



# Tadpole diet selection varies with the ecological context in predictable ways

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## Summary

Ecological conditions and food quality have influence on age and size at metamorphosis of organisms with complex life cycles. However, little is known about the foraging behaviour and how diet choice is influenced by the ecological conditions.

The present study poses two major questions: (1) how do different diets (high protein, low protein and both diets together) influence larval performance, and (2) how does diet choice change with ecological conditions (interference competition, predation and pond drying)? To address the second question, we offered both types of food to tadpoles under the different circumstances. We measured food consumption of the two food types, along with the growth rate and developmental stage of tadpoles. We expected that under unfavourable growth conditions, larvae would select high-protein food, which would promote development and allow individuals to escape these high-risk environments.

High-protein food promotes development, but results in smaller tadpoles, whereas low-protein food promotes growth with slower development. The mixture of the two is better only in terms of growth rate. Our study of tadpoles showed that diet selection may not be constant but can vary depending on the ecological context in predictable ways. When exposed to interference competition and drying ponds, tadpoles fed on food that enhanced development, whereas in the control group and in predation treatments, they fed selectively on food that favoured growth. Our data indicate that diet selection by tadpoles may confer adaptive responses to ecological changes. Such selection/responses would increase growth, development, and survival.

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## Zusammenfassung

Die ökologischen Bedingungen und die Nahrungsqualität haben Einfluss auf das Alter und die Größe bei der Metamorphose von Organismen mit komplexen Lebenszyklen. Dennoch ist wenig darüber bekannt, wie das Nahrungssuchverhalten und die Nahrungswahl durch die ökologischen Bedingungen beeinflusst wird. Die vorliegende Untersuchung stellt zwei Fragen: (1) wie beeinflusst unterschiedliche Nahrung (proteinreich, proteinarm und beides zusammen) das Gedeihen der Larven, und (2) wie verändert sich die Nahrungswahl mit den ökologischen Bedingungen (Interferenz-Konkurrenz, Prädation und Austrocknen des Gewässers)? Um die zweite Frage zu beantworten, boten wir den Kaulquappen beide Nahrungstypen unter verschiedenen Bedingungen an. Wir maßen die Nahrungsaufnahme für beide Nahrungstypen, zusammen mit der Wachstumsrate und den Entwicklungsstadien der Kaulquappen. Wir erwarteten, dass die Kaulquappen unter ungünstigen Wachstumsbedingungen proteinreiche Nahrung wählen würden, die das Wachstum fördert und den Individuen erlauben würde, die risikoreiche Umwelt zu verlassen. Proteinreiche Nahrung beschleunigt die Entwicklung, führt aber auch zu kleineren Kaulquappen, während proteinarme Nahrung bei langsamerer Entwicklung das Wachstum fördert. Die Mischung der beiden ist nur in Bezug auf die Wachstumsrate vorteilhafter. Unsere Untersuchung der Kaulquappen zeigte, dass die Nahrungswahl nicht unveränderlich war, sondern in Abhängigkeit von den ökologischen Zusammenhängen in vorhersehbarer Weise variieren konnte. Wenn die Kaulquappen interferierender Konkurrenz und austrocknenden Gewässern ausgesetzt waren, ernährten sich die Kaulquappen von Nahrung, welche die Entwicklung förderte, während sie in der Kontrollgruppe und der Prädatorenvariante selektiv Nahrung fraßen, die das Wachstum förderte. Unsere Daten zeigen, dass die Nahrungswahl der Kaulquappen eine adaptive Antwort auf ökologische Veränderungen darstellen kann. Solch eine Selektion/Antwort würde das Wachstum, die Entwicklung und das Überdauern der Art erhöhen.

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## Introduction

Diet is a fundamental aspect of an animal's ecological niche, and from the community point of view, forager diets potentially play a central role in determining the dynamics of competition (Pianka, 1981), predatory-prey interactions (Sih, Crowley, McPeck, Petranka, & Strohmeier, 1985), and indirect community interactions (Werner & Peacor, 2003). An understanding of diets and the ability to predict diet shifts in response to changes in different ecological contexts is thus a major issue in modern biology (Sih & Christensen, 2001).

The phenotypic plasticity in foraging behaviour in response to different environments can be one of the principal causes of variation in growth and life history parameters (Gotthard & Nylin, 1995; Kause, Haukioja, & Hanhimäki, 1999; Nylin & Gotthard, 1998). The duration of larval growth and the timing of metamorphosis are critical aspects of postembryonic development in most organisms with complex life cycles (Hall & Wake, 1999). Examples include holometabolous insects, many marine invertebrates (Greene, 1999; Nijhout, 1999), and amphibians (e.g. Wilbur & Collins, 1973; Werner,

1986). Because such traits affect an individual's fitness, variations of them have attracted considerable theoretical and experimental interest in the past 25 years (e.g. Alford & Harris, 1988; Hensley, 1993; Leips & Travis, 1994; Morey & Reznick, 2000; Rowe & Ludwig, 1992). The ecological model proposed by Wilbur and Collins (1973) suggests that recent growth history determines age and size at metamorphosis. Paralleling ecological models, many biologists focus attention on developmental and physiological studies to explore internal and external cues that regulate the duration of larval growth and development (e.g. Denver, 1997, 1998; Nijhout, 1999; Shi, 2000).

Due to the important effect of food quantity on rates of growth and development, laboratory manipulations of food resources during the larval phase have been used to test the predictions of the ecological model (e.g. Alford & Harris, 1988; Leips & Travis, 1994). In addition, some studies have shown that food quality can influence growth and time of metamorphosis (Álvarez & Nicieza, 2002a; Babbitt & Meshaka, 2000; Kupferberg, 1997; Pryor, 2003; Skelly & Golon, 2003). Experimental studies have demonstrated that high-protein diets can

produce a two-fold effect by accelerating both growth (during pre-metamorphosis phase) and development rates by influencing thyroid hormone functions (Pandian & Marian, 1985; Kupferberg, 1997; Steinwascher & Travis, 1983; but see Álvarez et al., 2002a and Crump, 1990). Many studies have reported that tadpoles are indiscriminate feeders that adjust feeding rates to food availability (see a review in Hoff, Blaunstein, McDiarmid, & Altig, 1999). Few studies have addressed the selective feeding behaviour of tadpoles under different ecological conditions (Kupferberg, 1997). If tadpoles are capable of choosing food that varies in quality, as demonstrated by some studies (Babbitt & Meshaka, 2000; Kupferberg, 1997; Taylor, Altig, & Boyle, 1995), then one can expect selective foraging in relation to ecological conditions.

Plasticity in foraging behaviour can be particularly important in species that occupy temporary habitats with a time constraint on metamorphosis. Selective feeding behaviour allows such species to escape from these habitats when there is a risk of mortality due to pond drying or overpopulation. The two principal objectives of the present study were to test (1) the effects of diet quality on growth and development of tadpoles, and (2) if diet quality choice changes in response to larval ecological conditions. We expected that diet quality promote growth and development rate of tadpoles as has been indicated in previous studies (Álvarez et al., 2002a; Crump, 1990; Kupferberg, 1997; Pandian & Marian, 1985; Steinwascher & Travis, 1983). We hypothesised that under unfavourable conditions in which growth opportunities are constrained by different factors, individuals would select a diet rich in proteins, to escape from these unfavourable conditions.

We considered three unfavourable conditions: pond drying, interference by a competitor and predation. Pond desiccation is considered the major cause of larval mortality in temporary ponds (Newman, 1989). Competition and predation strongly affect tadpole biology and development (reviewed by Alford, 1999). In drying ponds, growth opportunities are clearly time constrained. In interference competition (chemical detection of the presence of a competitor), organisms modify their behaviour and this has an influence on tadpole performance (Bardsley & Beebee, 2001). We expected the same response from our tadpole species to chemical competition as to physical competition, for which an acceleration of metamorphosis has been observed (Richter-Boix, Llorente, & Montori, 2004). Presence of a predator affects growth via behavioural changes. All models predict that under these circumstances, individuals

minimise the larval period and metamorphose earlier than individuals under "optimal" conditions (reviewed by Benard, 2004). In the absence of unfavourable conditions, individuals extend the larval period while they capitalise on rich aquatic growth opportunity. We hypothesised that individuals could regulate development and larval period by feeding on food that promotes growth or development under these four conditions.

We tested these ideas on *Pelodytes punctatus* (Daudin 1802; Parsley Frog) tadpoles. The potential for evolving selective foraging and adaptive responses to distinct diet quality is highlighted by the occurrence of tadpole larvae in a range of temporary aquatic habitats (Toxopeus, Ohm, & Arntzen, 1993) and the tendency of tadpoles to prey on other anuran spawn and conspecifics (Tejedo, 1991; personal field observations).

## Material and methods

### Animals and breeding conditions

On 28 February 2003, two *P. punctatus* spawns were collected from a natural temporary rainfall pool in the *Parc Natural del Garraf*, near Barcelona, Catalonia, in the north-eastern Iberian Peninsula. Egg masses were hatched in outdoor buckets, and the experiments were started when the tadpoles had reached Gosner stage 24–25 (Gosner, 1960). At this stage, external gills are reabsorbed and the operculum is well developed. Also, an effective tail and mouth have developed allowing an active search for food.

We designed a total of six treatments grouped in two experiments (Table 1). Each treatment was replicated four times. Experimental units consisted of tanks (1.2 × 0.45 × 0.40 m) that held 30 l of dechlorinated tap water. Thirty tadpoles, drawn from the two spawns in equal proportions, were randomly assigned to each aquarium. In the middle of each tank, we added two mesh cages elevated 5 cm above the bottom which allowed tadpoles to move freely from one side to the other. Thus, the same space for swimming was available in all treatments (see design of experiment 2 for more details), and the possibility of the cages acting as experimental factor was excluded. All treatments were performed during the same time period at the University of Barcelona, under the same laboratory conditions. Aquaria in both experiments were arranged on a pallet rack shelving system under 11 h light: 13 h dark intervals, and under uncontrolled thermal conditions following daily

**Table 1.** Schematic overview of the two experiments with the six treatments

|              |  | Treatment                | Diet    | Individuals per tank | Stress factor              | Duration of ex |
|--------------|--|--------------------------|---------|----------------------|----------------------------|----------------|
| Experiment 1 |  | LP only                  | LP      | 30                   |                            | 37 days        |
|              |  | HP only                  | HP      | 30                   |                            | 37 days        |
|              |  | Control mixed diet       | LP – HP | 30                   |                            | 37 days        |
| Experiment 2 |  | Interference competition | LP – HP | 30                   | 40 <i>Bufo bufo</i> larvae | 37 days        |
|              |  | Predation                | LP–HP   | 30                   | 2 <i>Aeshma</i> larvae     | 37 days        |
|              |  | Drying                   | LP–HP   | 30                   | decreasing water level     | 37 days        |

All treatments were conducted simultaneously and under the same conditions.

oscillations (maximum 21 °C, minimum 9 °C, with a mean water temperature of 16 °C). In all treatments, food was maintained constant and ad libitum according to the body mass of tadpoles. We offered tadpoles two types of food that differed in protein and carbohydrate composition: commercial rabbit food with low-protein and high-carbohydrate content (hereafter LP) (16% protein, 3% lipids, 17% carbohydrates, 10% ash), and commercial fish food (Sera granumeat, Spain) with high-protein and low carbohydrate content (hereafter HP) (40.3% protein, 6.1% lipids, 2.2% carbohydrates, 9.9% ash). Each tank received one or both types of food according to the experimental design (Table 1). The two types of food were solid pellets that remain intact in water for 24 h. Tadpoles fed on the pellets scraping them with their mouthparts. Pellets not consumed and tadpole faeces were pipetted out of the water daily to minimise the possibility of re-ingestion. Every day new pellets were added in proportion to the pellets consumed to maintain constant supply to larval demands. We estimated the amount of each food type consumed from the number and the weight of pellets added and consumed.

Larvae were weighed to the nearest 0.1 mg at the start of the experiments and at day 37 when the experiments were ended. All tadpoles were removed from the tanks and part of them preserved in formalin 4% for future histological studies. Body mass and Gosner stage were recorded for all individuals. Because food composition may affect the length of the digestive tract (Altig & Kelly, 1974; unpublished data), we weighed 12 tadpoles from each replicate after extracting the tract. This measurement, referred to as net body mass,

excludes gut weight and gut contents and was used as an indicator of body mass status.

Because growth is usually non-linear, we estimated the mean growth rate as  $(\ln \text{weight day } 37 - \ln \text{weight day } 1) / \text{development time}$ . For calculating growth rates, we used absolute body mass, which included the gut, to compare with weights at the start of the experiment (correlation between body mass and net body mass was significant  $r = 0.9616$ ;  $p < 0.001$ ).

### Experiment 1: consequences of diet quality

To evaluate the effects of food quality on tadpole growth and development, tadpoles were randomly assigned to three dietary treatments (Table 1): two treatments with only one type of food (LP and HP), and a treatment with both food types (LP–HP). In this mixture treatment, called “control group” LP and HP food were distributed in the same quantity at opposite ends of the aquaria. We estimated consumption of each type, tadpole growth and development.

### Experiment 2: diet choice influenced by ecological conditions

To examine the change in diet selectivity, we exposed tadpoles to ecological factors that can influence growth and development rates in nature. The experiment consisted of four treatments (Table 1). All treatments were conducted with the two types of food (LP and HP), which were offered at opposite sides of the tanks with positions varying

randomly. The LP–HP treatment from experiment 1 also served as control in experiment 2.

The control group consisted of an aquarium with 30 tadpoles and constant water volume. In the drying treatment tanks were drained according to Wilbur's (1987) formula  $D_j = 1 - (j/t)^a P$ , where  $D_j$  is the depth we need to take out on day  $j$  from initial depth,  $j$  the time in days since the start of the experiment,  $t$  the target date for the depth to reach zero (60 in our case),  $a$  a shape parameter (0.4 in our treatment), and  $P$  the depth (25 cm) at the start of the experiment. At day 37 ( $D_{37} = -19.6$ ) when we stopped the experiment, water level was approximately 5.4 cm ( $25 \text{ cm} - D_{37}$ ).

In the interference competition treatment 40, *Bufo bufo* (Common Toad) tadpoles were set into the mesh cages, so they were separated from the *Pelodytes* tadpoles, while water and chemical signals could pass between compartments. Direct competition for food by *Bufo* was thus avoided.

In the predation treatment, one *Aeshna cyanea* (Aeschnidae, Odonata) larva was introduced to each of the cages in the middle of the aquaria. Thus, *Pelodytes* tadpoles could detect the chemical cues from the predators or from injured prey. Predators were fed two or three tadpoles of *Pelodytes* taken from non-experimental aquaria every 2 days.

Tadpole behaviour (spatial distribution and activity level) was monitored by recording the number of individuals observed on both sides of the aquaria (LP or HP side) and the proportion of active tadpoles (swimming or feeding). We made a minimum of 100 recordings for each aquarium with a break of at least 20 min between observations during the second and fourth week of study. Food selection was estimated indirectly by spatial distribution on the HP or LP side and was defined as the number of tadpoles on the HP side divided by the total number of tadpoles. Activity was defined as the percentage of active tadpoles. We differentiated between observations made in the daytime (between 10:00 and 17:00 h) and those made at night (between 17:01 and 22:00 h), because we suspected that circadian rhythms could influence tadpole activity. As in experiment 1, we estimated food consumption for each type: tadpole growth, development and behaviour.

## Statistical analyses

Tank means were used as the unit of analysis to ensure the statistical independence of data. All data were log-transformed to achieve normality except for the proportional behaviour scores,

which were arcsine square root transformed before analysis.

For experiment 1, we used a one-way ANOVA to analyse total food ingested in the three treatments. Secondly, we used a MANOVA test and successive ANOVAs to test for differences in total proteins, carbohydrates and lipids ingested in the different treatments (calculated from the known proportion of elements included in each pellet). Effects of diet composition on growth and development were tested with one-way ANOVA. In all cases differences between treatments were explored using the Bonferroni post hoc test.

In experiment 2, we used a one-way ANOVA to analyse the effect of different treatment conditions in HP food ingested, net body mass, growth rate and development of tadpoles. A two-way ANOVA (treatments, time period of day) was used to examine larval spatial distribution and activity.

To establish relationships between food properties and their effects on larval growth and development, we calculated the correlation between food compounds ingested (total protein, carbohydrates and lipids) and the body mass and developmental stage of the tadpoles. For these correlations we used data from the six treatments together (experiments 1 and 2).

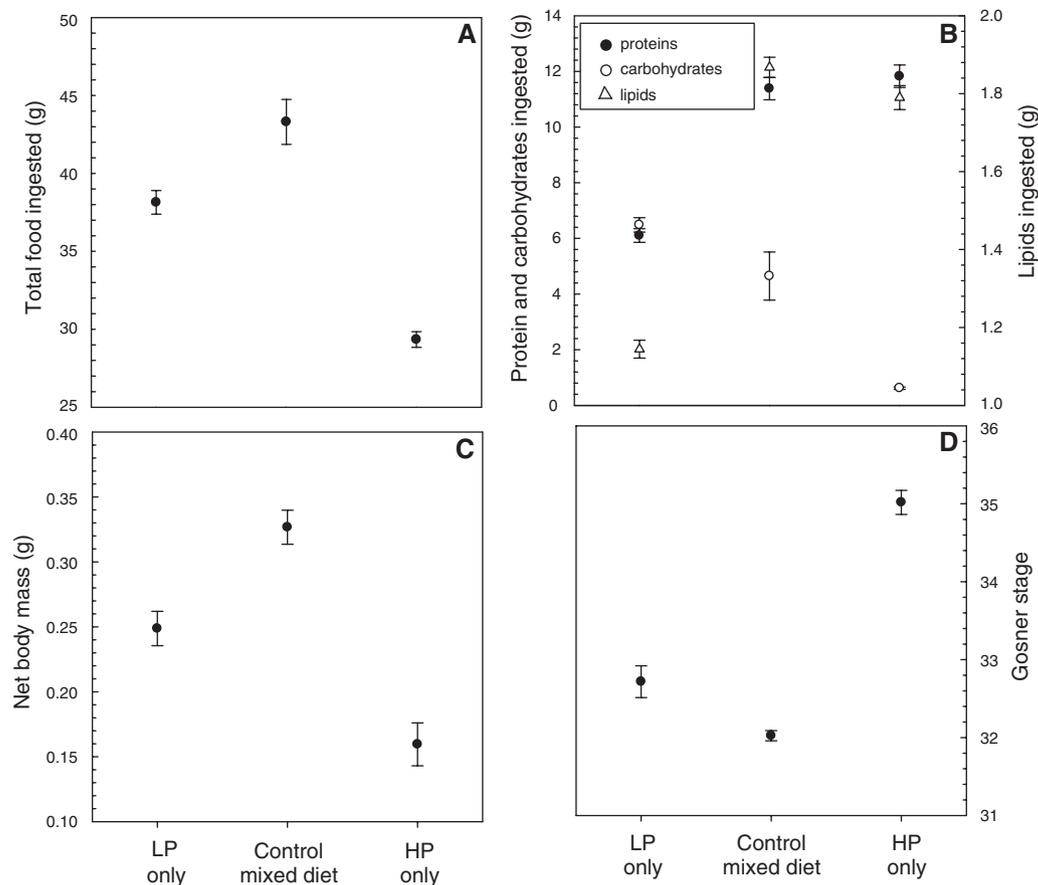
## Results

### Experiment 1

The three treatments differed in the total amount of food ingested ( $F_{2, 9} = 63.53$ ;  $p < 0.001$ ). The control group showed the highest values, whereas HP gave the lowest (Fig. 1A). The total protein, carbohydrates and lipids consumed in the treatments also differed ( $\lambda = 0.0002$ ;  $F_{4, 16} = 275.68$ ;  $p < 0.001$ ). Successive ANOVAs demonstrated differences between treatments in the consumption of these compounds (Fig. 1B). Quality of food affected net body mass ( $F_{2, 9} = 24.04$ ;  $p < 0.001$ ), growth rate ( $F_{2, 9} = 318.7$ ;  $p < 0.001$ ) and development of tadpoles ( $F_{2, 9} = 105$ ;  $p < 0.001$ ). The control group showed the highest body mass and growth rate values, whereas HP treatment showed the highest values for development (Figs. 1C and D).

### Experiment 2

The amount of HP food ingested by tadpoles differed between treatments ( $F_{3, 12} = 7.88$ ;  $p = 0.003$ ). Individuals from the drying treatment



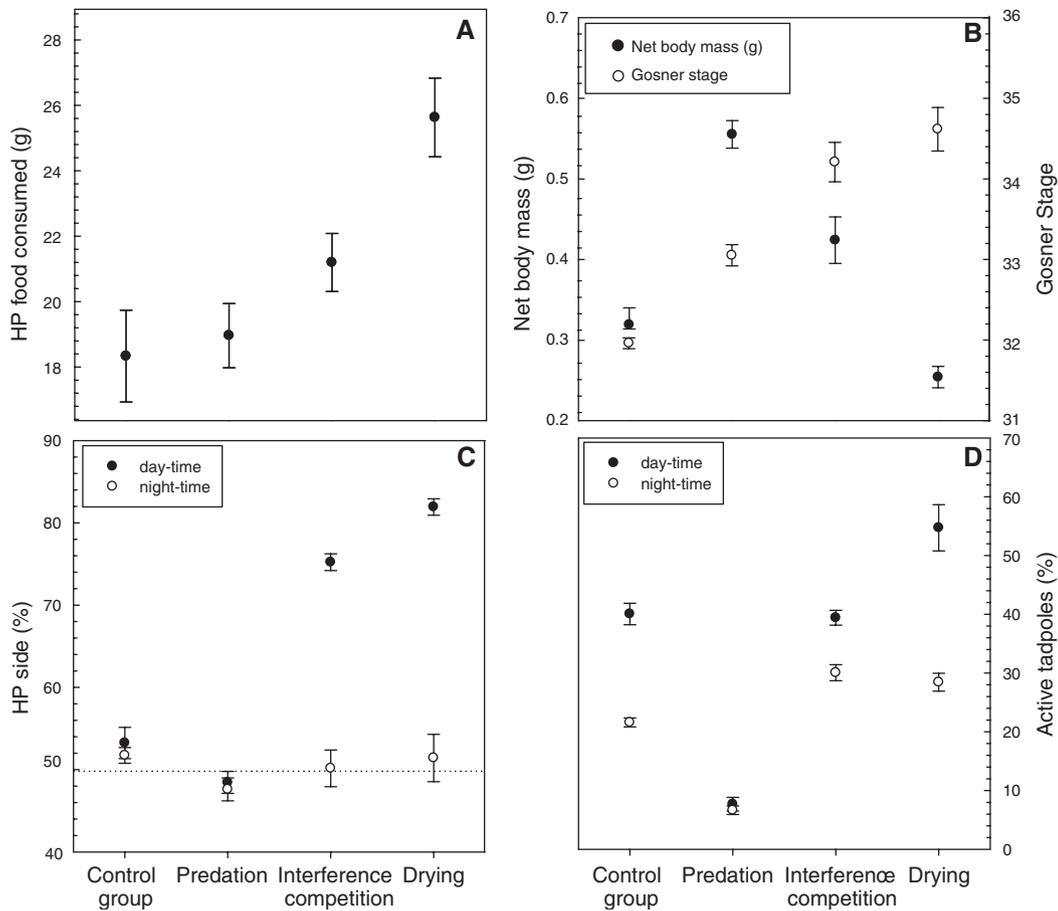
**Figure 1.** Food consumed and larval performance in experiment 1: (A) total amount of food consumed by the three treatments, (B) quantity of compounds ingested by treatments, (C) net body mass of tadpoles and (D) development stage. Error bars represent standard errors.

showed the highest values, whereas the control group and predation treatment showed the lowest (Fig. 2A). The results of the ANOVA suggested that the type of food ingested affected the weight and growth rate of tadpoles at the end of the experiment ( $F_{3, 12} = 48.24$ ;  $p < 0.001$  and  $F_{3, 12} = 294.7$ ;  $p < 0.001$  respectively). Also the final development stage of larvae was affected by treatments ( $F_{3, 12} = 39$ ;  $p < 0.001$ ). Tadpoles from the drying treatment were smaller but in a more advanced developmental stage, whereas tadpoles from the control group exhibited retarded development (Fig. 2B).

A significant interaction was detected between treatments and time of day for spatial distribution and activity levels (Table 2). Activity was higher in all treatments during the daytime, with the exception of the predation treatment in which tadpoles showed little activity all the time (Fig. 2D). Differences between treatments for spatial distribution were only significant during the daytime when tadpoles were active. In the

drying and interference competition treatments, tadpoles showed preferences for the HP food side of the tank, whereas in the other two treatments activity was equally distributed to both sides of the tank (Fig. 2C). A positive correlation was found between HP food consumed and the percentage of tadpoles on the HP side of tank ( $r = 0.7048$ ;  $p = 0.002$ ).

The relationship between all the factors considered is summarised by the correlation between the proteins and carbohydrates consumed and development (Gosner stage) and growth (net body mass). Development was positively correlated with protein ingestion ( $r = 0.426$ ;  $p = 0.037$ ) and negatively correlated with carbohydrates ( $r = -0.705$ ;  $p < 0.001$ ). Net body mass at day 37 showed a positive slope with respect to carbohydrates ingested ( $r = 0.629$ ;  $p < 0.001$ ) and no statistical significance with respect to the amount of proteins ingested ( $r = 0.133$ ;  $p = 0.534$ ). No correlation was found between these variables and the total of



**Figure 2.** Results of experiment 2: (A) high-protein food (HP) consumed in the different treatments, (B) net body mass (black circles) and development stage (open circles) of tadpoles, (C) spatial distribution of tadpoles on the HP side of aquarium during the two time periods in the day. Dotted line at 50% indicates the non-selective distribution, (D) percentage of tadpoles active during the two time periods in the four treatments.

**Table 2.** Two-way ANOVA test (treatments and time of day) for the behavioural variables: percentage of active individuals and percentage of individuals positioned on the HP side of the aquarium (see Figs. 2C and 2D)

| Source                      | df | MS    | F      | P      |
|-----------------------------|----|-------|--------|--------|
| <i>Spatial distribution</i> |    |       |        |        |
| Treatment (T)               | 3  | 0.069 | 55.93  | <0.001 |
| Time period of day (P)      | 1  | 0.191 | 155.02 | <0.001 |
| T × P                       | 3  | 0.056 | 45.41  | <0.001 |
| Error                       | 24 | 0.001 |        |        |
| <i>Activity</i>             |    |       |        |        |
| Treatment (T)               | 3  | 0.287 | 171.94 | <0.001 |
| Time period of day (P)      | 1  | 0.174 | 104.07 | <0.001 |
| T × P                       | 3  | 0.024 | 14.82  | <0.001 |
| Error                       | 24 | 0.001 |        |        |

lipids consumed ( $r = 0.343$ ;  $p = 0.106$  with respect to Gosner stage, and  $r = 0.221$ ;  $p = 0.229$  to body mass).

## Discussion

### Effects of diet quality on larval growth and development

This study demonstrates that diet quality has distinct effects on the growth and development of *P. punctatus* tadpoles. The HP diet favoured the acceleration of differentiation mechanisms. Metamorphosis is a thyroxine-dependent process, and many studies indicate that protein alters thyroid function in a number of organisms (Eales, 1988; Marine, Hershman, Maxwell, Dornfeld, & Schroth, 1991; Riley, Higgs, Dosanjh, & Eales, 1993). Contrary to previous studies on *Rana*, *Hyla*, *Bufo*, *Discoglossus* and *Crinia* (Álvarez & Nicieza, 2002a,b; Doughty & Roberts 2003; Kupferberg, 1997; Nathan & James, 1972; Pandian & Marian, 1985; Steinwascher & Travis, 1983), HP diet did not promote growth in the present experiment. But our results are consistent with those of Crump (1990)

for *Hyla pseudopuma*, a species adapted to habitat desiccation: faster development and low growth. Contrary to all these studies *Scaphiopus couchii* did not reduce the larval period but lost mass and body length when reared on HP food (Buchholz & Hayes, 2000).

Individuals from the LP treatment showed a greater growth rate and mass than those in the HP treatment. This may be due to sequestration of larger lipid stores (Pfennig, 1992). However, the LP group showed a low rate of development. The LP diet appeared to affect growth, whereas the HP diet facilitated development, creating a trade-off between the two diets. If we compare these treatments with the control group we can conclude that, considering growth, the two simple diets are sub-optimal compared to a mixed diet. This mixture diet may allow individuals to forage for complementary resources (Pfennig, 1992).

Response of the control group is consistent with the predictions made by Wilbur and Collins (1973) and Werner (1986), who proposed that in the absence of unfavourable ecological factors rapidly growing individuals delay metamorphosis and extend their larval period while capitalising on a rich growth opportunity.

### Diet choice influenced by ecological conditions

In contrast to the control group, tadpoles subjected to habitat desiccation showed a high preference for the HP diet during their active period. At the same time, these individuals were the most active. A possible explanation for this is that as the water volume is reduced, tadpole crowding increases, which leads to more interactions and displacements of individuals. In an environment where food resources are distributed unevenly there is potential for selective foraging. Tadpoles preferred food with relatively high-protein contents, a resource that contributes to accelerate development (Kupferberg, 1997). These tadpoles showed characteristics similar to those in the HP treatment: higher development stages and low level of growth. This is not in concordance with the results obtained by Doughty and Roberts (2003) where *Crinia georgiana* tadpoles exposed to deteriorating treatments metamorphosed early while the larval period was independent of food quality. Accelerating development may be an adaptive response of species that breed in temporary ponds, like *Pelodytes* (Crump, 1989; Denver, 1997; Doughty & Roberts, 2003; Newman, 1989; Richter-Boix, Llorente, & Montori, 2006). A short pre-

metamorphic stage reduces the risk of mortality by desiccation for temporary pond breeders but also results in smaller juveniles with lower fitness (Smith, 1987). So selective foraging allows tadpoles to minimise risk during the larval phase in species which need to forage after hatching to complete development. *C. georgiana* larvae, on the other hand, have sufficient reserves at hatching to complete metamorphosis (Doughty, 2002). This could be the explanation of the difference between the two species. *Crinia* do not need extra resources to accelerate development whereas *Pelodytes* do.

In the interference competition, treatment tadpoles also selected HP diet. This result is consistent with previous studies, in which *Pelodytes* tadpoles in presence of *B. bufo* accelerated development (Richter-Boix et al., 2004). This study reported that *Pelodytes* tadpoles alter their feeding strategy in the presence of a competitor. These changes correspond to a reduction in bottom feeding, with a slight increase in the use of middle and surface waters and grazing. Water surface films are higher in protein and lipids than bottom detritus (Nathan & James, 1972). Our data indicate that HP diet selection is one of the possible mechanisms that can accelerate development enabling tadpoles to escape from a hostile environment with poor growth opportunities.

We expected that in the predator treatment tadpoles would select the HP diet, thereby accelerating development to escape and decreasing mortality during the larval phase, as suggested by Werner's (1986) model. Our observations did not support this hypothesis but indicated that the trade-offs between mortality, growth and development are rather related to activity than to habitat or food selection per se. Larval activity decreased strongly, a common tadpole response to the presence of predators (reviewed by Alford, 1999), because increasing activity clearly increases vulnerability to predators (Werner & Anholt, 1993). Tadpoles spent less time swimming and searching for food because to them feeding activity appeared risky. The random distribution of tadpoles among the two diets had probably been caused by this low activity. Tadpoles tend to remain in a patch with food, regardless of its quality, in order to maximise growth (Anholt & Werner, 1995). A low rate of activity without resource limitations allows the food ingested to be allocated to growth at low energy cost (Babbitt, 2001; Tolonen, 1999), resulting in bigger tadpoles. Laurila, Kujasalo, and Ranta (1998) and Babbitt (2001) have reported a similar response. Since prey vulnerability and anti-predatory response decrease

with prey size (Eklöv, 2000; Eklöv & Werner, 2000), low activity not only prevents tadpole localisation by predators but favours relatively rapid growth, which can protect them from a size-limited predator (Richards & Bull, 1990).

To our knowledge, this is the first study to provide evidence of tadpole food selection in response to ecological hazards. The study demonstrates that diet selection may not be constant for a species but varies according to the ecological context. Results suggest a possible trade-off between feeding on protein and on carbohydrates, the former being associated with rapid development and small size at metamorphosis, the latter with a long larval period and high body mass. This suggests the need of feeding on both types of diet to optimise growth and development depending on larval conditions. Effects of diet quality on larval stages of organisms with complex-life cycles are well documented (e.g. MacNeil, Dick, & Elwood, 1997; Patt, Patt, Wainright, Hamilton, Whittinghill, Bosley et al., 2003; Wissinger, Steinmetz, Alexander, & Brown, 2004); however, active selection by individuals under different ecological hazards was not previously reported as a mechanism relevant to optimise larval development and growth rates. Diet selection may change during larval ontogeny, and in this manner the individual optimises growth when the developmental trajectory is fixed at an advanced Gosner stage (Hensley, 1993). For example, we can speculate that an individual can forage on high-protein food during the early stages to accelerate development and forage on high carbohydrate food in later stages when development time is fixed, adjusting diet during ontogeny to follow an optimal strategy.

Although the results of this study are compelling, there is substantial debate as to the relevance of laboratory and mesocosm studies to natural systems (e.g. Chalcraft, Binckley, & Resentaris, 2005; Skelly, 2005). The results presented here cannot be taken as evidence of tadpole diet selection in natural ponds. However, with the mechanistic approach we developed, we expected to contribute to the identification of a critical set of causal relations responsible for a particular result. While a large number of factors could be involved in structuring a given community, a combination of deductive and inductive reasoning will often suggest "fundamental" causal relations that are critical to a given ecological pattern (Resentaris & Bernardo, 1998). Feeding behaviour and diet choice of tadpoles could be mechanisms that explained the high variability described in developmental and growth rates in natural ponds under different ecological situations.

Knowledge of diet selection in different ecological contexts is of central importance to the understanding of trait-mediated indirect effects. The ecological role of a species depends on what other species (predators or competitors) or ecological factors are present, and this will change the way we have to look at food-web dynamics (Křivan & Schmitz, 2003; Schmitz, Křivan, & Ovadia, 2004).

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