Contrasting effects of environmental factors during larval stage on morphological plasticity in postmetamorphic frogs.

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Running Head: Environmental induced plasticity in frog morphology

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ABSTRACT: In organisms with complex life cycles, environmentally induced plasticity across sequential stages can have important consequences on morphology and life history traits such as developmental and growth rates. However, previous research in amphibians and other ectothermic vertebrates suggests that some morphological traits are generally insensitive to environmental inductions. We conducted a literature survey to examine the allometric responses in relative hind leg length and head shape of postmetamorphic anuran amphibians to induced environmental (temperature, resource level, predation and desiccation risk) variation operating during the larval phase in 44 studies using 19 species. To estimate and compare plastic responses across studies we employed both an index of plasticity and effect sizes from a meta-analysis. We found contrasting trait responses to different environmental cues. Higher temperatures increase development more than growth rate and induce smaller heads but not overall shifts in hind leg length. By contrast, an increment in resource availability increases growth more than development, with a parallel increase in hind leg length but no change in head shape. Increase in predation risk decreases both development and growth rates and slightly reduces relative hind leg length, but there is no change in head shape. Pond desiccation induces quick development and low growth rates, with no changes in morphology. Across environments, both hind leg and head shape plasticity were positively correlated with growth rate plasticity. However, plasticity of developmental rate was only correlated with head shape plasticity. Overall, these results suggest that environmental trends predicted by global warming projections, as increasing pond temperature and accelerating pond desiccation, will significantly influence hind leg and head morphology in metamorphic frogs, which may affect performance and, ultimately, fitness.

KEY WORDS: morphology, plasticity, temperature, resources, pond desiccation, predation risk, meta-analysis, global warming.

1. INTRODUCTION

Environmentally-induced variation in body shape occurs in many taxa and phenotypic plasticity in morphology has been found in response to several environmental factors such as diet (Wimberger 1992, Thompson 1999), temperature (de Jong et al. 2010, Trotta et al. 2010), and resource allocation (Nijhout & Emlen 1998, Stern & Emlen 1999, Canale & Henry 2010). However, previous research on amphibians and other ectothermic vertebrates has suggested that size-independent metric shapes are generally insensitive to environmental induction (Arnold & Peterson 1989, Blouin & Loeb, 1991, Forsman 1996, Blouin & Brown 2000).

Development is a branching process in which undifferentiated precursor tissues may determine different phenotypes occurring later. Therefore, environmental influence on phenotypes may be especially relevant when this happens at early stages of the ontogeny (e.g. Lindström 1999). This may be of particular interest in animals with complex life cycles, as in most invertebrates and amphibians, where environmental induction during the embryo, larval or pupal stage can have strong effects on morphology after metamorphosis (Emerson 1986, Giménez 2006).

In amphibians, four major ecological factors, commonly encountered during the larval stage, can drastically affect metamorphic traits: temperature, trophic resources (via food availability or larval competition), habitat permanence (via desiccation of temporary ponds, the common breeding environment for most amphibian species) and predator pressure (via behavioural trade-offs between growth and activity), (Alford 1999, Bruce 2005). Global warming will result in a general rise in pond temperatures, but it will also affect the rainfall regimes and environmental predictability across the globe, thus resulting

in shorter pond durations during dry years (McMenamin et al. 2008). Increased severe droughts may also affect biotic interactions presumably with a combined increase in both resource competition and predation. Therefore, climatic change is likely to affect all the main ecological factors affecting amphibian plasticity at metamorphosis.

Much of the research on amphibian developmental plasticity has concentrated on environmental induction on size and time to metamorphosis (Wells 2007). Only recently studies have reported on the allometric (size independent) shifts in hind leg length and head shape to varying growth conditions during the larval stages (Tejedo et al. 2000a, Relyea 2001, Van Buskirk & Saxer 2001, Gómez-Mestre & Buchholtz 2006, Nicieza et al. 2006, Richter-Boix et al. 2006a, Orizaola & Laurila 2009), which are partly due to allometric differences in the relative growth rates of the body and either hind leg or head (Emerson 1986, Emerson et al. 1988). In frogs, hind leg length and head shape are well suited traits for analysing environmental effects on morphological variation since both traits have clear and testable morphofunctional implications. Relatively longer hind legs increase jumping performance (Zug 1978, Emerson 1978, Tejedo et al. 2000a,b, Gomes et al. 2009), and rapid adaptive coevolution between hind leg length and rate of movement has been suggested in the invasive toad *Rhinella marina* (Phillips et al., 2006). In addition, wider skulls and longer jaws may facilitate the intake of larger prey (Emerson 1985 Emerson & Bramble, 1993).

To predict the environmental outcome of climatic change, especially on low dispersal organisms such as amphibians, it is necessary to assess the magnitude and direction of plasticity in fitness related traits in response to different environmental factors, and the potential of populations to evolve (Parmesan 2006, Chown et al. 2010). Current

93 results in amphibians have revealed contrasting patterns in morphological inductions
94 between different environmental factors. For instance, although increase in temperature and
95 resource availability is predicted to boost both developmental and growth rates, their effects
96 on hind leg length appear to be the opposite: longer legs when tadpoles are raised at
97 increased resources (Emerson 1986, Tejedo et al. 2000a) and shorter when growing at
98 higher temperatures (Gómez-Mestre & Buchholtz 2006). Therefore, it is currently difficult
99 to establish a general pattern of how larval environment affects the morphological plasticity
100 at metamorphosis.

101 In this study we used meta-analytic techniques to describe the magnitude and
102 direction of plasticity in hind leg length and head shape of postmetamorphic juvenile frogs
103 induced by four main ecological factors operating during the larval phase: temperature,
104 desiccation risk, resource availability and predation risk. All these factors will presumably
105 be affected by global climate warming.

106 **2. METHODS**

107 **2.1. Data**

108 We examined a total of 44 experiments to test whether variation in these four
109 environmental factors determine the allometric response in morphological shape after
110 metamorphosis in frogs. We considered information for 19 different taxa (including the
111 Klepton *Pelophylax* kl. *esculenta*; see Annex I) reported in 11 published studies (24
112 experiments) between 1991-2009 and 10 unpublished studies carried out between 1995-
113 2007 (20 experiments). All these studies, covering 20 mesocosms and 24 laboratory
114 experiments, manipulated environmental conditions the larvae experienced. Resource
115 availability (17 experiments), temperature (11 experiments), non-lethal predation risk (11

116 experiments), and pond desiccation risk (5 experiments), are known agents imposing
117 substantial effects on larval growth and development in amphibians (Alford, 1999). Forty-
118 one and forty of the considered studies provided quantitative data on relative size of hind
119 leg length / tibiofibula length, and head width, respectively, together with information on
120 time to and size at metamorphosis as well as larval growth rates (see Annex I).

121 We estimated adjusted mean differences in morphology between environments by
122 using an ANCOVA (GLM module of the Statistica software; Statsoft, Inc., 2007). Body
123 mass (ln mass$^{1/3}$) was used as a covariate for most of the studies. However in *Scaphiopus*
124 *holbrooki, Spea mutiplicata, Spea intermontana, Pelobates cultripes* (Gomez-Mestre &
125 Buchholtz 2006, Gomez-Mestre & Buchholtz, unpublished; *Hyla cinerea* (Blouin & Loeb
126 1991); and *Rana cascadae* (Blouin & Brown 2000), snout-vent length (SVL) was employed
127 as covariate, and the first principal component (PC1) was used as a covariate in
128 *Discoglossus galganoi* (Nicieza et al. 2006). The environment x body size interaction term
129 was included in the model to test for heterogeneity of slopes. Initial analyses showed that,
130 in most occasions, this interaction was not significant ($P > 0.25$). Thus, the treatment term
131 tests whether frogs raised in contrasting environments differed in size-independent shape.
132 In mesocosm experiments, individual responses were analysed and a mixed model was
133 fitted, treating environment as a fixed factor and tank as a random variable nested within
134 environments.

135 We were also interested in analysing the dependence of post-metamorphic shape on
136 larval developmental and growth rates across species and experiments. Thus, we considered
137 developmental time as the time elapsed from the start of larval feeding phase (Gosner stage
138 25, Gosner 1960) to metamorphic climax with foreleg protrusion (Gosner stage 42). Size at

139 metamorphosis was estimated as mass at metamorphosis after full tail resorption (Gosner
140 stage 46), or mass at Gosner stage 42 (Capellán & Nicieza 2007), or SVL (Blouin & Loeb
141 1991, Gómez-Mestre & Buchholz 2006, Gómez-Mestre & Buchholtz unpublished data).
142 Growth rate was estimated as body size at metamorphosis divided by developmental time.

143 **2.2. Analyses**

144 To estimate and compare plastic responses across studies, we employed both an
145 index of plasticity providing the change in percent, and effect sizes derived from a meta-
146 analysis (Rosenberg et al. 2000). To estimate the index of plasticity we first removed the
147 differences in mean size-adjusted hind leg length and head width, and mean time and size
148 to metamorphosis and growth rates, at low temperature or resource level, or at no
149 desiccation or predation risk treatments (Low treatments) by setting these variables to 100
150 % (i.e. Hind leg $length_{Low}$ = 100). Subsequently, we expressed the same variables at the
151 high temperature or resource level, and at predation or desiccation risk treatments (High
152 treatments) as a fraction of this total, and plasticity was estimated as the difference between
153 mean traits under High and Low environmental conditions (Plasticity Hind leg length =
154 ((Hind leg $length_{High}$ / Hind leg $length_{Low}$) -1) * 100). Since this value of plasticity
155 represents a dimensionless estimate of relative change it can be used to compare different
156 traits and experiments. Positive values of plasticity indicate that the trait increases at the
157 High environments (high temperature or resource level, presence of desiccation or
158 predation risk), whereas a negative value indicates that the increase occurred at the Low
159 environments (low temperatures or resource level, no risk of desiccation or predation).
160 Significant values of plasticity were considered if 95 % confidence limits do not overlap
161 with zero.

In addition, we estimated the magnitude of plasticity in morphological and life history traits by parallel analyses conducted with effect sizes from a meta-analysis (Metawin 2.1, Rosenberg et al. 2000). *Hyla versicolor* and *H. cinerea* were excluded from some of the analyses because lack of information on sample sizes and standard errors prevented us from estimating effect sizes. The magnitude of the overall effect size is generally interpreted as "small" if Hedges' $d = 0.2$, "medium" if $d = 0.5$, "large" if $d = 0.8$, and "very large" for values of $d > 1.0$ (Cohen 1969). Effect sizes were considered significant if 95 % confidence intervals did not cross zero

The associations between plasticity estimates in hind leg length and head shape with developmental time, mass and growth rates plasticities were analyzed by using Pearson's correlation and multiple regression analyses to tease apart the partial contributions of plasticity in developmental or growth rates to morphological plasticity. All the analyses were performed using the STATISTICA 8.0 Statistical Package (Statsoft, Inc 2007).

3. RESULTS

Ecological factors acting during the larval phase induce strong changes in larval life history traits in anuran amphibians (Table 1, Fig. 1). Increasing resource levels and temperature strongly accelerated both larval development and growth rates. However, we found contrasting trait responses to different environmental cues. Higher temperatures increase development more than growth rates, whereas an increment in resource availability results in greater enhancement of growth than development. An increase in predation risk induced a small decrease in both development and growth rates, and pond desiccation increased developmental rate and reduced growth rate slightly. Mass at metamorphosis

responds differentially depending on the ecological factor, with larger size when resources are plenty but smaller size with increases in temperature, predation or pond desiccation risk.

Larval environmental conditions affected the morphology of anurans at metamorphosis (Table 1, Fig. 1). For hind leg length, 32 studies out of 43 (74.4 %) reported significant results, whereas only 24 out of 41 studies (58.5%) reported significant allometry in head shape (test of comparison between proportions, P = 0.126, see Annex I). Most of the experiments found that allometric plasticity in morphology was low or moderate for both traits (hind leg: plasticity index range: - 5.6 to + 10.3 %, Hedges' *d* range: - 0.64 to + 2.63; head: plasticity index range, - 13.3 to + 17.3 %, Hedges' *d* range. - 2.12 to + 2.04, Annex I). Resource availability and the presence of non-lethal predators induced the strongest changes in hind leg length by either elongating hind legs with increasing resource levels or shortening them with predation risk (Table 1, Fig. 1). Head shape allometry was only affected by temperature, implying a reduction in head size with increasing temperatures (Table 1, Fig. 1).

Hind legs were relatively longer when either growth rate or mass at metamorphosis was environmentally enhanced (r = 0.52, P = 0.0005, N = 41, Fig. 2a, r = 0.52, P = 0.0004, N = 43, respectively). However, there was no significant relationship between plasticity in hind leg length and plasticity in developmental time (r = - 0.20, P = 0.20, N = 41, Fig. 2b). Allometric changes in head width covaried positively with growth rate (r = 0.35, P = 0.027, N = 40, Fig. 3a) and mass at metamorphosis (r = 0.53, P = 0.0003, N = 41), and also with developmental time, although this result was marginally non significant (r = 0.29, P = 0.06, N = 40, Fig. 3b).

208 Time to metamorphosis and growth rate plasticity were negatively correlated (r = -
209 0.44, P = 0.0036, N = 42). Hind leg length plasticity was explained by the partial
210 contribution of growth rate plasticity after controlling for variation in developmental rate
211 plasticity (*Beta* = 0.502, P = 0.0007), but the partial contribution of developmental rate was
212 not significant (*Beta* = 0.211, P = 0.129). Head width plasticity was explained by partial
213 contributions of both growth rate (*Beta* = 0.593, P = 0.0002) and developmental rate (*Beta*
214 = 0.552, P = 0.0005). Parallel analyses conducted with effect sizes from the meta-analysis
215 (Metawin 2.1, Rosenberg et al. 2000) provided similar trends to those found with our
216 plasticity index and are not shown in detail here.
217

218 **4. DISCUSSION**

219 In anurans, environmental variation in the aquatic larval habitat promotes shifts in
220 growth and differentiation rates that influence morphological shape at metamorphosis. This
221 is an indication that ecological conditions determine allometric growth between body size,
222 hind legs and head throughout development (Emerson 1986). The environmentally induced
223 plasticity in morphological shape found in anurans via alteration of growth and
224 developmental rates may be widespread also in other organisms (e.g. Strathmann et al.
225 1992, Elphick & Shine 1998, Zijlstra 2003, Moriuchi & Winn 2005).

226 The increase in resource availability induces a consistent response with elongation
227 of hind legs with the exception of *Discoglossus galganoi,* which exhibits a slight non-
228 significant reduction (Nicieza et al. 2006). However, the pattern of increased resource
229 induction on head shape appears inconsistent across the species as some species exhibit
230 wider (e.g. *Rana* species, *Agalychnis callidryas* and *Discoglossus galganoi,* see Annex I)

231 and other narrower heads (*Pelobates cultripes* and *Pelodytes ibericus,* see Annex I). The
232 morphological pattern observed at reduced resource levels (i.e. metamorphs with shorter
233 hind legs and wider heads in some species) seems to mirror less developed morphology as
234 tadpoles approaching metamorphosis tend to elongate the hind legs and narrow the head
235 (Sokol 1984, Hall et al. 1997, Cannatella 1999). A similar trend is found when larvae
236 develop under predation risk (see below). Hence, stressful conditions operating during
237 larval stages (lower resource levels or predation risk) seem to promote a faster whole-body
238 developmental rate that allows larvae to escape from a poor growing environment at the
239 cost of incomplete development of some body parts (e.g. hind legs).

240 Higher temperature during the larval phase induces a significant reduction in
241 metamorph head width. Results across species appear strongly consistent, with the
242 exception of *Rana cascadae* and *Xenopus laevis* which increase head size, however, both
243 plasticity values were non-significant (Blouin & Brown 2000, Gómez-Mestre et al.
244 unpublished). A similar reduction in head width was found in *Xenopus laevis* when
245 temperature was increased only during the metamorphic climax (Walsh et al. 2008), which
246 agrees with the general trend of head reduction at higher developmental temperatures.
247 These results are similar to those found in other ectotherms, showing reduced size of
248 several morphological traits, such as the wings, thorax and head under higher
249 developmental temperatures (French et al. 1998, Ottenheim & Volmer 1999, Stevens 2004,
250 Santos et al. 2006, Trotta et al. 2010). In amphibians, a reduction of head size may have
251 some negative consequences on individual performance, since most species are gape-
252 limited predators and reduced head size may decrease ingestion capability in juveniles and
253 reduce the size and type range of potential prey (Emerson & Bramble 1993, Maglia, 1996).

254 Interestingly, increasing temperature did not induce a response in hind leg length with an
255 effect size not different from zero. Although developmental time was clearly reduced and
256 growth rate was enhanced, an expected hind leg elongation similar to that found with
257 increasing resources, was only found for ranid frogs (*Rana cascadae*, Blouin & Brown
258 2000, and *R. lessonae*, Orizaola & Laurila 2009) whereas a shortening in hind legs was
259 found for the rest of species. This contrasting pattern may reflect a phylogenetic signal
260 although the small sample size (six species) precludes any power in the statistical analysis
261 of phylogenetic autocorrelation (Abouheif et al. 1999). Therefore, more information is
262 required to depict a general trend of temperature effect on hind legs in amphibians and its
263 proximate mechanisms.

264 Exposure to predation risk during larval development promoted changes in
265 allometric shape of metamorphs. High predation risk generally induces shorter relative hind
266 legs. In the present study the data are highly consistent with the exception of the longer
267 hind legs of *Rana sylvatica* frogs emerging from predator treatment (Relyea 2001). This
268 disparity may be explained by the high growth rates exhibited by this species (*R. sylvatica*
269 raised with predators metamorphoses later but at similar size), contrasting with other
270 species which exhibit a strong reduction in growth rates (see Annex I, Fig. 1).

271 Desiccation risk induced a plastic acceleration of developmental rate, with a parallel
272 decline in growth rates and size at metamorphosis. Pond desiccation poses a strong time
273 constraint for development of larval amphibians. The increase in developmental rate and
274 reduction in growth rate is the common response to pond desiccation expressed by larval
275 anurans both at the intraspecific and interspecific level (Brady & Griffiths 2000, Leips et al.
276 2000, Merilä et al. 2004, Richter-Boix et al. 2006b, Richter-Boix, Tejedo and Rezende,

277 unpublished data). The consequences of pond desiccation on allometric shape seem to be a
278 decrease in relative hind legs, although this effect was not significant, probably due to the
279 small sample size (five contrasts for three species). However, we propose that this trend is
280 general as other studies have reported shorter hind legs under pond desiccation risk, for
281 example, in *Scaphiopus couchii* (Newman 1989) and *Rhinella spinulosa* (Márquez-García
282 et al. 2009).

283 Plasticity of hind leg length and head shape was of relatively low or moderate
284 magnitude, especially if compared with plasticity in development, growth rate, or mass at
285 metamorphosis. Therefore, the direct consequences for fitness will require further testing.
286 Interspecific comparisons have suggested that an increase of at least 10% in leg length is
287 needed to have a substantial influence on locomotion (Zug 1972, Emerson 1978). In fact,
288 several recent morphofunctional analyses, where the relative hind leg lengths were
289 experimentally manipulated, have revealed that a small (1-2%) increase of relative hind leg
290 length did not result in a significantly enhanced locomotor performance (Van Buskirk &
291 Saxer 2001, Richter-Boix et al. 2006a; see Annex I). By contrast, a larger increase of
292 relative hind leg length in *R. esculenta* (7.2 %) and *P. punctatus* (8.8 %) under high
293 resource availability (Annex I) determined a concomitant increase of 32.4 % and 34 % in
294 size-adjusted maximum jumping distance, respectively (Tejedo et al. 2000, M. Tejedo, F.
295 Marangoni & C. Pertoldi, unpublished data). Similarly, increases in relative leg length (5.8
296 - 10.3 %) in warm larval environments in *Rana lessonae* populations, increased relative
297 jumping performance by 15.1 - 29.4 % in two out of three studied populations (Orizaola &
298 Laurila 2009). These latter studies suggest that environmentally induced allometries in hind
299 leg length may have important consequences on performance, once a minimum amount of

hind leg elongation is attained. Therefore, we can expect that any small advantage may be selectively important considering the intense predation that amphibians suffer especially during metamorphosis and early juvenile life (Arnold & Wassersug, 1978). Recent studies have found that population variation in relative hind leg length correlates with locomotor performance (Ficetola et al. 2006, Phillips et al. 2006). The role that plasticity induced during the larval phase may play in driving this adaptive divergence (e.g. through genetic assimilation) deserves more research (Gómez-Mestre & Buchholtz 2006, Wund et al. 2008).

In general, plasticity of shape in juvenile frogs across environments is dependent on variation in either developmental and/or growth rate plasticities. Environments promoting higher larval growth rates produce juvenile frogs with relatively longer hind legs and wider heads. Poor growing environments, contrarily, will produce stumpy juveniles with relatively poor jumping performance. However the pattern of integration of developmental rates with postmetamorphic morphology differs between traits. Environmentally induced variation in developmental rates translated in changes in relative head size, but not on relative hind leg length. The variation in elongation of hind leg length at metamorphosis was only affected by variation in growth rates. This conclusion agrees with an experiment designed to tease apart both growth and developmental rate by altering larval growth rates while keeping the pace of developmental rate unchanged. The results (M. Tejedo, F. Marangoni & C. Pertoldi, unpublished data) revealed that the treatment where larval growth was diminished at late pre-metamorphosis (33-34 Gosner stage) resulted in similar developmental rates as in the control but, in contrast to expectations, overall size and relative hind legs were smaller than the control. As a result, and coincident with our

analyses, final hind leg shape was more dependent on variations in growth rates than on variation in developmental rate.

A final consideration is the persistence of the plasticity: whether the level of plasticity found in hind leg length and head width at metamorphosis can be relatively transient and disappear during the early juvenile growth. In holometabolous insects, the morphological effects of larval and pupae environments on adults are fixed (Boggs 1981). However, environmentally induced changes in amphibians may not be permanent and concomitant to their fitness consequences. In reptiles, duration of thermally induced allometries is short (Shine et al. 1997, Elphick & Shine 1998). This may be the general pattern also in amphibians as found in two pelodytids (*Pelodytes punctatus* and *P. ibericus*; M. Tejedo, F. Marangoni & C. Pertoldi, unpublished data) and one pelobatid frog (*Pelobates cultripes*; M. Tejedo & I. Gomez-Mestre, unpublished). Consequently, compensatory growth processes can result in a more canalised phenotype during the adult stage (Emerson 1986). Thus, in terms of fitness, the biological significance of the developmental plasticity for hind leg shape found at metamorphosis may be time-limited.

Global warming will probably increase both air temperature and decrease rainfall amount in many areas of the world (IPCC 2007) which indirectly will determine increasing pond desiccation rates. As our results suggest, increased temperature and pond desiccation risk during anuran larval phase can be predicted to produce smaller-headed and possibly more shorter-legged frogs. However, climate change is also going to affect resource availability, primary production, competition and predation risk in unpredictable ways. These effects are going to be highly system-specific and therefore, the effects of global warming on froglet morphology and fitness are difficult to predict.

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	Hind leg length	Head width	Developmental time	Mass at metamorphosis	Growth rate
Plasticity index	*Mean (SE) N*	*Mean (SE) N*	*Mean (SE) N*	*Mean (SE) N*	*Mean (SE) N*
Resources	+5.27 (0.85) 17	+1.43 (1.46) 16	-16.18 (4.61) 17	+82.65 (15.54) 17	+122.97 (15.67) 17
Temperature	+0.96 (1.37) 11	-4.24 (1.61) 11	-38.22 (4.41) 11	-11.95 (4.76) 11	+53.61 (16.63) 11
Predation risk	-1.89 (0.76) 10	-0.92 (0.92) 9	+5.89 (3.66) 9	-8.86 (3.33) 11	-17.36 (5.13) 9
Desiccation risk	-1.14 (1.18) 5	+2.38 (3.86) 5	-7.81 (2.04) 5	-17.41 (5.99) 5	-11.27 (6.22) 5
Effect sizes	*d (95 % bias CI) N*	*d (95 % bias CI) N*	*d (95 % bias CI) N*	*d (95 % bias CI) N*	*d (95 % bias CI) N*
Resources	+1.02 (+0.75, +1.29) 16	+0.09 (-0.36, +0.45) 16	-1.87 (-2.88,-0.82) 16	+3.36 (+2.39,+4.54) 16	+4.17 (+3.23,+5.26) 16
Temperature	+0.17 (-0.21, +0.60) 11	-0.56 (-1.08,-0.07) 11	-10.24 (-16.28,-6.25) 11	-3.41 (-7.47,-0.95) 11	+2.78 (+0.03,+4.79) 11
Predation risk	-0.35 (-0.48, -0.17) 8	-0.11 (-0.35,+0.25) 8	+0.70 (+0.04,+1.55) 9	-1.02 (-2.01,-0.31) 8	-1.01 (-2.48,-0.43) 8
Desiccation risk	-0.13 (-0.39, +0.06) 5	+0.20 (-0.46,+1.19) 5	-0.68 (-0.96,-0.49) 5	-0.88 (-1.46,-0.36) 5	-0.58 (-1.36,-0.06) 5

Table 1. The numbers present the mean, standard error (SE) and sample size of the plasticity index (%, see main text) and Hedges' d effect sizes (*d*), bias-corrected 95 % bootstrap confidence intervals (95 % bias CI) and sample size (N) from a meta-analysis, of size-adjusted hind leg length, size-adjusted head width, developmental time, mass at metamorphosis and growth rates in amphibians at the metamorphosis, at different experimental conditions during the larval phase. Positive values of plasticity index and effect sizes indicate that the trait increases at the High environments (high temperature or resource level, presence of desiccation or predation risk), whereas a negative value indicates that the increase occurred at the Low environments (low temperatures or resource level, no risk of desiccation or predation).

Species Treatment (References)	Hind leg † x ± SD, N (high/low)	Head width‡ x ± SD, N (high/low)	Developmental time (days) x ± SD, N (high/low)	Mass at metamorphosis (g)§ x ± SD, N (high/low)	Growth rate x ± SD, N (high/low)	Hind leg plasticity % d ± var	Head width plasticity % d ± var	Time plasticity % d ± var	Mass plasticity % d ± var	Growth plasticity % d ± var
Xenopus laevis RES (1)	27.45 ± 1.79, 30[H] 25.95 ± 1.76, 29	5.88 ± 0.44, 30 5.95 ± 0.44, 29	40.43 ± 3.29, 30 50.03 ± 3.28, 29	0.12 ± 0.02, 30 0.04 ± 0.02, 29	0.0300 ± 0.0049, 30 0.0085 ± 0.0048, 29	5.82* 0.84 ± 0.07	-1.19 -0.16 ± 0.07	-19.19 -2.88 ± 0.14	189.58 4.59 ± 0.25	252.94 4.34 ± 0.23
Discoglossus galganoi RES (2)	5.51 ± 0.19, 5[T] 5.55 ± 0.19, 5	4.57 ± 0.24, 35 4.65 ± 0.24, 35	56.89 ± 2.68, 5 68.02 ± 4.25, 5	0.39 ± 0.01, 5 0.34 ± 0.03, 5	0.0037 ± 0.0003, 5 0.0027 ± 0.0004, 5	-0.76 -0.21 ± 0.40	-1.75 -0.34 ± 0.06	-16.37 -2.83 ± 0.80	15.48 2.34 ± 0.67	40.51 2.69 ± 0.76
Discoglossus galganoi RES (2)	5.74 ± 0.26. 5[T] 5.81 ± 0.26, 5	4.73 ± 0.30, 35 4.48 ± 0.30, 35	51.23 ± 3.95, 5 57.26 ± 4.17, 5	0.49 ± 0.03, 5 0.32 ± 0.01, 5	0.0065 ± 0.0005, 5 0.0030 ± 0.0002, 5	-1.11 -0.22 ± 0.40	5.54* 0.81 ± 0.06	-10.54 -1.34 ± 0.49	52.00 7.24 ± 3.02	118.06 7.81 ± 3.45
Discoglossus pictus RES (3)	17.28 ± 0.18, 3[H] 16.70 ± 0.18, 3	4.81 ± 0.09, 3 4.82 ± 0.09, 3	44.36 ± 2.72, 3 48.64 ± 2.43, 3	0.18 ± 0.04, 3 0.17 ± 0.01, 3	0.0041 ± 0.0009, 3 0.0034 ± 0.0003, 3	3.45* 2.63 ± 1.24	-0.22 -0.09 ± 0.67	-8.80 -1.33 ± 0.81	9.00 0.36 ± 0.68	19.99 0.81 ± 0.72
Pelobates cultripes RES (4)	25.30 ± 1.56, 52[H] 23.72 ± 1.52, 79	7.90 ± 0.49, 52 8.38 ± 0.48, 79	84.77 ± 22.82, 53 129.04 ± 29.79, 89	1.24 ± 0.47, 52 0.85 ± 0.24, 79	0.0147 ± 0.0037, 52 0.0072 ± 0.0029, 79	6.67* 1.03 ± 0.04	-5.78* -0.99 ± 0.04	-34.31 -1.61 ± 0.04	45.96 1.11 ± 0.04	103.50 2.32 ± 0.05
Pelobates cultripes RES (5)	35.17 ± 1.70, 264[H] 34.27 ± 1.70, 297	10.20 ± 0.60, 267 10.24 ± 0.60, 297	157.98 ± 9.33, 270 165.57 ± 9.39, 301	2.14 ± 0.39, 264 1.57 ± 0.40, 297	0.0137 ± 0.0027, 264 0.0095 ± 0.0027, 297	2.62* 0.53 ± 0.01	-0.43 -0.07 ± 0.01	-4.58 -0.81 ± 0.01	36.37 1.44 ± 0.01	43.51 1.55 ± 0.01
Pelodytes punctatus RES (6)	20.29 ± 1.12, 124[H] 18.59 ± 1.11, 130	4.01 ± 0.39, 117 4.42 ± 0.39, 123	51.18 ± 4.66, 131 89.43 ± 11.06, 126	0.25 ± 0.03, 132 0.17 ± 0.02, 124	0.0049 ± 0.0006, 124 0.0019 ± 0.0002, 130	9.15* 1.52 ± 0.02	-9.23* -1.05 ± 0.02	-42.77 -4.52 ± 0.06	49.60 3.25 ± 0.04	161.67 7.18 ± 0.12
Pelodytes punctatus RES (7)	21.82 ± 0.88, 98[H] 20.05 ± 0.91, 79	4.88 ± 0.25, 98 4.60 ± 0.26, 78	38.38 ± 3.39, 100 58.51 ± 6.36, 96	0.21 ± 0.02, 98 0.17 ± 0.02, 79	0.0054 ± 0.0004, 98 0.0030 ± 0.0003, 79	8.82* 1.98 ± 0.03	6.23* 1.11 ± 0.03	-34.40 -3.96 ± 0.06	21.03 1.80 ± 0.03	82.14 6.94 ± 0.16
Pelodytes ibericus RES (7)	20.70 ± 0.83, 115[H] 19.34 ± 0.83, 110	5.17 ± 0.20, 115 5.43 ± 0.20, 110	44.98 ± 3.11, 115 66.24 ± 7.29, 115	0.18 ± 0.02, 115 0.15 ± 0.02, 110	0.0040 ± 0.0003, 115 0.0023 ± 0.0002, 110	7.00* 1.63 ± 0.02	-4.76* -1.30 ± 0.02	-32.10 -3.78 ± 0.05	19.57 1.54 ± 0.02	74.49 6.19 ± 0.10
Agalychnis callidryas RES (1)	33.38 ± 2.93, 28[H] 30.60 ± 3.59, 17	6.86 ± 0.57, 28 6.27 ± 0.48, 17	36.39 ± 5.77, 28 60.93 ± 5.57, 17	0.09 ± 0.02, 28 0.05 ± 0.02, 17	0.0250 ± 0.0074, 28 0.0075 ± 0.0070, 17	9.06* 0.85 ± 0.10	9.49* 1.08 ± 0.11	-40.28 -4.23 ± 0.29	94.15 1.90 ± 0.13	233.33 2.37 ± 0.16
Hyla cinerea RES (8)	9.79 ± 0.69, 20[T] 9.58 ± 0.63, 25	6.38 ± 0.68, 27 6.74 ± 0.71, 25	36 64.5	24 § 16	?	2.18 0.31 ± 0.09	-5.35 -0.51 ± 0.08	-44.19	50.00	168.75
Hyla versicolor RES (9)	?	?	43.76 ± 0.49, 5 48.08 ± 0.72, 5	0.38, 5 0.20, 5	0.0088 ± 0.0003, 5 0.0042 ± 0.0002, 5	2.00*	?	-8.99 -6.38 ± 2.44	92.51	111.54 17.25±15.28

Species Treatment (Reference)	Hind leg †	Head width‡	Developmental time (days)	Mass at metamorphosis (g)§	Growth rate	Hind leg plasticity	Head width plasticity	Time plasticity	Mass plasticity	Growth plasticity
	x ± SD, N (high/low)	x ± SD, N (high/low)	x ± SD, N (high/low)	x ± SD, N (high/low)	x ± SD, N (high/low)	% d ± var	% d ± var	% d ± var	% d ± var	% d ± var
Pelophylax esculenta RES (10)	31.97 ± 2.05, 65 [H] 29.83 ± 1.95, 75	8.03 ± 0.73, 49 7.82 ± 0.72, 52	47.75 ± 4.34, 65 48.44 ± 4.44, 75	0.96 ± 0.15, 65 0.41 ± 0.10, 75	0.0203 ± 0.0037, 65 0.0085 ± 0.0022, 75	7.16* 1.06 ± 0.03	2.58* 0.28 ± 0.04	-1.42 -0.16 ± 0.03	135.96 4.51 ± 0.10	138.73 3.98 ± 0.09
Pelophylax esculenta RES (10)	31.01 ± 1.79, 62 [H] 28.59 ± 1.73, 68	7.79 ± 0.75, 58 7.41 ± 0.71, 68	50.10 4.31, 62 51.27 ± 4.65, 68	0.86 ± 0.12, 62 0.34 ± 0.07, 68	0.0173 ± 0.0032, 62 0.0067 ± 0.0017, 68	8.43* 1.36 ± 0.04	5.09* 0.51 ± 0.03	-2.28 -0.26 ± 0.03	153.98 5.33 ± 0.14	157.59 4.14 ± 0.10
Pelophylax esculenta RES (10)	31.78 ± 1.82, 65 [H] 29.51 ± 1.82, 65	7.96 ± 0.57, 65 7.49 ± 0.59, 57	55.19 ± 3.75, 65 47.61 ± 4.66, 65	0.84 ± 0.13, 65 0.39 ± 0.06, 65	0.0153 ± 0.0026, 65 0.0082 ± 0.0017, 65	7.70* 1.24 ± 0.04	6.32* 0.81 ± 0.04	15.92 1.78 ± 0.04	117.54 4.48 ± 0.11	86.39 3.20 ± 0.07
Pelophylax lessonae RES (10)	28.47 ± 2.80, 26 [H] 26.08 ± 1.83, 80	7.66 ± 0.98, 26 7.01 ± 0.70, 58	54.69 ± 6.65, 26 47.61 ± 6.35, 81	0.89 ± 0.09, 28 0.35 ± 0.05, 82	0.0166 ± 0.0026, 26 0.0076 ± 0.0020, 80	9.15* 1.13 ± 0.06	9.24* 0.80 ± 0.06	14.89 1.10 ± 0.06	155-33 8.75 ± 0.40	119.05 4.14 ± 0.13
Pelophylax ridibunda RES (10)	32.51 ± 2.08, 38 [H] 31.77 ± 2.17, 34	7.78 ± 0.64, 38 7.26 ± 0.67, 34	60.21 ± 4.05, 38 63.83 ± 4.88, 35	0.93 ± 0.18, 38 0.35 ± 0.08, 35	0.0156 ± 0.0030, 38 0.0056 ± 0.0018, 34	2.30 0.34 ± 0.06	7.08* 0.78 ± 0.06	-5.67 -0.80 ± 0.06	167.07 4.12 ± 0.17	178.35 3.89 ± 0.16
Xenopus laevis TEM (1)	26.62 ± 1.39, 26 [H] 27.35 ± 1.51, 27	5.67 ± 0.32, 26 5.55 ± 0.32, 27	29.58 ± 3.77, 26 53.63 ± 3.79, 27	0.07 ± 0.02, 26 0.06 ± 0.02, 27	0.0230 ± 0.0051, 26 0.0120 ± 0.0052, 27	-2.66* -0.49 ± 0.08	2.15 0.37 ± 0.08	-44.84 -6.26 ± 0.45	7.28 0.26 ± 0.08	91.67 2.10 ± 0.12
Scaphiopus holbrooki TEM (11)	25.06 ± 2.64, 47 [H] 25.63 ± 2.50, 50	2.19 ± 0.58, 47‡ 2.19 ± 0.53, 50	16.02 ± 3.17, 47 21.90 ± 2.47, 50	12.41 ± 1.30, 47 § 13.22 ± 1.29, 50	0.7790 ± 0.0993, 47 0.6290 ± 0.0289, 50	-2.23* -0.22 ± 0.04	-0.33 -0.01 ± 0.04	-26.83 -2.06 ± 0.06	-6.09 -0.62 ± 0.04	23.85 2.06 ± 0.06
Spea mutiplicata TEM (11)	26.34 ± 1.02, 6 [H] 26.72 ± 1.02, 15	2.84 ± 0.17, 6‡ 2.91 ± 0.19, 15	16.02 ± 0.53, 6 28.15 ± 1.54, 15	18.02 ± 1.29, 6 § 19.13 ± 1.29, 15	1.2960 ± 0.0644, 6 0.7380 ± 0.0577, 15	-1.42 -0.36 ± 0.24	-2.35 -0.36 ± 0.24	-43.08 -8.61 ± 2.00	-5.80 -0.82 ± 0.25	75.61 9.00 ± 2.16
Spea intermontana TEM (12)	26.74 ± 1.01, 12 [H] 27.35 ± 0.97, 14	2.60 ± 0.19, 12‡ 2.67 ± 0.21, 14	22.72 ± 1.04, 12 30.91 ± 0.98, 14	19.29 ± 1.29, 12 § 21.12 ± 1.29, 14	0.8340 ± 0.0520, 12 0.6730 ± 0.0569, 14	-2.22* -0.60 ± 0.16	-2.69 -0.34 ± 0.16	-26.49 -7.88 ± 1.35	-8.67 -1.37 ± 0.19	23.92 2.85 ± 0.31
Pelobates cultripes TEM (12)	30.14 ± 1.09, 6 [H] 30.42 ± 1.08, 9	3.07 ± 0.25, 6‡ 3.43 ± 0.25, 9	36.13 ± 4.73, 6 42.42 ± 4.74, 9	24.17 ± 1.06, 6 § 25.17 ± 1.58, 9	0.5610 ± 0.0414, 6 0.5520 ± 0.0749, 9	-0.94 -0.25 ± 0.28	-10.67* -1.38 ± 0.34	-14.82 -1.25 ± 0.33	-3.99 -0.67 ± 0.29	1.63 0.13 ± 0.28
Agalychnis callidryas TEM (1)	32.66 ± 2.54, 21 [H] 33.87 ± 2.38, 15	6.75 ± 0.45, 21 7.15 ± 0.45, 15	29.21 ± 3.30, 21 49.53 ± 3.14, 15	0.08 ± 0.01, 21 0.07 ± 0.01, 15	0.0262 ± 0.0037, 21 0.0140 ± 0.0035, 15	-3.57* -0.48 ± 0.12	-5.58* -0.87 ± 0.12	-41.03 -6.14 ± 0.64	8.39 0.59 ± 0.12	87.14 3.32 ± 0.27
Rana cascadae TEM (12)	8.75 ± 0.38, 24 [T] 8.49 ± 0.30, 23	6.29 ± 0.21, 24 6.18 ± 0.21, 23	24.57 ± 1.56, 22 57.45 ± 2.06, 22	0.78 ± 0.10, 22 0.86 ± 0.11, 22	0.0318 ± 0.0039, 22 0.0149 ± 0.0017, 22	3.05* 0.74 ± 0.09	1.80 0.52 ± 0.09	-57.23 -17.64 ± 3.63	-8.70 -0.69 ± 0.10	114.18 5.59 ± 0.45

Species Treatment (Reference)	Hind leg †	Head width‡	Developmental time (days)	Mass at metamorphosis (g)§	Growth rate	Hind leg plasticity	Head width plasticity	Time plasticity	Mass plasticity	Growth plasticity
	x ± SD, N (high/low)	x ± SD, N (high/low)	x ± SD, N (high/low)	x ± SD, N (high/low)	x ± SD, N (high/low)	% d ± var	% d ± var	% d ± var	% d ± var	% d ± var
Pelophylax lessonae TEM (13)	7.20 ± 0.40, 75 [T] 6.80 ± 0.50, 106	0.89 ± 0.14, 106 0.91 ± 0.04, 75	32.81 ± 0.60, 106 49.31 ± 0.48, 75	0.61 ± 0.01, 106 0.82 ± 0.02, 75	0.0338 ± 0.0010, 106 0.0280 ± 0.0004, 75	5.88* 0.86 ± 0.02	-2.20 -0.18 ± 0.02	-33.46 -29.68 ± 2.46	-25.61 -13.97 ± 0.56	21.00 7.42 ± 0.17
Pelophylax lessonae TEM (13)	7.50 ± 0.70, 13 [T] 6.80 ± 0.40, 77	0.84 ± 0.05, 77 0.95 ± 0.06, 13	44.41 ± 0.91, 77 67.88 ± 1.31, 13	0.60 ± 0.02, 77 0.94 ± 0.06, 13	0.0240 ± 0.0005, 77 0.0228 ± 0.0008, 13	10.29* 1.53 ± 0.10	-11.58* -2.12 ± 0.11	-34.58 -23.88 ± 3.26	-36.17 -11.66 ± 0.84	5.36 2.19 ± 0.12
Pelophylax lessonae TEM (13)	7.30 ± 0.60, 15 [T] 6.90 ± 0.50, 60	0.85 ± 0.05, 60 0.98 ± 0.10, 15	42.95 ± 0.64, 60 62.60 0.90, 15	0.59 ± 0.01, 60 0.98 ± 0.02, 15	0.0235 ± 0.0004, 60 0.0274 ± 0.0006, 15	5.80* 0.76 ± 0.09	-13.27* -2.05 ± 0.11	-31.39 -27.89 ± 5.27	-39.80 -30.75 ± 6.39	-14.22 -8.15 ± 0.53
Rana temporaria TEM (14)	4.84 ± 0.45, 64 [T] 4.91 ± 0.45, 61	6.03 ± 0.54, 64 6.14 ± 0.54, 61	45.86 ± 3.28, 64 137.51 ± 17.23, 61	0.41 ± 0.06, 64 0.47 ± 0.07, 61	0.0090 ± 0.0012, 64 0.0035 ± 0.0006, 61	-1.44 -0.16 ± 0.03	-1.89 -0.22 ± 0.03	-66.65 -7.43 ± 0.25	-12.31 -0.90 ± 0.04	159.57 5.55 ± 0.16
Discoglossus galganoi PRE (2)	5.87 ± 0.23, 35 [T] 5.98 ± 0.23, 35	4.78 ± 0.28, 35 4.80 ± 0.28, 35	56.89 ± 2.68, 5 51.23 ± 3.95, 5	0.39 ± 0.01, 5 0.49 ± 0.03, 5	0.0037 ± 0.0003, 5 0.0065 ± 0.0005, 5	-1.83* -0.48 ± 0.06	-0.45 -0.08 ± 0.06	11.05 1.51 ± 0.51	-19.30 -4.33 ± 1.34	-42.43 -6.09 ± 2.26
Discoglossus galganoi PRE (2)	5.32 ± 0.19, 5 [T] 5.45 ± 0.19, 5	4.53 ± 0.22, 35 4.33 ± 0.22, 35	68.02 ± 4.25, 5 57.26 ± 4.17, 5	0.34 ± 0.03, 5 0.32 ± 0.01, 5	0.0027 ± 0.0004, 5 0.0030 ± 0.0002, 5	-2.40* -0.64 ± 0.42	4.65* 0.92 ± 0.06	18.78 2.31 ± 0.67	6.22 0.84 ± 0.44	-10.66 -0.80 ± 0.43
Pelobates cultripes PRE (15)	37.94 ± 1.46, 153 [H] 37.86 ± 1.61, 149	10.24 ± 0.43, 152 10.37 ± 0.47, 146	201.86 ± 8.77, 161 206.78 ± 9.66, 156	2.09 ± 0.64, 153 2.47 ± 0.71, 149	0.0104 ± 0.0032, 153 0.0120 ± 0.0036, 149	0.22 0.06 ± 0.01	-1.33* -0.31 ± 0.01	-2.38 -0.53 ± 0.01	-15.31 -0.56 ± 0.01	-13.23 -0.47 ± 0.01
Pelobates cultripes PRE (16)	10.19 ± 0.99, 34 [T] 10.49 ± 0.77, 35	11.36 ± 0.70, 34 11.57 ± 0.71, 35	166.58 ± 11.87, 34 163.22 ± 16.68, 35	1.58 ± 0.38, 34 1.61 ± 0.44, 35	0.0095 ± 0.0021, 34 0.0098 ± 0.0024, 35	-2.85* -0.33 ± 0.06	-1.84* -0.30 ± 0.06	2.06 0.23 ± 0.06	-1.88 -0.07 ± 0.06	-3.77 -0.16 ± 0.06
Pelobates cultripes PRE (16)	10.11 ± 0.69, 32 [T] 10.45 ± 0.88, 41	11.90 ± 0.63, 32 11.84 ± 0.70, 41	180.65 ± 11.89, 32 172.40 ± 11.89, 41	2.02 ± 0.38, 32 2.41 ± 0.38, 40	0.0112 ± 0.0021, 32 0.0140 ± 0.0021, 40	-3.31* -0.43 ± 0.06	0.50 0.09 ± 0.06	4.79 0.69 ± 0.06	-16.09 -1.00 ± 0.06	-20.27 -1.33 ± 0.07
Hyla versicolor PRE (9)	?	?	46.16 ± 0.71, 5 45.68 ± 0.49, 5	0.29, 5 0.30, 5	0.0065 ± 0.0003, 5 0.0065 ± 0.0002, 5	?	?	1.05 0.71 ± 0.43	-2.04	0.00 0.00 ± 0.40
Bufo calamita PRE (17)	2.57 ± 0.19, 48 [T] 2.61 ± 0.19, 43	3.66 ± 0.19, 50 3.75 ± 0.19, 44	41.29 ± 5.02, 50 44.25 ± 5.02, 44	0.05 ± 0.01, 50 0.06 ± 0.01, 44	0.0013 ± 0.0003, 50 0.0015 ± 0.0003, 44	-1.50* -0.21 ± 0.04	-2.23* -0.43 ± 0.04	-6.69 -0.59 ± 0.04	-16.96 -1.13 ± 0.05	-14.73 -0.79 ± 0.05
Bufo calamita PRE (17)	2.56 ± 0.18, 52 [T] 2.65 ± 0.18, 45	3.66 ± 0.19, 53 3.70 0.19, 47	44.62 ± 5.03, 53 45.72 ± 5.04, 48	0.06 ± 0.01, 53 0.06 ± 0.01, 48	0.0013 ± 0.0003, 53 0.0015 ± 0.0003, 48	-3.43* -0.49 ± 0.04	-1.17* -0.23 ± 0.04	-2.41 -0.22 ± 0.04	-11.19 -0.75 ± 0.04	-8.69 -0.44 ± 0.04

Species Treatment (Reference)	Hind leg (mm)†	Head width (mm)‡	Time to metamorphosis (days)	Mass at metamorphosis (g)§	Growth rate	Hind leg plasticity	Head width plasticity	Time plasticity	Mass plasticity	Growth plasticity
	x ± SD, N (high/low)	x ± SD, N (high/low)	x ± SD, N (high/low)	x ± SD, N (high/low)	x ± SD, N (high/low)	% d ± var	% d ± var	% d ± var	% d ± var	% d ± var
Rana temporaria PRE (18)	5.68 ± 0.53, 7 [T] 6.01 ± 0.48, 7	4.20 ± 0.37, 7 4.47 ± 0.37, 7	75.31 ± 4.86, 7 59.39 ± 5.40, 7	0.27 ± 0.04, 7 0.36 ± 0.04, 7	0.0035, 7 0.0061, 7	-5.54* -0.62 ± 0.30	-5.92* -0.67 ± 0.30	26.81 2.90 ± 0.59	-27.00 -2.24 ± 0.46	-42.44
Pelophylax ridibunda PRE (19)	?	?	?	?	?	-1.20*	-0.52	?	?	?
Rana sylvatica PRE (20)	?	?	?	?	?	3.40*	?	?	?	?
Pelobates cultripes DES (16)	10.19 ± 0.99, 34 [T] 10.11 ± 0.69, 32	11.36 ± 0.70, 34 11.90 ± 0.63, 32	166.58 ± 11.87, 34 180.65 ± 11.89, 32	1.58 ± 0.38, 34 2.02 ± 0.38, 32	0.0095 ± 0.0021, 34 0.0112 ± 0.0021, 32	0.85 0.10 ± 0.06	-4.53* -0.79 ± 0.07	-7.79 -1.17 ± 0.07	-21.72 -1.13 ± 0.07	-15.32 -0.80 ± 0.07
Pelobates cultripes DES (16)	10.49 ± 0.77, 35 [T] 10.45 ± 0.88, 41	11.57 ± 0.71, 35 11.84 ± 0.70, 41	163.22 ± 16.68, 35 172.40 ± 11.89, 41	1.61 ± 0.44, 35 2.41 ± 0.38, 40	0.0098 ± 0.0024, 35 0.0140 ± 0.0021, 40	0.37 0.05 ± 0.05	-2.26* -0.38 ± 0.05	-5.32 -0.64 ± 0.06	-33.06 -1.92 ± 0.08	-29.83 -1.84 ± 0.08
Pelodytes punctatus DES (21)	5.32 ± 0.51, 36 [T] 5.63 ± 0.50, 28	5.81 ± 0.42, 26 4.95 ± 0.41, 38	62.93 ± 17.75, 28 74.28 ± 17.75, 36	0.16 ± 0.04, 26 0.21 ± 0.06, 38	0.0026 ± 0.0010, 36 0.0031 ± 0.0010, 28	-1.12* -0.61 ± 0.07	0.90* 2.04 ± 0.10	-15.28 -0.63 ± 0.07	-24.94 -0.93 ± 0.07	-15.81 -0.50 ± 0.07
Bufo calamita DES (17)	2.57 ± 0.19, 48 [T] 2.56 ± 0.18, 52	3.66 ± 0.19, 50 3.66 ± 0.19, 53	41.29 ± 5.02, 50 44.62 ± 5.03, 53	0.05 ± 0.01, 50 0.06 ± 0.01, 53	0.0013 ± 0.0003, 50 0.0013 ± 0.0003, 53	0.31 0.04 ± 0.04	0.14 0.03 ± 0.04	-7.46 -0.66 ± 0.04	-6.90 -0.41 ± 0.04	-1.21 -0.06 ± 0.04
Bufo calamita DES (17)	2.61 ± 0.19, 43 [T] 2.65 ± 0.18, 45	3.75 ± 0.19, 44 3.70 ± 0.19, 47	44.25 ± 5.02, 44 45.72 ± 5.04, 48	0.06 ± 0.01, 44 0.06 ± 0.01, 48	0.0015 ± 0.0003, 44 0.0015 ± 0.0003, 48	-1.66* -0.24 ± 0.05	1.23 0.24 ± 0.04	-3.22 -0.29 ± 0.04	-0.43 -0.03 ± 0.04	5.79 0.29 ± 0.04

Annex I Dataset

Size-adjusted hind leg length and head width, developmental time, mass at metamorphosis and growth rates in amphibians at the metamorphosis at different experimental conditions during the larval phase: RES: Resource level; TEM: temperature; PRE: predation risk, DES: Desiccation risk. High and Low indicates values for “high” levels of resources and temperatures and presence of non-lethal predators and pond

desiccation; “low” indicates low levels of resources and temperatures and absence of either predation risk or pond desiccation risk. Data are expressed as mean ± 1 Standard Deviation. Plasticity in size-adjusted hind leg, size-adjusted head width, time to metamorphosis, mass at metamorphosis and growth rate was expressed both by a plasticity index (%, see text) and by Hedges’ d effect sizes (d), expressed as mean d ± variance from meta-analysis. *Comparison of either relative hind leg length or head width reported as significant in original paper or unpublished study. †: ^{T}: Tibio-fibula length, ^{H}:Total hind leg length. ‡: Size-adjusted head snout length. §: Snout vent length (mm). ?: Information unknown or not provided.

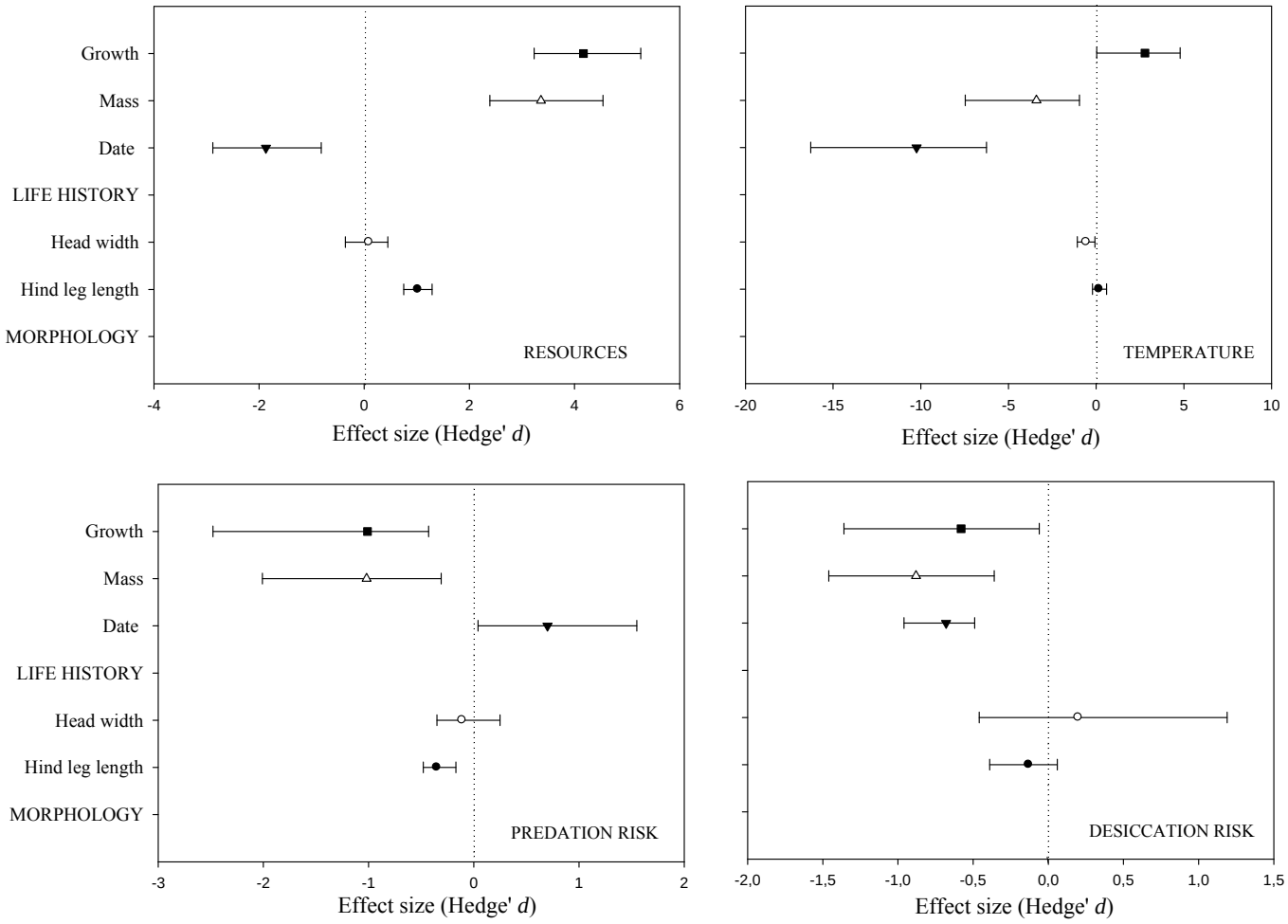
References: (1) Gómez-Mestre et al. (unpublished), (2) Nicieza et al. (2006), (3) Richter-Boix, Llorente , Franch and Montori (unpublished), (4) Tejedo and Gómez-Mestre (unpublished), (5) Marangoni and Tejedo (unpublished), (6) Tejedo, Sánchez-Herráiz, Pertoldi and Marangoni (unpublished), (7) Tejedo, Marangoni, Pertoldi (unpublished), (8) Blouin and Loeb (1991), (9) Relyea and Hoverman (2003), (10) Tejedo, Semlitsch and Hotz (2000a, b unpublished), (11) Gómez-Mestre and Buchholz (2006, unpublished), (12) Blouin and Brown (2000), (13) Orizaola and Laurila (2009, unpublished), (14) Nicieza et al. (unpublished), (15) Tejedo, Cruz, Rebelo and Marangoni (unpublished), (16) Tejedo, Graciá and Iriarte (unpublished), (17) Tejedo, Iriarte and Graciá (unpublished), (18) Capellán and Nicieza (2007), (19) Van Buskirk and Saxer (2001), (20) Relyea (2001), (21) Richter-Boix, et al. (2006, unpublished).

FIGURE LEGENDS

Figure 1. Mean effect sizes (Hedge's *d*) and bias-corrected bootstrapped 95% confidence intervals, for morphological (size-adjusted hind leg length and head width) and life history traits (date of metamorphosis, mass at metamorphosis and growth rates), in amphibians at the metamorphosis at different experimental conditions during the larval phase. Effects are statistically significant ($P < 0.05$) if confidence intervals excluded zero. Positive values of *d* indicate that the trait increases at the High environments (high temperature or resource level, presence of desiccation or predation risk), whereas a negative value indicates that the increase occurred at the Low environments (low temperatures or resource level, no risk of desiccation or predation).

Figure 2. Correlation between size- adjusted hind leg length plasticity and plasticity in either growth rate (a) ($r=0.52$, $P=0.0005$, $N=41$), or developmental time (b) ($r=-0.20$, $P=0.20$, $N=41$) in amphibians at the metamorphosis at different experimental conditions during the larval phase: RES: Resource level; TEM: temperature; PRE: predation risk, DES: Desiccation risk.

Figure 3. Correlation between size- adjusted head width plasticity and plasticity in either growth rate (a), ($r=0.35$, $P=0.027$, $N=40$) or developmental time (b) ($r=0.29$, $P=0.06$, $N=40$), in amphibians at the metamorphosis at different experimental conditions during the larval phase: RES: Resource level; TEM: temperature; PRE: predation risk, DES: Desiccation risk.


Growth
Mass
Date
LIFE HISTORY
Head width
Hind leg length
MORPHOLOGY
RESOURCES
-4
-2
0
2
4
6
Effect size (Hedge' d)
TEMPERATURE
-20
-15
-10
-5
0
5
10
Effect size (Hedge' d)
PREDATION RISK
-3
-2
-1
0
1
2
Effect size (Hedge' d)
DESICCATION RISK
-2,0
-1,5
-1,0
-0,5
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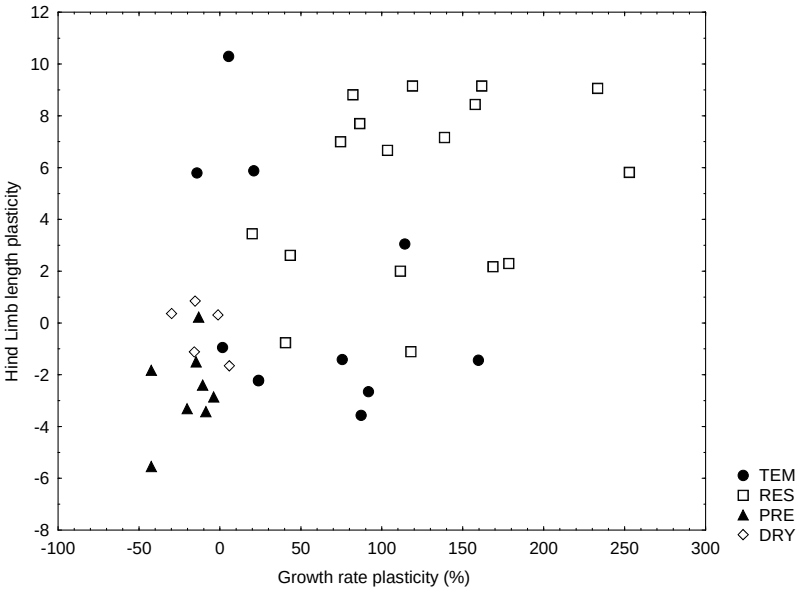
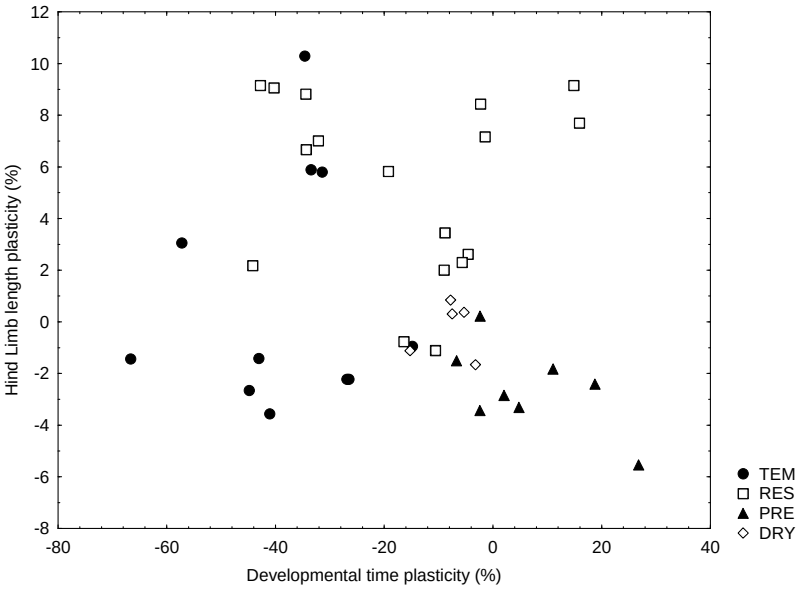
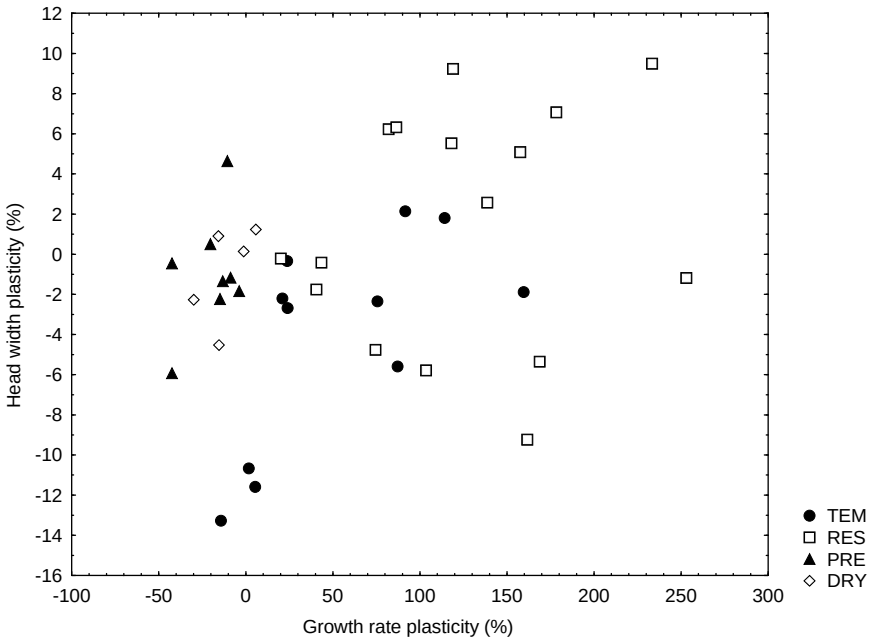
Effect size (Hedge' d)


Hind Limb length plasticity
Growth rate plasticity (%)
TEM
RES
PRE
DRY

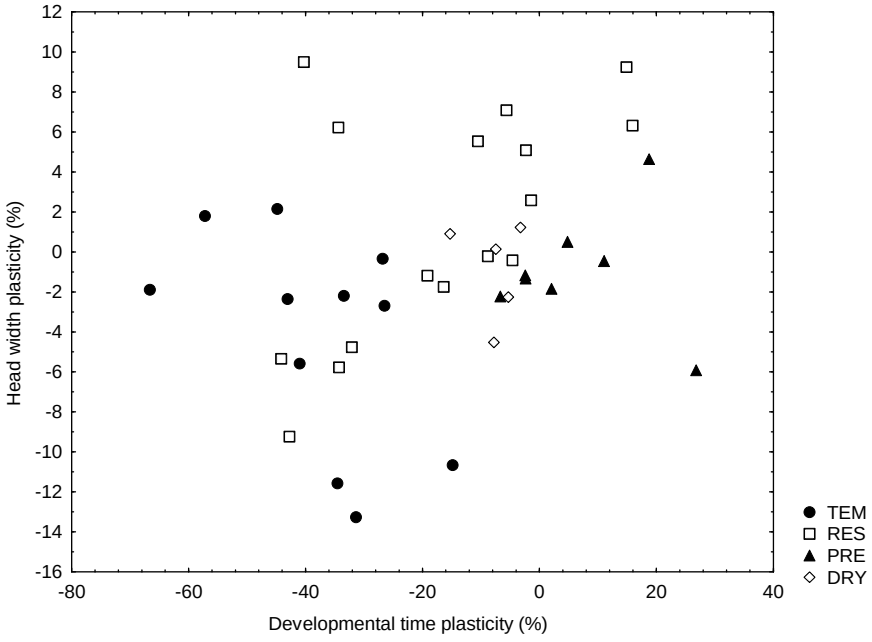
a


Hind Limb length plasticity (%)
Developmental time plasticity (%)
TEM
RES
PRE
DRY

b


Head width plasticity (%)
Growth rate plasticity (%)
TEM
RES
PRE
DRY

a


Head width plasticity (%)
Developmental time plasticity (%)
TEM
RES
PRE
DRY

b