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Spatial variation in abiotic and biotic factors in a floodplain determine anuran body size and growth rate at metamorphosis

Lukas Indermaur · Benedikt R. Schmidt ·
Klement Tockner · Michael Schaub

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Abstract Body size at metamorphosis is a critical trait in the life history of amphibians. Despite the wide-spread use of amphibians as experimental model organisms, there is a limited understanding of how multiple abiotic and biotic factors affect the variation in metamorphic traits under natural conditions. The aim of our study was to quantify the effects of abiotic and biotic factors on spatial variation in the body size of tadpoles and size at metamorphosis of the European common toad (*Bufo b. spinosus*). Our study population was distributed over the riverbed (active tract) and the fringing riparian forest of a natural floodplain. The riverbed had warm ponds with variable hydroperiod and few predators, whereas the forest had ponds with the opposite characteristics. Spatial variation in body size at

metamorphosis was governed by the interactive effects of abiotic and biotic factors. The particular form of the interaction between water temperature and intraspecific tadpole density suggests that abiotic factors laid the foundation for biotic factors: intraspecific density decreased growth only at high temperature. Predation and intraspecific density jointly reduced metamorphic size. Interspecific density had a negligible affect on body size at metamorphosis, suggesting weak inter-anuran interactions in the larval stage. Population density at metamorphosis was about one to two orders of magnitudes higher in the riverbed ponds than in the forest ponds, mainly because of lower tadpole mortality. Based on our results, we conclude that ponds in the riverbed appear to play a pivotal role for the population because tadpole growth and survival is best in this habitat.

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L. Indermaur (✉)
Department of Aquatic Ecology,
Swiss Federal Institute of Aquatic Science and Technology
(EAWAG), Überlandstrasse 133, 8600 Dübendorf, Switzerland
e-mail: lukas.indermaur@eawag.ch

L. Indermaur
Institute of Integrative Biology, Swiss Federal
Institute of Technology, 8092 Zurich, Switzerland

B. R. Schmidt
Institut für Evolutionsbiologie und Umweltwissenschaften,
Universität Zürich, Winterthurerstrasse 190,
8057 Zurich, Switzerland

B. R. Schmidt
KARCH, Passage Maximilien-de-Meuron 6,
2000 Neuchâtel, Switzerland

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K. Tockner
Leibniz-Institute of Freshwater Ecology and Inland Fisheries,
Müggelseedamm 310, 12587 Berlin, Germany

K. Tockner
Institute of Biology, Freie Universität Berlin,
Mueggelseedamm 310, 12587 Berlin, Germany

M. Schaub
Swiss Ornithological Institute, 6203 Sempach, Switzerland

M. Schaub
Institute of Ecology and Evolution–Conservation Biology,
University of Bern, Baltzerstrasse 6, 3012 Bern, Switzerland

Introduction

Size and growth are fundamental traits that control the performance of plants and animals (Stearns 1992). Such life history traits vary in time and space within and among populations because species occupy habitats that differ in both abiotic and biotic factors (Petranka 1984; Wellborn et al. 1996; Amézquita and Lüddecke 1999; Van Buskirk 2009). This spatiotemporal variation ultimately affects population growth, abundance and distribution (Savage et al. 2004; Loehle 2006). Variation in life history traits is predominantly studied along gradients formed by a single environmental factor, such as predation or altitude. In some instances, such simple environmental gradients explain the spatial phenotypic variation very well (Wellborn et al. 1996; Angilletta et al. 2004b), but many species live in places where multiple environmental gradients intersect (Van Buskirk 2009). Under these conditions, one factor may dominate over others, or environmental factors may reinforce each other or even cancel each other out (Laugen et al. 2003).

The aim of our study was to study phenotypic variation in amphibian body size and growth, two key life history traits, in a natural habitat with multiple environmental gradients. Amphibians have become model systems for the study of life history variation and the ecological determinants thereof, and several of these models have been successfully used to explain the variation in the life histories of other taxa with complex life histories (Alford and Harris 1988; Bradshaw and Johnson 1995; Twombly 1996; Moehrlin and Juliano 1998). The factors that determine variation in amphibian larval body size have been well explored experimentally, both in the laboratory and in outdoor mesocosms (Alford 1999).

Concern does exist, however, on whether experimental conditions appropriately reflect natural conditions (Skelly and Kiesecker 2001). For example, Skelly (2002) showed that density is an important predictor of amphibian size at metamorphosis in experimental settings, but this is not the case in natural ponds. Hence, quantifying and explaining variation in life history traits under natural conditions is essential for the feedback loop between field studies, experiments and theory (Werner 1998). Unfortunately, only a few studies have been performed to date that quantify the variation in body size of amphibians under natural conditions (Petranka 1984; Reading and Clarke 1999; Gray and Smith 2005; Van Buskirk 2009).

We quantified among-pond variation in body size at metamorphosis of tadpoles of the European common toad (*Bufo b. spinosus*) under natural conditions. This trait was chosen because it is critical in the complex life cycle of amphibians (Wilbur 1980). Individuals that are relatively larger at metamorphosis are expected to perform better

later in life than smaller individuals (Smith 1987; Berven 1990; Goater 1994; Altwegg and Reyer 2003). Furthermore, equilibrium densities and population growth rates can be highly sensitive to variation in post-metamorphic performance, especially that of juveniles (Lampo and De Leo 1998; Biek et al. 2002).

Our study population was patchily distributed in the temporary and permanent ponds of a dynamic braided floodplain in Italy (Kuhn 2001; Tockner et al. 2006; Indermaur et al. 2010). Braided floodplains are composed of two major habitats: the active tract, which is the open riverbed frequently reworked by floods, and the fringing riparian forest. Ponds in the active tract contain no or few predators and are sun exposed and hydrologically variable; consequently, they provide a warm and productive environment. Ponds in the riparian forest have the opposite characteristics (Indermaur et al. 2010). These factors constitute major environmental gradients that affect metamorphic traits and thereby the structure of freshwater communities (Wellborn et al. 1996).

The expectation is that warm ponds with a short hydroperiod select for rapid development and hence small metamorphs. In contrast, cool and more permanent ponds select for slow development and large metamorphs (Newman 1988; Berrigan and Charnov 1994). However, different predation risks may override the effects of temperature on growth. For example, low predation risk in the active tract may select for long larval periods and large size at metamorphosis, while high predation risk in the riparian forest may select for the opposite characteristics (Travis et al. 1985; Skelly and Werner 1990). While we can formulate clear predictions about the impacts of single factors on metamorphic size for the active tract and the riparian forest, when multiple factors come into play, it is unclear whether and how metamorphic traits will differ between the two major habitats.

Our specific goals were: (1) to quantify the interactive effects of abiotic and biotic factors on variation in body size among ponds during the larval period and at metamorphosis, and (2) to determine whether there are differences in tadpole performance (body size at metamorphosis, growth rates) and population density at metamorphosis in the two main habitat types.

Materials and methods

Study site

The study was conducted between 14 March and 2 July 2006 in an island-braided floodplain along the seventh-order Tagliamento river in north-eastern Italy (46°N, 12°30'E) [see Electronic Supplementary Material (ESM)

S1]. The Tagliamento (catchment area 2,580 km²) originates at 1,000 m a.s.l. in the southern fringe of the European Alps and flows almost unimpeded by dams for 172 km to the Adriatic Sea. Unlike most European rivers, the river retains its essentially pristine morphological and hydrological characteristics (Ward et al. 1999).

The study site at river-km 79.8–80.8 (135 m a.s.l.) was 1.6 km² and comprised an 800-m-wide active tract, with the adjacent riparian forest on the north bank. The active tract was a spatio-temporally complex mosaic of vegetated islands, a braided network of main and secondary channels and backwaters and ponds, embedded within a matrix of exposed gravel sediments (Ward et al. 1999) (see [ESM S1](#)). Within the riparian forest, the ponds were distributed along an alluvial channel. The habitat mosaic was frequently reworked by floods. We choose this particular river section for study because both habitat heterogeneity (Arscott et al. 2002) and amphibian diversity are high (Tockner et al. 2006).

Study species

The European common toad (referred to as common toad hereafter) was selected for study because it is abundant within both the active tract and the riparian forest (Tockner et al. 2006). The common toad is widespread in Mediterranean countries and is an early breeder with a fixed breeding time and a preference for large permanent waters (Giacoma and Castellano 2006; Indermaur et al. 2010). However, the species shows considerable behavioral plasticity when breeding in unpredictable environments (Kuhn 2001). The tadpoles of the common toad, which was the predominant species in our study area, often co-occurred with those of the Italian Agile frog (*Rana latastei*) and less frequently with those of the European common frog (*Rana temporaria*) and the green toad (*Bufo viridis*) (Tockner et al. 2006; Indermaur et al. 2010).

Pond selection

To document the range of environmental conditions, we sampled all ponds with a surface water area ≥ 1 m² and water depth >0.05 m in the active tract ($n = 92$) and in the riparian forest ($n = 49$) on four separate occasions between February and July 2006. The common toad laid eggs in about half of the ponds of both the active tract and the riparian forest.

For measuring tadpole growth and metamorph size, we randomly selected 27 ponds in the active tract and 13 ponds in the riparian forest. More ponds were sampled in the active tract than in the riparian forest because we expected that many ponds in the former location would dry up before the tadpoles completed metamorphosis. Egg laying within

each of the selected ponds was completed within 1 week, thus tadpoles from the same pond were of nearly the same age.

Data collection

Pond attributes

We measured 15 abiotic and biotic factors that are expected to affect body size of tadpoles (Alford 1999) (Table 1). A number of factors were strongly correlated, and these were removed from further analysis (see [ESM S2, S3](#)). The nine factors retained for the analysis were intra- and interspecific density (a surrogate for competition), predation risk (an index excluding fish), fish presence, mean pond surface area, oxygen concentration, maximum temperature, hydroperiod length and habitat type (active tract, riparian forest).

The predation risk index was based on the total number of individual adult newts (*Triturus carnifex*, *Triturus vulgaris*), predatory insects (larvae and adults of *Dytiscus marginalis*, *Aeshna* sp.), and snakes (*Natrix natrix*) caught in individual ponds. The total number of individuals was normalized so that the pond with the highest predation risk had an index value of 1, and the pond with no predators had an index value of 0. Fish were not part of the predation index as toad tadpoles appear unpalatable to fish (Denton and Beebee 1997; Laurila 1998); frog tadpoles, however, are heavily preyed upon by fish. Due to this ambiguity we decided to evaluate the separate effect of fish presence on tadpole body size. We used oxygen concentration as a surrogate for primary productivity as most of the oxygen in standing waters derives from the photosynthesis of macrophytes and algae.

Pond surface area and hydroperiod length, and oxygen concentration and temperature were correlated. Nevertheless, we considered each of these individually because each factor has its own merit. To avoid collinearity problems, we did not use these correlated factors in the same model. Age at metamorphosis was included in the analysis to account for variation in developmental rates. A detailed description of the abiotic and biotic factors monitored and the sampling intervals are presented in Table 1.

Tadpole sampling

We quantified population density and body size; the former was used as a measure of competition, and we derived growth rates from the latter. Tadpoles were caught on two consecutive days at weekly intervals. Sampling was performed over a period of 4–14 weeks, depending on the duration of the larval period. Funnel traps were exposed for at least 0.5 h when trapping success was high, and up to 4 h when trapping success was low. Traps were randomly distributed and between 1 and 14 were placed per pond, the

Table 1 Factors used for quantifying among-pond variation in log-body size during the larval period

Code ^a	Factor	Sampling interval ^b	Measuring details
Age	Number of days from egg laying until sampling	W	Weekly egg clutch surveys of all ponds
(Al)	Algae availability (%)	M 4 times	Visually
Ar	Mean pond surface area (m ²)	M 4 times	Differential global positioning system (Trimble GeoXT, Sunnyvale, CA)
Ca	Intraspecific density (competition) (no. of tadpoles of <i>B. b. spinosus</i> /m ²)	W	Sweep netting and funnel traps proportional to water area
Ci	Interspecific density (competition) (no. of tadpoles other than <i>B. b. spinosus</i> /m ²)	W	Sweep netting and funnel traps proportional to pond surface area
(Cy)	Specific conductance (μS/cm)	M 4 times	WTW LF 340 (Wissenschaftlich-Technische Werkstätten, Weilheim, Germany)
(De)	Water depth (m)	W	Maximum water depth
Fi	Fishes ≥ 10 cm (present/absent)	M 4 times	Visually
Hp	Hydroperiod length (number of days ponds contained water)	W	
Ht	Habitat type (two levels: active tract, forest)		Once classified
Ox	Oxygen concentration (mg/l)	M (4 times 3–4 p.m.)	WTW Oxi 340 (Wissenschaftlich-Technische Werkstätten GmbH)
(Ph)	pH [H ⁺]	M 4 times 3–4 p.m.	WTW pH 340 (Wissenschaftlich-Technische Werkstätten GmbH)
Pr	Predation risk (index: 0–1)	Once	Sweep netting and funnel traps proportional to pond surface area
(Sh)	Shading (%)	M 4 times	Visual quantification of canopy cover
T	Mean maximum water temperature (°C)	H	Maxim thermochron ibutton loggers DS1921G (Sunnyvale, CA)

^a Parentheses indicate that the factor was correlated with other factors (see [ESM S3](#)) and hence not used in the analyses. Ca and Ci were estimated for every sampling interval (weekly). For other factors, we used mean values in the analyses as they were not measured at weekly intervals, or the measurements did not overlap temporally with tadpole sampling

^b H hourly; M monthly; W weekly

number being in proportion to the water area. Dip-netting was used in addition to funnel traps when <10 tadpoles were caught in the traps.

Sampling started when tadpoles were swimming, which is Gosner (1960) stage 25, which was, on average, 26 days after egg laying in the active tract and 31 days after egg laying in the riparian forest. Sampling ended shortly before metamorphosis (Gosner stage 41). In two ponds in the active tract and one pond in the riparian forest, all tadpoles died before metamorphosis. These ponds were excluded from analyses.

Body size

Tadpole body size was quantified from digital photographs taken at the weekly sampling times. We randomly selected and photographed 12–35 tadpoles per pond; the tadpoles

were removed from pond, placed in a shallow flat dish (50 × 40 × 3 cm) with a millimeter scale attached to the bottom and photographed. The millimeter scale was used to correct for the spatial scale during processing of the photographs with software ImageJ V 1.4.0 (Abramoff et al. 2004). The software automatically records the size of each tadpole (number of pixels) and counts the number of tadpoles. All tadpoles were horizontally oriented due to the shallow water layer in the basin. When the tail of a tadpole was twisted in any way it was not used in the analyses. Consequently, tadpole orientation had no impact on the number of pixels measured (see [ESM S4](#)).

There were 4,117 individual measurements of tadpole body size. From these, we derived mean body size per pond and sampling occasion, which we used for the analyses (n = means across all ponds and occasions = 209).

Population density

We used the population density of common toad tadpoles as an index for intraspecific competition and the population density of tadpoles of all other species to quantify interspecific competition. We estimated tadpole population density using capture-mark-recapture methods. On the first capture occasion within the first week of the study period, all of the tadpoles caught were batch-marked with a temporary visible neutral red dye staining solution (Viertel 1980) and released into their ponds immediately after marking. The following day tadpoles were caught again at the same ponds. The number of marked and unmarked tadpoles were counted and then again released.

We estimated population size per square meter using Baileys' formula (Williams et al. 2002): $(n \text{ individuals caught and marked at first capture occasion} + 1) \times (n \text{ individuals caught at second capture occasion} + 1) / (n \text{ individuals caught at first and second capture occasion} + 1)$. This formula is a variant of the Peterson–Lincoln index (Williams et al. 2002) and allows unbiased estimates of population size when detection is not perfect. This estimate was then divided by pond surface area.

The use of Baileys' formula requires that the population is closed, meaning that population size is not influenced by mortality or emigration and that tags are neither lost nor overlooked. We minimized mortality-related bias by separating the marking and recapture occasions by only 1 day. Bias due to permanent emigration was unlikely as we stopped sampling when the proportion of tadpoles with forelegs was at most 10%. Tags were clearly visible up to 3 days after tagging, but disappeared within less than 1 week. By sampling at weekly intervals we avoided double-counting of tadpoles that were tagged the previous week. Hence, all underlying assumptions of the method were met as closely as possible. We did not find any impact of marking method on mortality and behavior.

Statistical analysis

Explaining among-pond variation in body size

Model selection: We used an information–theoretical approach (Burnham and Anderson 2002) to find a model that best explained among-pond variation in larval body size in relation to environmental factors. As combining the factors in all possible combinations is considered a poor modeling strategy (Burnham and Anderson 2002), we emphasized framing a small set of a priori candidate models that reflect the biological hypotheses we were interested in (Burnham and Anderson 2002). As a first step, we formulated groups of candidate models to include either biotic factors (Table 2, nos. 1–12), abiotic factors (nos. 13–

20), or both abiotic and biotic factors (nos. 21–28). Second, we duplicated models from the first step that included biotic factors and changed these to include only intraspecific density (nos. 29–36) or only interspecific density (nos. 37–44). Model 45, solely included the factors “age” at metamorphosis and “habitat type”. Model 46 included only the intercept as a fixed effect with the nested random effects “pond” and “sampling occasion”. These factors were included in every model to correct for their potential effects on log-body size. In this way, we were able to evaluate the effects of intra- and interspecific density.

We fitted linear mixed effects models (package lme4) in R (V 2.4.0) (R Development Core Team 2005) to the data. The repeated body-size measures over time (occasion) were specified as nested random effects per pond. All continuous explanatory factors were z-standardized prior to analysis. Body size was log-transformed, and residuals were normally distributed.

Predictions: We predicted body size at metamorphosis to graphically explore the direct and interactive effects of factors from the best selected candidate model. Log-body size was calculated at metamorphosis for 161 density values (0–8,000 tadpoles/m²) and for 100 temperature values spanning the range of observed values (3–21°C). Other factors in the model were held constant using mean values (i.e., zero for standardized explanatory factors). We used 80 days for the factor “age”, which corresponds to occasion eight and the point where mean body size was the largest. Predictions were made for the habitat type “riparian forest”. Confidence intervals were obtained by bootstrapping (1,000 iterations).

Differences in tadpole performance and population density between the two major habitats

Body size: Using *t* tests, we tested for differences in body size (1) at first sampling (Gosner stage 25, shortly after hatching) and (2) at metamorphosis, between the active tract and the riparian forest.

Growth rate: We calculated the growth rate as a daily proportion of body size, solving the following equation for “rate”: $\text{body size at metamorphosis} = \text{body size at first sampling} \times (1 + \text{rate})^{\text{age}}$ (Anholt et al. 2000). Differences in growth rate between tadpoles from the active tract and the riparian forest were analyzed using analysis of covariance (ANCOVA), taking “log-body size at first sampling” as a covariate and “habitat type” as a fixed factor. Growth rates were log-transformed to assure normally distributed residuals.

Population density: We tested for differences in population density at first sampling and at metamorphosis between the active tract and the riparian forest using *t* tests.

Table 2 Candidate models used for quantifying among-pond variation in log-body size during the larval period of tadpoles of the European common toad

Model no.	Factors
Biotic factors	
1	Ca + Ci + Pr + Fi + Ca*Ci + Ca*Pr + Ci*Pr
2	Ca + Ci + Pr + Fi + Ca*Pr + Ci*Pr
3	Ca + Pr + Fi + Ca*Pr
4	Ci + Pr + Fi + Ci*Pr
5	Ca + Ci + Pr + Fi + Ca*Ci
6	Ca + Ci + Pr + Fi
7	Ca + Ci + Pr
8	Ca + Ci
9	Ca
10	Ci
11	Pr
12	Fi
Abiotic factors	
13	Ox + Ar
14	Ox + Hp
15	T + Ar
16	T + Hp
17	Ox
18	T
19	Ar
20	Hp
Biotic and abiotic factors	
21	Ca + Ci + Pr + Fi + Ca*Ci + Ca*Pr + Ci*Pr + Ox + Ar
22	Ca + Ci + Pr + Fi + Ca*Ci + Ca*Pr + Ci*Pr + Ox + Hp
23	Ca + Ci + Pr + Fi + Ca*Ci + Ca*Pr + Ci*Pr + T + Ar
24	Ca + Ci + Pr + Fi + Ca*Ci + Ca*Pr + Ci*Pr + T + Hp
25	Ca + Ci + Pr + Fi + Ca*Ci + Ca*Pr + Ci*Pr + Ox + Ar + Ca*Ox + Ci*Ox
26	Ca + Ci + Pr + Fi + Ca*Ci + Ca*Pr + Ci*Pr + Ox + Hp + Ca*Ox + Ci*Ox
27	Ca + Ci + Pr + Fi + Ca*Ci + Ca*Pr + Ci*Pr + T + Ar + Ca*T + Ci*T
28	Ca + Ci + Pr + Fi + Ca*Ci + Ca*Pr + Ci*Pr + T + Hp + Ca*T + Ci*T
Biotic and abiotic factors with intraspecific density	
29	Ca + Pr + Fi + Ca*Pr + Ox + Ar
30	Ca + Pr + Fi + Ca*Pr + Ox + Hp
31	Ca + Pr + Fi + Ca*Pr + T + Ar
32	Ca + Pr + Fi + Ca*Pr + T + Hp
33	Ca + Pr + Fi + Ca*Pr + Ox + Ar + Ca*Ox
34	Ca + Pr + Fi + Ca*Pr + Ox + Hp + Ca*Ox
35	Ca + Pr + Fi + Ca*Pr + T + Ar + Ca*T
36	Ca + Pr + Fi + Ca*Pr + T + Hp + Ca*T
Biotic and abiotic factors with interspecific density	
37	Ci + Pr + Fi + Ci*Pr + Ox + Ar
38	Ci + Pr + Fi + Ci*Pr + Ox + Hp
39	Ci + Pr + Fi + Ci*Pr + T + Ar
40	Ci + Pr + Fi + Ci*Pr + T + Hp
41	Ci + Pr + Fi + Ci*Pr + Ox + Ar + Ci*Ox
42	Ci + Pr + Fi + Ci*Pr + Ox + Hp + Ci*Ox
43	Ci + Pr + Fi + Ci*Pr + T + Ar + Ci*T
44	Ci + Pr + Fi + Ci*Pr + T + Hp + Ci*T
Null models	
45	(Age and habitat type)
46	Null model

See Table 1 for a description of other factors

Tadpole mortality was calculated from population density at first sampling and at metamorphosis.

Results

Range of environmental conditions

Low-predation-risk ponds (Fig. 1a, b) with temperatures >22°C (Fig. 1c, d) were more common in the active tract than in the riparian forest. Ponds with hydroperiods of <40 days (Fig. 1e, f) and ponds with a surface area >500 m² (Fig. 1g, h) were only found in the active tract. Predation risk increased with hydroperiod length ($r = 0.214$) and water depth ($r = 0.214$), and hydroperiod length increased with increasing pond surface area ($r = 0.663$; ESM S3).

Characterization of ponds

The ponds in the two habitats differed most with respect to temperature, pond surface area, hydroperiod length, and

predation risk. Ponds in the active tract were warmer and larger than ponds in the riparian forest (Table 3). Furthermore, hydroperiod length, which was positively related to water depth, was more variable and, on average, 1 week shorter in the active tract than in the riparian forest (Table 3; Fig. 1). Predation risk was on average about sixfold lower in the active tract than in the riparian forest, while intraspecific density was similar in the two major habitat types.

Explaining among-pond variation in body size of tadpoles

Model ranking

The top-ranked model that best explained among-pond variation in body size during the larval period was model 36 (Akaike weight = 0.772) (Table 4). This model included the additive and interactive effects of abiotic and biotic factors, such as temperature, hydroperiod length, age, habitat type, intraspecific density, presence of fish, and predation, as well as the interactions intraspecific density × predation risk and intraspecific density × temperature.

The second-ranked model was number 28 (Akaike weight = 0.169) (Table 4), which included all factors and interactions present in the best model plus the factor interspecific density and the interactions interspecific density × predation risk and interspecific density × temperature. Despite these additional explanatory factors, model no. 28 was about 4.6-fold less supported than the top-ranked model (evidence ratio $0.772/0.169 = 4.6$). In general, the model selection process favored models that included intraspecific density instead of interspecific density (Table 4; ESM S5). Models including only abiotic or biotic factors were poorly supported by the data (ESM S5).

In the best model, the confidence intervals of some factors did not include zero, namely, age, hydroperiod length, intraspecific density, predation risk, and the interactions intraspecific density × predation risk and intraspecific density × temperature (Table 5). The confidence intervals of other factors did include zero, namely, presence of fish, habitat type, and temperature. Thus, these latter factors were unsuitable predictors for among-pond variation in body size.

Predictions

Body size at metamorphosis decreased with increasing hydroperiod length (Table 5; Fig. 2a). The effect of intraspecific density depended interactively both on temperature, and on predation risk (Fig. 3a, b). At low temperature, intraspecific density had no effect (Fig. 3a), but

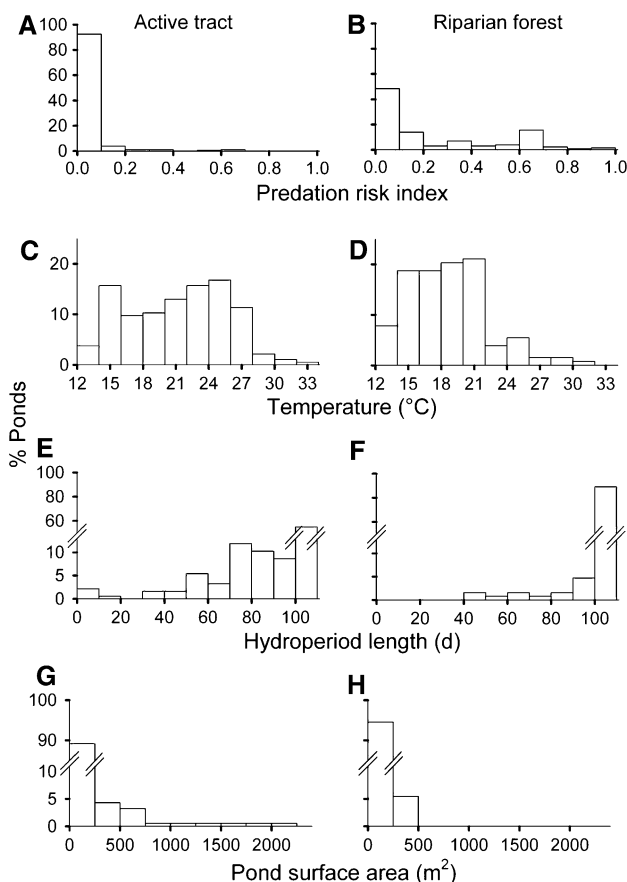


Fig. 1 The frequency distribution of ponds in the open riverbed (active tract, left column) and riparian forest (right column) in relation to predation risk (a, b) (see data collection), temperature (c, d), hydroperiod length (e, f), and pond surface area (g, h). These graphs are based on a total of 141 ponds

Table 3 Descriptive statistics for life history traits and abiotic and biotic factors for the active tract and riparian forest

Code ^a	Factor	Habitat type								Test statistics		
		Active tract				Riparian forest				<i>t</i>	<i>df</i>	<i>P</i>
		Mean	Standard deviation	Range		Mean	Standard deviation	Range				
Age	Age at metamorphosis	56.71	17.73	35	93	82.68	12.45	62	100	5.059	26.7	<0.001
(Al)	Algae availability	24.5	10.5	0	91.25	22.25	8.75	0	82.5	0.512	22.5	0.613
Ar	Pond surface area	65.66	120.24	0.99	506.41	55.46	47.08	21.95	189.02	2.194	34.8	0.034
Ca	Intraspecific density	731.20	1588.48	0.00	7137.09	549.24	1427.82	0.00	8274.86	1.890	25.0	0.070
Ci	Interspecific density	37.27	98.91	0.00	625.76	106.01	313.95	0.00	2364.12	0.904	26.2	0.373
(Cy)	Specific conductance	546.16	108.09	152.25	652.62	470.36	113.94	291.25	598.83	1.734	18.9	0.099
(De)	Water depth	0.28	0.15	0.09	0.69	0.39	0.24	0.20	1.00	1.402	14.3	0.165
Hp	Hydroperiod length	97.23	12.92	56.00	104.00	104.00	0.00	104.00	104.00	2.811	25.0	0.009
Ox	Oxygen concentration	8.82	2.52	3.95	20.80	8.39	2.87	5.18	14.45	0.448	19.1	0.664
(Ph)	pH	7.83	0.24	7.57	8.86	7.80	0.28	7.50	8.32	0.452	18.2	0.656
Pr	Predation risk	0.09	0.09	0.00	0.34	0.51	0.32	0.12	1.00	4.452	10.6	0.001
(Sf)	Log-body size at first sampling	4.87	0.37	3.91	5.90	4.69	0.26	4.20	5.15	1.159	28.5	0.256
(Sh)	Shading	38.25	12.75	0	68.75	48.00	13.75	0	65.00	2.011	17.7	0.059
Sm	Log (body size at metamorphosis)	5.27	0.42	3.91	6.18	5.10	0.26	4.20	5.72	2.020	26.7	0.053
T	Temperature	23.55	2.53	17.43	26.75	21.09	1.59	17.88	23.43	3.579	29.5	0.001

All factors, except age, Sf, and Sm are mean values over the entire study period

^a Parentheses indicate that the factor was correlated with other factors (see [ESM S3](#)) and hence not used in the modeling analyses

Table 4 Model selection results for quantifying among-pond variation in log-body size during the larval period of tadpoles of the European common toad, sorted after Akaike's small sample information criterion scores (ΔAICc)

Model no.	Factors	<i>K</i>	ΔAICc		Akaike weight	ER	
			Dev	Res			
36	Ca + Pr + Fi + Ca*Pr + T + Hp + Ca*T	13	-39.48	2.4E-14	0.00	0.772	1.0
28	Ca + Ci + Pr + Fi + Ca*Ci + Ca*Pr + Ci*Pr + T + Hp + Ca*T + Ci*T	17	-45.79	1.1E-13	3.03	0.169	4.6
35	Ca + Pr + Fi + Ca*Pr + T + Ar + Ca*T	13	-33.90	2.0E-14	5.58	0.047	16.3

Only models with an Akaike weight >0.04 are shown (for full results see [ESM S5](#)). The top ranked model with $\Delta\text{AICc} = 0$ best approximates the data, and models with $\Delta\text{AICc} \leq 2$ are considered to receive substantial support from the data

Only models 35, 36, and 28 are given in the table

See [Table 1](#) for description of factors

^a *K*, Number of estimated parameters

^b Dev = $-2 \times \log\text{-likelihood}$

^c Res = sum of residual deviance

^d ER Evidence ratio; the ratio of model weight of a particular model in relation to the top ranked model. When one model receives a weight ≥ 0.9 , there is no apparent model selection uncertainty

at high temperature, increasing intraspecific density negatively affected body size at metamorphosis. Tadpoles metamorphosed at the largest size in ponds with a low

density and low predation risk and at the smallest size in ponds with a high density and high predation risk ([Fig. 3b](#)).

Table 5 Regression slopes (beta) of the best-selected model (no. 36, Table 4) that was used to predict among-pond variation in log-body size at metamorphosis

Code	Factor	Beta	SE	LCL	UCL
	Intercept ^a	5.256 ^a	0.092 ^a	5.076 ^a	5.436 ^a
Age ^a	Age ^a	0.292 ^a	0.018 ^a	0.257 ^a	0.327 ^a
Ca ^a	Intraspecific density ^a	-0.235 ^a	0.041 ^a	-0.315 ^a	-0.155 ^a
Ca × Pr ^a	Intraspecific density × predation risk ^a	0.138 ^a	0.027 ^a	0.085 ^a	0.191 ^a
Ca × T ^a	Intraspecific density × temperature ^a	-0.132 ^a	0.030 ^a	-0.191 ^a	-0.073 ^a
Fi	Presence of fish	-0.016	0.063	-0.139	0.107
Hp ^a	Hydroperiod length ^a	-0.177 ^a	0.057 ^a	-0.289 ^a	-0.065 ^a
Ht	Habitat type	-0.133	0.200	-0.525	0.259
Pr ^a	Predation risk ^a	-0.202 ^a	0.072 ^a	-0.343 ^a	-0.061 ^a
T	Temperature	0.111	0.067	-0.020	0.242

SE Standard error; LCL, UCL lower and upper limits, respectively, of 95% confidence intervals of the regression slopes

^a Factors that do not include zero in their confidence intervals and are hence reliable for predicting among-pond variation in body size at metamorphosis

See Table 1 for description of factors

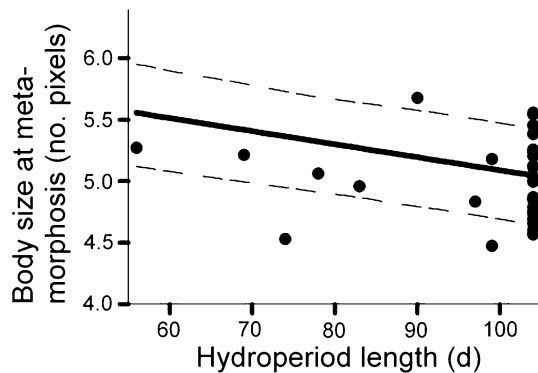


Fig. 2 Predicted body size at metamorphosis of the European common toad (*Bufo b. spinosus*) in relation to hydroperiod length. The model that best explained among-pond variation in log-body size was used (no. 36, Table 4). Predictions were calculated within the range of observed factor values. Upper and lower dashed lines are 95% confidence limits. Filled circles Observed data. Note: log scale (base = 10) for body size at metamorphosis

Differences in tadpole performance and population density between the two habitat types

Body size

Body size at first sampling did not significantly differ between the active tract and the riparian forest ($t = 1.159$, $P = 0.256$, $df = 28.5$). Body size at metamorphosis was larger in the active tract than in the riparian forest (Table 3; Fig. 4a), although the differences were not statistically significant ($t = 2.020$, $P = 0.053$, $df = 26.7$).

Growth rate

Tadpoles in the active tract grew significantly faster [mean ± standard deviation (SD); $0.94 \pm 0.49\%$ pixels/

day] than did tadpoles in the riparian forest ($0.57 \pm 0.21\%$ pixels/day) [ANCOVA; “log(body size at first sampling)” $F_{1,34} = 7.461$, $P = 0.010$, “habitat type” $F_{1,34} = 7.697$, $P = 0.009$] (Fig. 4b). In addition, the larval period of tadpoles (age at metamorphosis) in the active tract was on average 26 days shorter than that of tadpoles in the riparian forest (Table 3) ($t = 5.06$, $P < 0.001$).

Population density

Mean population density (±SD) at first sampling was similar in ponds of the active tract and the riparian forest (active tract: $1,256.1 \pm 2,125.9/m^2$, range 2.3–7,137.1/ m^2 ; riparian forest: $1,610.1 \pm 2,458.4/m^2$, range 130.6–8,274.8/ m^2 ; $t = 1.476$, $P = 0.149$) (Fig. 4c). However, mean population density (±SD) at metamorphosis of ponds in the active tract was one to two order of magnitude higher than that in ponds of the riparian forest (active tract: $489.1 \pm 1,286.2/m^2$, range 0–4,855.4/ m^2 ; riparian forest: $12.1 \pm 19.6/m^2$, range 0–59.9/ m^2 ; $t = 2.767$, $P = 0.010$) (Fig. 4d). The mean percentage of hatchlings (±SD) that died before metamorphosis was on average 16% lower in the active tract than in the riparian forest (active tract: $82.3 \pm 22.4\%$, range 28.8–100%; riparian forest: $98.9 \pm 1.8\%$, range 94.2–100%).

Discussion

In this study, we quantified the spatial variation in body size of tadpoles at metamorphosis in relation to multiple abiotic and biotic factors in ponds in two contrasting habitats of a braided floodplain, namely, the active tract

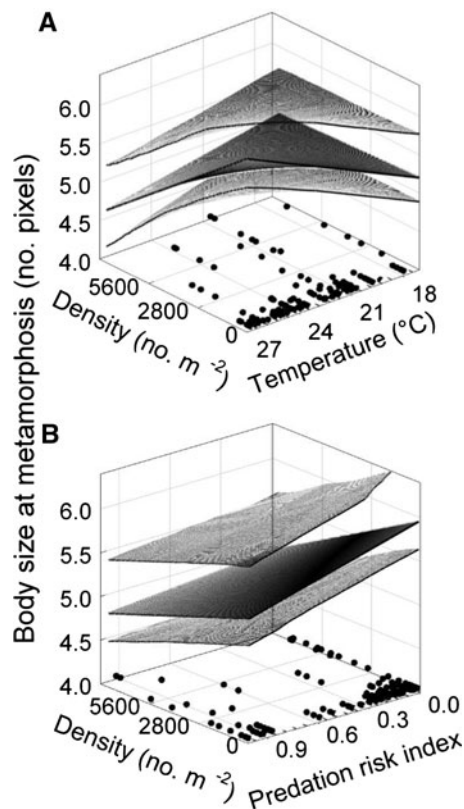


Fig. 3 Predicted body size at metamorphosis of European common toad (*Bufo b. spinosus*) in relation to combined effects of intraspecific tadpole density and temperature (a) and combined effects of intraspecific tadpole density and predation risk (b). The model that best explained among-pond variation in log-body size was used (no. 36, Table 4). Predictions were calculated within the range of observed factor values. *Upper and lower meshes (a, b)* are 95% confidence limits. To ease interpretation, we plotted the range of observed data (*filled circles*) to the bottom. *Note:* log scale (base = 10) for body size at metamorphosis in both panels

and the riparian forest. We focused on body size at metamorphosis because it is an important trait that affects fitness, survival later in life and population growth (Smith 1987; Berven 1990; Goater 1994; Altwegg and Reyer 2003).

Variation in body size is of fundamental importance for the distribution of species and, consequently, for the dynamics of populations (Savage et al. 2004). The underlying factors of variation in body size have previously been quantified experimentally under laboratory and mesocosm conditions, although most of these studies considered only a few individual environmental factors (Allan 1976; Mitchell-Olds 1987; Alford 1999; Charnov and Gillooly 2004). Though multiple abiotic and biotic factors act in concert on life history in nature, their combined impacts have been rarely studied (Petranka 1984; Reading and Clarke 1999; Gray and Smith 2005; Van Buskirk 2009). In addition, it is unclear whether differences in habitat

conditions translate into differences in life history traits among habitats.

Explaining among-pond variation in body size

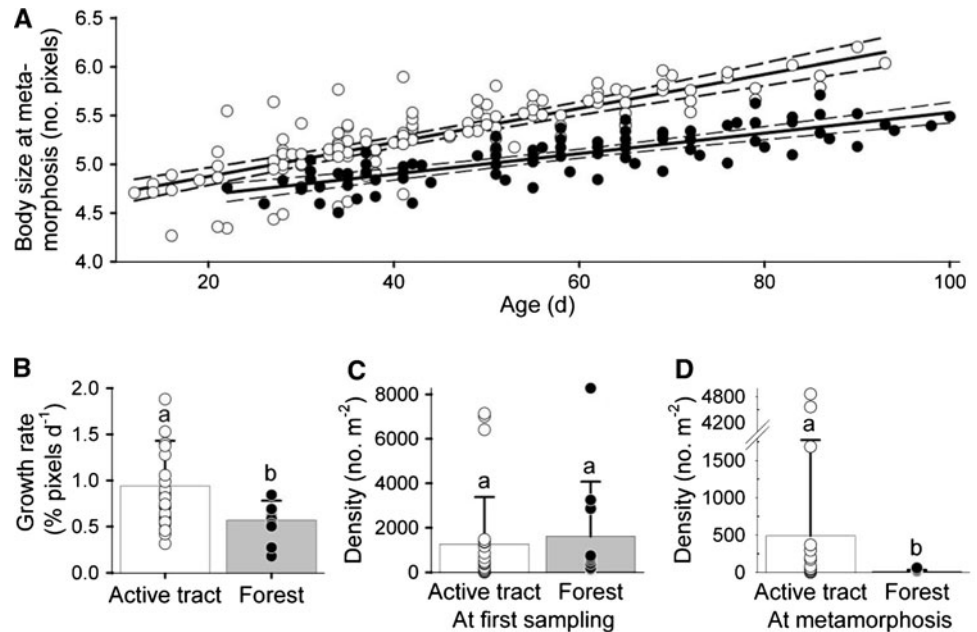
Body size at metamorphosis was largest in ponds that had a short hydroperiod, were warm and were characterized by a low intraspecific density and low predation risk (Table 5). These conditions were characteristic for the active tract in our study area (Table 3; Fig. 1). Hydroperiod is a major environmental gradient affecting traits of freshwater organisms (Wellborn et al. 1996), as confirmed by our results (Table 5; Fig. 2). The highest growth and survival rates in the short-lived ponds of the active tract suggests that these ponds are the most productive environments in our study (Wellborn et al. 1996; Skelly et al. 2002).

Interactions between abiotic and biotic factors determined the growth and size of the tadpoles in our study. We found strong interactive effects on body size at metamorphosis due to intraspecific density and temperature as well as to intraspecific density and predation risk (Fig. 3a, b). Temperature largely determines biological reaction times, thereby affecting metabolism and hence the growth rates of organisms. At low temperatures, we found that body size was not affected by tadpole density (Fig. 3a). This results suggests that low temperatures limited growth such that density was unimportant. However, at high temperatures, when abiotic conditions for growth were favorable, body size was negatively affected by tadpole density, indicating that while both temperature and intraspecific tadpole density may affect growth, abiotic conditions are the most influencing important factors in ectotherms (Angilletta et al. 2004a).

Predation risk and intraspecific tadpole density interactively affected tadpole growth and size (Fig. 3b). The growth rates were lowest when both predation risk and intraspecific tadpole density were high. Increasing predation risk decreased growth rates, and the effect was stronger at a low competitor density than at a high competitor density. It would therefore appear that the effects of predation risk were strong when growth conditions were relatively favorable because tadpole density was low. However, when tadpole density was high, growth rates were already depressed such that the effect of predation risk was weaker than that at a low tadpole density.

Between the two major types of competition that we tested, only intraspecific density affected growth, with interspecific density playing only a minor role (ESM S5). This result suggests that the different anuran species in the floodplain have limited interactions in the larval stage. Indeed, the four species of anurans living in the Tagliamento floodplain co-occur more often than expected by

Fig. 4 Differences in performance measures between tadpoles from the active tract (*open circles*) and the riparian forest (*solid circles*). **a** Predicted body size at metamorphosis in relation to age (log scale, mean \pm 95% confidence intervals), **b** growth rates (no. pixels per day), **c** population density at first sampling, **d** population density at metamorphosis. Date points are estimates per pond, *vertical lines* (**b**, **c**, **d**) standard deviation. *Bars* that do not share a *subscript letter* were significantly different from each other (*t* test, $P < 0.05$)



chance, which shows that they do not avoid each other (Indermaur et al. 2010).

Our study on within-population, among-pond variation in larval growth demonstrated that the direct and interactive effects of abiotic and biotic factors determined the body size of the tadpoles at metamorphosis. This result is consistent with the conclusion of Van Buskirk (2005) based on an among-population study of the effects of biotic and abiotic factors on the distribution and abundance of larval anurans. Van Buskirk (2005) found that competition was unimportant and suggested that variation in general habitat quality was of greater importance. Our results suggest that temperature may be an abiotic condition that determines overall habitat quality. If temperature is of paramount importance, then we would expect that common toads would select warm ponds for breeding. This is in fact the result of a study on anuran breeding site selection on the Tagliamento floodplain (Indermaur et al. 2010). In contrast, neither Indermaur et al. (2010) and Van Buskirk (2005) found competitor density to determine breeding site selection.

Differences in tadpole performance and population density between the two major habitat types

Tadpoles in the active tract and the riparian forest primarily differed in growth and survival, rather than body size. Body size at metamorphosis was larger in the active tract than in the riparian forest (Table 3), although the difference was not significant (Fig. 4a). Tadpoles in the active tract had significantly higher growth rates (Fig. 4b) and completed metamorphosis on average 3 weeks earlier than

tadpoles from the riparian forest. Moreover, population density at metamorphosis in ponds of the active tract was one to two orders of magnitudes higher than that in ponds of the riparian forest (Table 3; Fig. 4d), mainly because tadpole survival until metamorphosis was 17% higher in the active tract than in the riparian forest.

These differences between the two habitat types may induce source–sink dynamics (Pulliam 1988), with ponds in the active tract acting as sources and ponds in the riparian forest acting as sinks. Year-to-year variation in rainfall, such that ephemeral ponds dry too early or are scoured by floods, may, however, reverse the observed pattern. Hence, the correct identification of source and sink habitats requires a multi-year study (Semlitsch et al. 1996; Runge et al. 2006), with fitness components measured in all life history stages (McPeck and Peckarsky 1998; Rohr et al. 2006).

Conclusions and conservation implications

We have demonstrated that the spatial variation in life history traits of a population of European common toads occurring in different habitat types in a dynamic floodplain was determined by the interactive effects of abiotic and biotic factors. Dunson and Travis (1991) suggested that abiotic factors operate immediately on larval traits, thereby explaining the rather weak impacts of biotic factors, such as competition (Loman 2001).

The particular form of the interaction between temperature and intraspecific density that we documented (Fig. 3a) suggests a hierarchy of effects regulating size and growth, namely, temperature determines whether tadpole

density affects growth. At low temperatures, there are no effects of intraspecific density on growth; at high temperatures, however, the effects of intraspecific density can be very strong. Thus, only if temperature conditions are favorable, competition may affect growth. Hence, the abiotic conditions set the stage for biotic interactions.

The importance of temperature, intraspecific density, predation risk and interactions, as shown in our field study, corroborates experimental findings (Alford 1999), which is essential for the feedback loop between experiments, observational studies and theory (Werner 1998). In other words, the factors that have been identified as important factors experimentally under laboratory and field conditions are indeed important under the full range of natural conditions. However, we show that some factors only matter in a range of conditions determined by other factors.

Our observational approach provides correlative evidence, while experimental studies provide causative evidence. Despite this limitation for inference, we argue that observational approaches are useful for identifying those factors that should be manipulated experimentally in amphibians and most likely in other taxa as well. Moreover, observational approaches are needed to justify experimental treatment levels (Werner 1998).

Differences among habitats in the dynamic floodplain translated into performance differences, as tadpole performance in the active tract was much better than that in the riparian forest. In particular, the short-lived, shallow, warm and low-predation-risk, ponds in the active tract led to improved tadpole performance. The flooding-mediated disturbance regime maintains the ponds in the active tract in a state that is favorable for amphibians, which is similar to findings reported earlier (Petranka and Sih 1986; Loman 2002). The creation and maintenance of ponds in early succession stages depends on a natural river bed and flow regime as well as an unconstrained river morphology. However, these ponds are among the first habitats that disappear as a consequence of flow regulation and channelization of rivers. Restoration of riverine floodplains is therefore a promising method to create and maintain habitats of early succession stages that are favorable for tadpole performance.

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