.02, $n = 9$; non-predator treatment: 0.44 ± 0.03, $n = 8$). However, activity was not correlated with tadpole weight (Pearson $r = 0.37$, $P = 0.15$, $n = 17$).

Discussion

In the present study, we found no direct evidence that morphology *per se* represents a trait that directly correlates with enhanced performance or acts as a predator distracter. However, the activity of tadpoles revealed significant differences between treatments, and body mass and developmental stage were also significantly affected by the presence of the predator, with tadpoles exposed to predators being less active and smaller than non-exposed tadpoles. However, in previous studies we observed that *P. thaul* tadpoles exposed to a scent signal indicating non-lethal risk of predation (caged predator) by the dragonfly *R. variegata* responded strongly by showing changes in their morphology such as deeper tails and bodies and enhanced survival, thus supporting the hypothesis of a fitness benefit (Jara 2010).

Predator-induced morphological changes that improve the swimming performance of tadpoles are not quite evident (Dayton et al. 2005; Teplitsky et al. 2005; Arendt 2009). We expected that tadpoles that increased their tail fin depth showed faster swimming performance (Van Buskirk and McCollum 2000). However, we found no significant relationship between morphology and performance. GLS models also confirmed these findings; although morphological traits influenced swimming performance differently in each treatment, the models showed no significant effect.

Previous studies showing no significant relationship between morphology and swimming in tadpoles later tested the tail lure tactic as a way to distract predators as an alternative hypothesis to understand this relationship. Some of these studies found that distractive tactics are a good intermediate predictor of enhanced survival (Van Buskirk et al. 2003; Johnson et al. 2008). However, in the present study, when we tested the lure effect based on different body vulnerability (see section "Methods"), we found no differences on strikes on the head or tail between tadpoles exposed and not exposed to the predator. Additionally, *P. thaul* tadpoles did not develop conspicuous tail coloration in the presence of the predator, as previously observed in other anuran species (Caldwell 1982; McCollum and Van Buskirk 1996; Skelly 1997). Instead, changes in morphology in *P. thaul* could be the result of the allometric growth that goes along with the abovementioned changes affecting life history features as observed in other vertebrates (Pettersson and Brönmark 1997, 1999; Andersson et al. 2006; Frommen et al. 2011).

Morphological changes could primarily be the result of physical constraints or biological interactions imposed on the developing organisms, ultimately affecting the expression of morphology (Abdala and Ponssa 2012). As suggested by Bourdeau and Johansson (2012), many examples of predator-induced morphological defenses in animals may actually be indirect effects (by-products) of alterations in prey behavior, rather than direct adaptive morphological responses to predation cues. They proposed that activity, growth rate, and morphology are often highly integrated traits. Then, as shown in previous studies (Jara and Perotti 2010), activity in *P. thaul* tadpoles seems to be the functional link that explains the increased survival of tadpoles in the presence of predation risk. Moreover, the reduction in activity can be interpreted as a change in the behavior of tadpoles, potentially resulting in morphological changes.

We know that *P. thaul* tadpoles pre-exposed to predators show enhanced survival (Jara 2010) and that they innately respond to conspecific alarm cues (Pueta et al. 2016) and to caged odonate larvae fed with mosquito larvae (Jara and Perotti 2010). Then, being less active can make these tadpoles less conspicuous when they are at risk of predation, and pre-exposure to caged predators and damaged conspecifics can give tadpoles an advantage when they face a free predator (Alvarez and Nicieza 2006; Mirza et al. 2006; Polo-Cavia and Gómez-Mestre 2014). However, more evidence is needed to find out whether the behavioral plasticity (low activity) of tadpoles exposed to predator risk affects traits (as the morphological changes observed) that are not necessarily related to a functional correlation (tadpole swimming).

We conclude that the morphological changes observed may be related to other unmeasured traits rather than serving as a functional link to swimming performance or lure distraction (Arendt 2003, 2010; Calsbeek and Kuchta 2011). *Pleurodema thaul* tadpoles occur in environments that vary in predator density and composition, and experimental studies have shown that they survive more if they have prior experience to predators (Jara 2010). Although our results do not elucidate the functional correlation of the traits, they provide evidence that tadpoles respond when they have previous predator risk experience.

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Appendix

Appendix 1. Generalized Least Square Models evaluating morphological traits (body length = BL, tail length = TL, body depth = BD, tail muscle depth = MD, tail fin depth = TD, and total tadpole length = TTL) on swimming performance of tadpoles from 2 predator treatments (SP = swimming from tadpoles exposed to predator, SNP = swimming from tadpoles non-exposed to predators)

Treatment	Model	Intercept	BD	BL	MD	TD	TL	TTL	R2	LL	AICc	Δi	Wi
SP	VEL ~ TD	0.202				−0.033			0.029	39.688	−72.454	0.000	0.082
SP	VEL ~ TL	0.273					−0.044		0.025	39.623	−72.322	0.132	0.077
SP	VEL ~ TTL	0.147						−0.003	0.019	39.526	−72.128	0.326	0.070
SP	VEL ~ BD	0.207	−0.039						0.012	39.421	−71.920	0.534	0.063
SP	VEL ~ BL + TL	0.452		0.259			−0.302		0.093	40.707	−71.814	0.640	0.060
SP	VEL ~ BL	0.196		−0.022					0.007	39.343	−71.763	0.691	0.058
SP	VEL ~ MD	0.152			−0.003				0.000	39.245	−71.566	0.888	0.053
SP	VEL ~ BL+ TD	0.063		0.131		−0.120			0.066	40.270	−70.940	1.514	0.038
SP	VEL ~ TD + MD	0.229			−0.022	−0.042			0.039	39.835	−70.070	2.384	0.025
SP	VEL ~ BD +TD	0.236	−0.027			−0.030			0.035	39.773	−69.946	2.508	0.023
SP	VEL ~ TTL + BL + TD	−0.193		0.284		−0.167		−0.008	0.120	41.162	−69.825	2.629	0.022
SP	VEL ~ TTL + TD	0.192				−0.027		−0.001	0.030	39.706	−69.812	2.642	0.022
SP	VEL ~ TD + TL	0.187				−0.039	0.009		0.029	39.690	−69.780	2.674	0.022
SP	VEL ~ BD + TL	0.290	−0.023				−0.038		0.029	39.681	−69.762	2.692	0.021
SP	VEL ~ MD + TL	0.293			−0.012		−0.048		0.028	39.673	−69.747	2.707	0.021
SP	VEL ~ TTL + TL	0.257					−0.039	0.000	0.025	39.626	−69.651	2.802	0.020
SP	VEL ~ BD + MD	0.246	−0.079		0.031				0.022	39.574	−69.548	2.906	0.019
SP	VEL ~ TTL + BL	0.100		0.021				−0.004	0.021	39.560	−69.520	2.934	0.019
SP	VEL ~ TTL + MD	0.142			0.007			−0.003	0.020	39.541	−69.482	2.972	0.019
SP	VEL ~ TTL + BD	0.155	−0.006					−0.002	0.019	39.527	−69.455	2.999	0.018
SP	VEL ~ BD + BL	0.227	−0.033	−0.014					0.014	39.457	−69.314	3.140	0.017
SP	VEL ~ BL + TD + TL	0.332		0.270		−0.058	−0.235		0.103	40.866	−69.233	3.221	0.016
SP	VEL ~ BD + BL+ TL	0.481	−0.032	0.266			−0.301		0.100	40.826	−69.152	3.302	0.016
SP	VEL ~ BD +TD + MD	0.065		0.181	−0.045	−0.171			0.099	40.813	−69.125	3.328	0.016
SP	VEL ~ BL+ MD	0.206		−0.025	−0.008				0.008	39.363	−69.125	3.329	0.016
SP	VEL ~ TTL + BL + TL	0.398		0.266			−0.289	−0.002	0.096	40.751	−69.002	3.452	0.015
SP	VEL ~ BL + MD + TL	0.467		0.257	−0.010		−0.304		0.095	40.744	−68.988	3.466	0.015
SP	VEL ~ BD + BL+ TD	0.098	−0.059	0.169		−0.138			0.089	40.635	−68.770	3.684	0.013
SP	VEL ~ TTL + BL + MD	−0.435		0.236	0.112			−0.020	0.060	40.168	−67.835	4.618	0.008
SP	VEL ~ TTL + TD + MD	0.342			−0.065	−0.094		0.005	0.050	40.004	−67.508	4.946	0.007
SP	VEL ~ TTL + MD + TL	0.852			−0.091		−0.226	0.013	0.044	39.914	−67.329	5.125	0.006
SP	VEL ~ TD + MD + TL	0.129			−0.031	−0.086	0.062		0.043	39.901	−67.302	5.152	0.006
SP	VEL ~ BD +TD + MD	0.194	0.063		−0.060	−0.065			0.042	39.884	−67.267	5.186	0.006
SP	VEL ~ TTL + BD + TD	0.288	−0.051			−0.040		0.002	0.037	39.804	−67.109	5.345	0.006
SP	VEL ~ BD + TD + TL	0.180	−0.033			−0.053	0.036		0.036	39.797	−67.095	5.359	0.006
SP	VEL ~ TTL + BD + TL	0.524	−0.080				−0.090	0.006	0.036	39.785	−67.070	5.384	0.006
SP	VEL ~ TTL + TD + TL	0.019				−0.070	0.085	−0.003	0.034	39.764	−67.028	5.426	0.005
SP	VEL ~ TTL + BD + BL + TD	−0.388	0.066	0.335		−0.176		−0.013	0.128	41.298	−66.944	5.510	0.005
SP	VEL ~ TTL + BL + TD + MD	−0.389		0.347	0.048	−0.150		−0.015	0.126	41.264	−66.875	5.579	0.005
SP	VEL ~ BD + MD + TL	0.291	−0.020		−0.002		−0.040		0.029	39.681	−66.862	5.592	0.005
SP	VEL ~ TTL + BL + TD + TL	−0.022		0.313		−0.130	−0.103	−0.007	0.125	41.241	−66.829	5.625	0.005
SP	VEL ~ BD + BL+ MD	0.237	−0.119	0.026	0.053				0.025	39.619	−66.738	5.716	0.005
SP	VEL ~ TTL + BD + MD	0.210	−0.053		0.024			−0.001	0.023	39.595	−66.689	5.765	0.005
SP	VEL ~ TTL + BD + BL	0.043	0.021	0.033				−0.005	0.022	39.573	−66.646	5.808	0.004
SP	VEL ~ BL + TD + MD + TL	0.271		0.275	−0.033	−0.110	−0.181		0.119	41.136	−66.620	5.834	0.004
SP	VEL ~ BD + BL + TD + TL	0.330	−0.047	0.286		−0.079	−0.210		0.117	41.104	−66.555	5.899	0.004
SP	VEL ~ BD + BL + MD + TL	0.482	−0.093	0.287	0.037		−0.294		0.105	40.913	−66.173	6.281	0.004
SP	VEL ~ BD + BL + TD + MD	0.027	0.069	0.182	−0.086	−0.196			0.103	40.875	−66.097	6.356	0.003
SP	VEL ~ TTL + BD + BL + TL	0.611	−0.065	0.260			−0.325	0.003	0.102	40.862	−66.072	6.382	0.003
SP	VEL ~ TTL + BL + MD + TL	0.355		0.272	0.007		−0.280	−0.003	0.096	40.752	−65.852	6.601	0.003
SP	VEL ~ TTL + BD + BL + MD	−0.386	−0.105	0.272	0.162			−0.019	0.073	40.379	−65.106	7.348	0.002
SP	VEL ~ TTL + BD + TD + MD	0.308	0.072		−0.109	−0.122		0.006	0.053	40.067	−64.481	7.973	0.002
SP	VEL ~ TTL + TD + MD + TL	0.613			−0.090	−0.068	−0.104	0.010	0.052	40.048	−64.443	8.010	0.001

(continued)

Appendix 1. Continued

Treatment	Model	Intercept	BD	BL	MD	TD	TL	TTL	R2	LL	AICc	Δi	Wi
SP	VEL ~ BD + TD + MD + TL	0.034	0.097		−0.091	−0.139	0.089		0.050	40.004	−64.355	8.098	0.001
SP	VEL ~ TTL + BD + MD + TL	0.879	−0.037		−0.076		−0.219	0.014	0.046	39.942	−64.232	8.222	0.001
SP	VEL ~ TTL + BD + TD + TL	0.317	−0.054			−0.036	−0.011	0.002	0.037	39.805	−63.957	8.496	0.001
SP	VEL ~ TTL + BD + BL + TD + MD	−0.408	0.054	0.344	0.014	−0.170		−0.014	0.128	41.302	−63.512	8.941	0.001
SP	VEL ~ TTL + BD + BL + TD + TL	−0.384	0.066	0.335		−0.176	−0.002	−0.013	0.128	41.298	−63.505	8.948	0.001
SP	VEL ~ TTL + BL + TD + MD + TL	−0.260		0.344	0.035	−0.137	−0.047	−0.012	0.127	41.273	−63.456	8.998	0.001
SP	VEL ~ BD + BL +TD + MD + TL	0.266	0.005	0.274	−0.036	−0.112	−0.179		0.119	41.136	−63.182	9.272	0.001
SP	VEL ~ TTL + BD + BL + MD + TL	0.366	−0.093	0.302	0.055		−0.269	−0.003	0.106	40.922	−62.752	9.701	0.001
SP	VEL ~ TTL + BD + TD + MD + TL	0.452	0.055		−0.111	−0.102	−0.052	0.008	0.054	40.075	−61.058	11.396	0.000
SP	VEL ~ TTL + BD + BL +TD + MD + TL	−0.418	0.055	0.344	0.014	−0.171	0.004	−0.014	0.128	41.302	−59.746	12.708	0.000
SNP	VEL ~ BD		0.105						0.023	28.946	−50.969	0.000	0.082
SNP	VEL ~ BL	−0.076		0.105					0.020	28.901	−50.878	0.091	0.078
SNP	VEL ~ TTL	0.161						0.003	0.009	28.743	−50.563	0.406	0.067
SNP	VEL ~ MD	0.142			0.037				0.006	28.700	−50.477	0.492	0.064
SNP	VEL ~ TD	0.126				0.025			0.001	28.624	−50.325	0.644	0.059
SNP	VEL ~ TTL + TL	1.718					−0.551	0.027	0.086	29.950	−50.299	0.670	0.059
SNP	VEL ~ TL	0.178					−0.005		0.000	28.604	−50.286	0.684	0.058
SNP	VEL ~ MD + TL	1.194			0.297		−0.419		0.055	29.455	−49.310	1.660	0.036
SNP	VEL ~ BL + TL	0.115		0.267			−0.195		0.052	29.400	−49.199	1.770	0.034
SNP	VEL ~ BD + TL	0.214	0.169				−0.105		0.037	29.173	−48.746	2.224	0.027
SNP	VEL ~ BL+ TD	−0.147		0.235		−0.143			0.036	29.152	−48.703	2.266	0.026
SNP	VEL ~ BD +TD	0.048	0.168			−0.086			0.031	29.080	−48.561	2.409	0.025
SNP	VEL ~ TTL + BL	−0.317		0.213				−0.005	0.024	28.974	−48.348	2.621	0.022
SNP	VEL ~ BL+ MD	−0.224		0.185	−0.058				0.024	28.973	−48.346	2.623	0.022
SNP	VEL ~ BD + MD	−0.014	0.127		−0.021				0.024	28.963	−48.325	2.644	0.022
SNP	VEL ~ TTL + BD	−0.013	0.119					−0.001	0.023	28.951	−48.303	2.667	0.022
SNP	VEL ~ BD + BL	−0.018	0.086	0.023					0.023	28.949	−48.298	2.671	0.022
SNP	VEL ~ TTL + TD	0.394				−0.152		0.010	0.020	28.912	−48.224	2.745	0.021
SNP	VEL ~ TD + MD	0.295			0.116	−0.126			0.013	28.801	−48.003	2.966	0.019
SNP	VEL ~ TTL + MD	0.203			−0.082			0.009	0.011	28.777	−47.954	3.015	0.018
SNP	VEL ~ TD + TL	0.382				0.175	−0.171		0.011	28.774	−47.948	3.021	0.018
SNP	VEL ~ TTL + TD + TL	1.754				0.074	−0.603	0.026	0.088	29.981	−47.462	3.507	0.014
SNP	VEL ~ TTL + MD + TL	1.746			0.064		−0.573	0.024	0.087	29.970	−47.440	3.529	0.014
SNP	VEL ~ TTL + BD + TL	1.616	0.031				−0.531	0.025	0.087	29.964	−47.427	3.542	0.014
SNP	VEL ~ TTL + BL + TL	1.832		−0.030			−0.568	0.029	0.086	29.953	−47.406	3.563	0.014
SNP	VEL ~ BL + MD + TL	0.829		0.169	0.202		−0.406		0.070	29.695	−46.889	4.080	0.011
SNP	VEL ~ BD + MD + TL	1.002	0.096		0.235		−0.389		0.065	29.609	−46.717	4.252	0.010
SNP	VEL ~ TD + MD + TL	1.207			0.284	0.047	−0.446		0.056	29.466	−46.433	4.536	0.008
SNP	VEL ~ BL + TD + TL	0.157		0.258		0.034	−0.221		0.052	29.405	−46.311	4.658	0.008
SNP	VEL ~ BD + BL+ TL	0.118	0.008	0.259			−0.193		0.052	29.400	−46.300	4.669	0.008
SNP	VEL ~ TTL + BD + TD	0.238	0.139			−0.183		0.006	0.039	29.195	−45.889	5.080	0.006
SNP	VEL ~ BD + BL+ TD	−0.097	0.071	0.164		−0.138			0.038	29.184	−45.868	5.101	0.006
SNP	VEL ~ BD + TD + TL	0.261	0.159			0.042	−0.139		0.038	29.181	−45.862	5.108	0.006
SNP	VEL ~ BD +TD + MD	−0.075		0.217	0.035	−0.175			0.037	29.165	−45.830	5.139	0.006
SNP	VEL ~ BD +TD + MD	0.173	0.153		0.081	−0.181			0.037	29.165	−45.830	5.139	0.006
SNP	VEL ~ TTL + BL + TD	−0.087		0.217		−0.156		0.001	0.036	29.155	−45.810	5.159	0.006
SNP	VEL ~ BD + BL+ MD	−0.158	0.066	0.111	−0.050				0.026	29.000	−45.500	5.469	0.005
SNP	VEL ~ TTL + BD + BL	−0.234	0.053	0.142				−0.004	0.025	28.989	−45.479	5.490	0.005
SNP	VEL ~ TTL + BD + MD	0.027	0.117		−0.074			0.004	0.025	28.979	−45.458	5.511	0.005
SNP	VEL ~ TTL + BL + MD	−0.285		0.205	−0.030			−0.003	0.025	28.978	−45.457	5.513	0.005
SNP	VEL ~ TTL + TD + MD	0.394			−0.015	−0.147		0.010	0.020	28.913	−45.326	5.643	0.005
SNP	VEL ~ TTL + BD + BL + TL	2.070	0.107	−0.182			−0.586	0.032	0.090	30.020	−44.387	6.582	0.003
SNP	VEL ~ TTL + BL + TD + TL	2.039		−0.072		0.096	−0.660	0.030	0.089	29.999	−44.347	6.623	0.003
SNP	VEL ~ TTL + TD + MD + TL	1.768			0.046	0.062	−0.610	0.024	0.088	29.991	−44.329	6.640	0.003
SNP	VEL ~ TTL + BD + TD + TL	1.700	0.015			0.064	−0.587	0.025	0.088	29.984	−44.315	6.654	0.003
SNP	VEL ~ TTL + BD + MD + TL	1.650	0.029		0.061		−0.553	0.022	0.088	29.982	−44.312	6.657	0.003
SNP	VEL ~ TTL + BL + MD + TL	1.825		−0.021	0.062		−0.583	0.025	0.087	29.972	−44.291	6.678	0.003
SNP	VEL ~ BL + TD + MD + TL	0.822		0.171	0.203	−0.009	−0.401		0.070	29.695	−43.738	7.232	0.002
SNP	VEL ~ BD + BL + MD + TL	0.830	0.004	0.165	0.201		−0.406		0.070	29.695	−43.737	7.232	0.002
SNP	VEL ~ BD + TD + MD + TL	0.993	0.099		0.236	−0.014	−0.380		0.065	29.610	−43.567	7.402	0.002
SNP	VEL ~ BD + BL + TD + TL	0.157	0.000	0.258		0.034	−0.221		0.052	29.405	−43.159	7.810	0.002
SNP	VEL ~ BD + BL + TD + MD	0.019	0.086	0.122	0.051	−0.184			0.040	29.211	−42.769	8.200	0.001
SNP	VEL ~ TTL + BD + BL + TD	0.098	0.100	0.083		−0.176		0.004	0.039	29.208	−42.763	8.206	0.001
SNP	VEL ~ TTL + BD + TD + MD	0.237	0.140		0.013	−0.188		0.006	0.039	29.195	−42.739	8.230	0.001
SNP	VEL ~ TTL + BL + TD + MD	−0.121		0.232	0.056	−0.174		−0.002	0.037	29.168	−42.684	8.286	0.001
SNP	VEL ~ TTL + BD + BL + MD	−0.162	0.065	0.113	−0.049			0.000	0.026	29.000	−42.348	8.621	0.001
SNP	VEL ~ TTL + BD + BL + TD + TL	2.204	0.093	−0.196		0.077	−0.657	0.033	0.092	30.048	−−41.005	9.964	0.001
SNP	VEL ~ TTL + BD + BL + MD + TL	2.048	0.099	−0.166	0.034		−0.594	0.030	0.090	30.025	−40.960	10.010	0.001
SNP	VEL ~ TTL + BL + TD + MD + TL	2.012		−0.062	0.031	0.085	−0.657	0.028	0.089	30.004	−40.916	10.053	0.001
SNP	VEL ~ TTL + BD + TD + MD + TL	1.709	0.017		0.047	0.051	−0.593	0.023	0.089	29.994	−40.897	10.072	0.001
SNP	VEL ~ BD + BL +TD + MD + TL	0.823	0.006	0.165	0.203	−0.011	−0.399		0.070	29.695	−40.299	10.670	0.000
SNP	VEL ~ TTL + BD + BL + TD + MD	0.066	0.094	0.101	0.035	−0.186		0.002	0.040	29.212	−39.334	11.635	0.000
SNP	VEL ~ TTL + BD + BL +TD + MD + TL	2.192	0.092	−0.191	0.010	0.073	−0.657	0.032	0.092	30.049	−37.240	13.729	0.000