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The plasticity of metamorphic traits in the Chinese brown frog tadpoles fails to obey Richards' hypothesis

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According to Richards' hypothesis, algae or cells in the intestinal tract has been considered the cellular inhibitory factor, when they fall off and hide in the faeces, excreted together with the faeces. If the animals feed on these faeces with algae or cells, and bring them into their systems, then the cellular inhibitory factor would play the main responsibility for growth inhibition. Here, we surveyed the effects of different combinations of faeces and food level on growth rates, survivorship, larval age and mass, and SVL at metamorphosis of the Chinese brown frog *Rana chensinensis*. Our results showed that food level can influence the length of the larval period of Chinese brown frog tadpoles, suggesting that delayed metamorphosis is caused by low food supply, indicative of a function of effective energy. Our data also clearly indicated that tadpoles in the presence of faeces were on average larger in body mass than those in the absence of faeces, which failed to obey Richards' hypothesis. Moreover, our results found evidence that faeces have a positive effect on the growth rate of tadpoles. Thus, there is no evidence for Richards' hypothesis, suggesting that this novel mechanism is selected for where coprophagy is likely to prove profitable, irrespective of the abundance of alternative food.

Keywords: Rana chensinensis, Richards' hypothesis, faecal material, mass at metamorphosis, growth rate

INTRODUCTION

In animals with complex life cycles, such as anurans, size and age at metamorphosis have a strong relationship with individual fitness (Arnold & Wassersug, 1978; Wilbur, 1980). Larval amphibians are more likely to experience variation in food availability because of the variety of spawning sites (Morey & Reznick, 2004; Skelly, 2004). In addition to energy uptake, food availability can be generally regarded as a major proximal cause of variation in metamorphic size and timing of metamorphosis (Newman, 1998; reviewed by Álvarez & Nicieza, 2002; Castano et al., 2010).

In the field or laboratory, high food availability can accelerate growth and developmental rates, thus permitting larvae either to maximise metamorphic size or minimise timing of metamorphosis (Pandian & Marian, 1985; Arendt & Hoang, 2005; Yu et al., 2015; Yu et al., 2016a; 2016b; 2016c; Yu & Han, 2020). Conversely, low food availability owing to low food supply, large population density of the larvae, or both, would also postpone metamorphosis, such that if the environmental conditions were poor in the ponds, then larvae would spend plenty of time to achieve the minimum size for metamorphosis because of slow growth rates (reviewed by Wilbur & Collins, 1973).

In addition, other factors can also affect timing of metamorphosis and growth rate, such as temperature, water volume and competitors and predators (Rose, 2005). The excretory material including something inhibitory to growth is a popular idea (Richards, 1958; 1962). Here, Richards' hypothesis predicted that the crowding effect would occur if tadpoles could eat their own excretory material and then the cellular inhibitory factor is introduced into their systems (Richards, 1958). It was later identified that a non-pigmented, unicellular alga can be detached from the faecal material of larvae which is linked with growth inhibition in British anuran tadpoles. Wong et al. (1994) proposed the name *Prototheca richardsi* sp. which belonged to the genus *Prototheca* (Beebee, 1991). The growth-inhibiting algae is not overtly parasitic, instead, its mode of action seems to rely on altering feeding behaviour. For example, large, superior tadpoles can release a large number of growth-inhibiting algae hidden in the faeces. Then, small tadpoles are attracted to feed on algae-rich faeces and are thereby diverted from other higher quality food resources, while large tadpoles do not alter feeding behaviour (reviewed by Griffiths et al., 1993). Up to now, some studies have proved that faeces are indeed inhibitory to the growth of anuran tadpoles (Griffiths et al., 1991; 1993; Baker & Beebee, 2000) and snails (Crabb, 1929). Further, high food level can ameliorate growth inhibition under crowded conditions, and the production of inhibitory cells is inversely correlated with food levels (Griffiths et al., 1993).

The question arises whether the faeces is the major factor leading to crowding effects in all organisms and

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under all conditions (Richards, 1958). However, few studies have examined how faecal material and food level can interact to affect amphibian larvae (Gromko et al., 1973). Here, we investigated the effects of food level and faecal material on size and age at metamorphosis of the Chinese brown frog *Rana chensinensis* tadpoles. Specifically, if the growth inhibition of faecal material is stronger at a low food level, and thus larger body length and mass at metamorphosis are rare, longer length of larval period might be expected. If, however, the growth inhibition of faecal material is weak at a high food level, and difference between the presence of faecal material and absence of faecal material may be undetectable.

MATERIALS & METHODS

Study species

Female frogs in *Rana chensinensis* are the larger sex and are widely distributed north of the Yangtze River in China (Yu et al., 2015). This animal belongs to a typically explosive breeder with a relatively short breeding season (8–16 days; Wells, 2007; Yu et al., 2015), and favours small and medium still-water bodies for breeding behaviour. *R. chensinensis* begins reproductive behaviour in early February when the water temperature is higher than 5 °C. The frogs usually amplexus and spawn at night, while male frogs demonstrate chorusing behaviour in warm breeding ponds. After two weeks, the tadpoles hatch in a natural pond, then feed on Spirogyra and *Potamogeton crispus* for three months (Cao et al., 2002) and finally, the metamorphosis go ashore and begin to live on land.

Field and laboratory procedures

Ten fresh egg clutches of *R. chensinensis* were collected in Xinyang (114° 06′ E, 32° 12′ N, elevation 22–100 m), Henan, the central plains of China, during 11–19 February 2021. Then, to obtain the experimental tadpoles, we selected 100 fresh eggs from each clutch and placed them in an opaque round plastic container (2000 ml, diameter = 15.8 cm) with 15 cm of fresh water to hatch. The experiment was carried out in the indoor laboratory which is 0.5 km away from the spawning site.

Experiment design

We used a 2 × 2 factorial design to analyse the influences of food level and faeces on larval growth and development. For every factorial treatment we used 30 tadpoles that were carefully chosen, ensuring that all individuals were the same size (3.55–3.65 mm) and development stage (absorption of external gills and formed spiracle, Gosner stage 26). Also, we randomly selected one tadpole from each clutch in each of the treatments (each representing a different family) housed individually in opaque round plastic bowls (500 ml) and three replicates were implemented, so that it could minimise any parental or genetic effects and intraspecific competition through the experiment. We used commercial fish food (Bieyanghong, Biological Co. Ltd., Hangzhou, China, medium protein content, MPC; 30 % protein, 10 % lipids, 18 % algae, 4 % fibre, 10 % ash) to feed the tadpoles. All tadpoles experienced the same temperature (room temperature = 17.3 ± 1.33 °C) and photoperiod (13L:11D) conditions throughout the study period. We changed the water in the containers once a week.

To assess the food level influences, we designed two treatments of feeding regime: (i) low mass-specific food level (6 % of per tadpole mass perday) and (ii) a high food level (12 % per tadpole mass per day) throughout the experiment (Zhang et al., 2007). For each food level, two different faeces regimen were chosen across the larval period: (i) presence of faeces (sucked into the faeces of other individuals where 12 or more large tadpoles were put into a litre of water within two days, diluted to 60 ml, then accelerated the movement of faeces by rotating the beaker, simultaneously sucked 1 ml of faecal liquid with a pipette gun and injected into one plastic bowl; Richards, 1958) and (ii) absence of faeces (sucked out the faeces by Pasteur pipette every four to six hours, thus there was very few or a few faeces at the bottom of the plastic bowls, Biologix 30-0138A1).

Five variables were measured: (1) age at metamorphosis [number of days from incubation until metamorphosis (the emergence of at least one forelimb, Gosner stage 42)]; (2) body length (snout-vent length, SVL), the tadpole was placed into a plastic basin of flat bottom with a caliper (error 0.05 mm) to get digital images, the SVL measure was obtained using the free computer software TpsDig 2; (3) body mass, which was measured with an electric balance (error 0.001 g); (4) growth rate, which was calculated with the following equation: mass at metamorphosis/age at metamorphosis (Laurila, 2000); (5) survivorship, which was classified two-point scales based on the number of tadpoles in a plastic bowl: 1 = one tadpole survived until metamorphosis; 0 = no tadpoles survived until metamorphosis.

Data analysis

One-Sample Kolmogorov-Smirnov Test was used to test whether data met normal distribution. Then, we analysed metamorphosis age, body length and mass at metamorphosis, growth rate and survivorship, by using a univariate two-way ANOVAs with type III mean squares and faeces, food level, and their interaction as fixed factors. If the effects of any fixed variable in univariate two-way ANOVAs were significant, the data were analysed with one-way ANOVA (four experimental treatments as factors) by using Fisher's LSD post-hoc multiple comparisons to test differences between food levels or between faeces levels (IBM SPSS Statistics 20.0, IBM Corp, Armonk, NY, USA). All probabilities were two-tailed, with values presented as means ± SE (standard error).

RESULTS

The effects of food level and faeces on age at metamorphosis

The effect of food level on age at metamorphosis was significant ($F_{1,101}$ = 7.936, p = 0.006; Table 1, Fig. 1a), revealing that age at metamorphosis with presence of

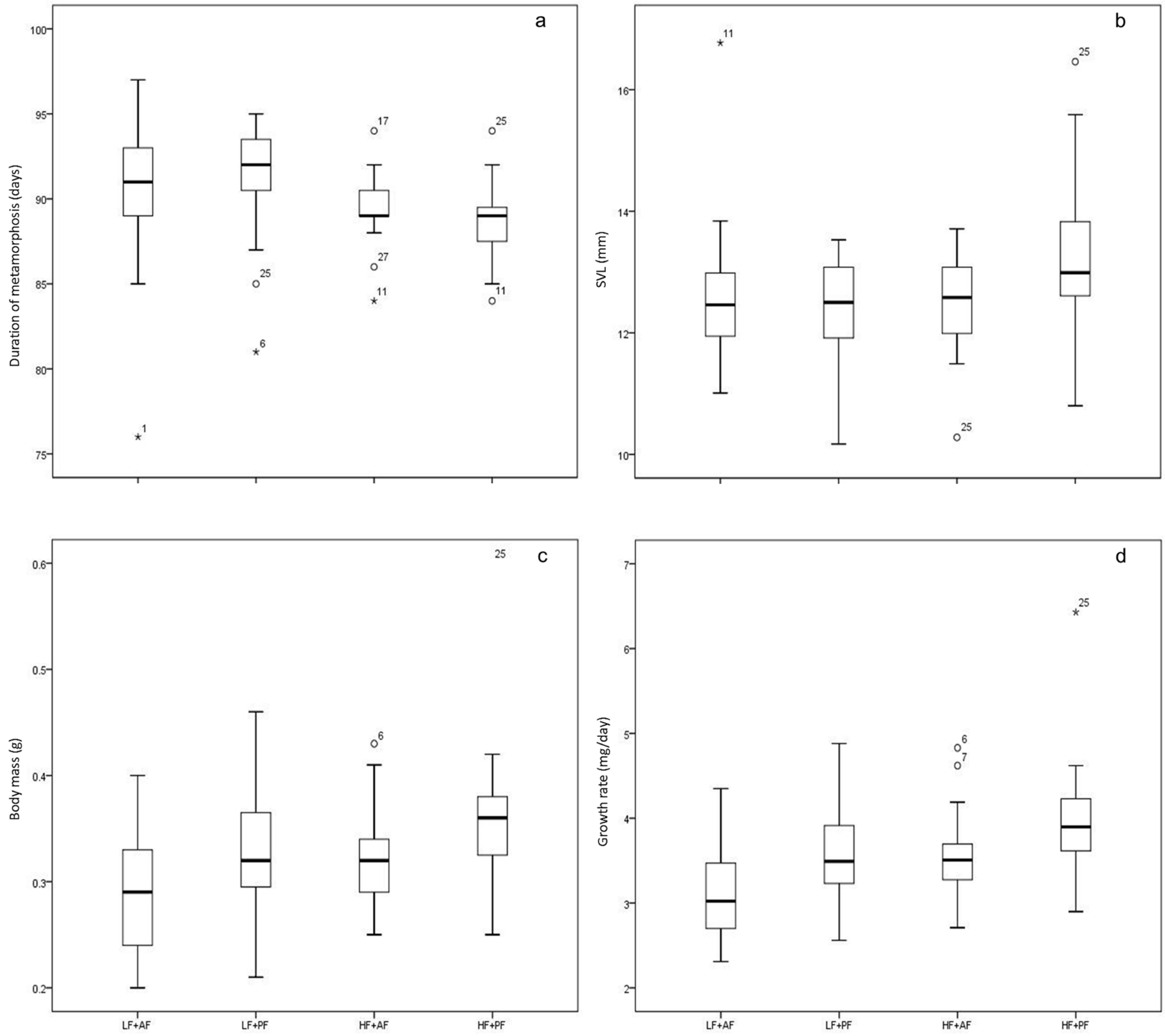

Figure 1. Influences of faecal material and food level on **(a)** age at metamorphosis, **(b)** SVL, **(c)** body mass, and **(d)** growth rate of the Chinese brown frog *Rana chensinensis* at forelimb emergence (Gosner stage 42; LF, low food level; HF, high food level; AF, absence of faecal material; PF, presence of faecal material; the box plots indicate median, 25th and 75th quartile and range).

faeces reared at a high food level was significantly shorter than those at a low food level ($p = 0.011$), but the effect of food quantity was negligible when faeces were absent ($p = 0.175$). However, there was not a significant effect of faeces ($F_{1,101} = 0.171$, $p = 0.680$; Fig. 1a), as well as an interaction between faeces and food level ($F_{1,101} = 0.840$, $p = 0.362$).

The effects of food level and faeces on body length and mass at metamorphosis

Body length was not significantly affected by food level ($F_{1,101} = 3.708$, $p = 0.057$; Table 1, Fig. 1b). The faeces was not statistically significant ($F_{1,101} = 1.436$, $p = 0.234$); however, there was a tendency for the difference in body length between faeces treatments to be greater at the same food level (Fig. 1b). The interaction between faeces and food level was not significant ($F_{1,101} = 1.087$, $p = 0.300$).

Mass at metamorphosis was affected by faeces ($F_{1,101} = 15.332$, $p < 0.001$; Table 1, Fig. 1c) and food level ($F_{1,101} = 9.481$, $p = 0.003$), indicative of increasing mass at metamorphosis at a high food level (both $p < 0.039$) or in presence of faeces (both $p < 0.008$). However, there was not a significant interaction between food level and faeces ($_{F1,101} = 0.005$, $p = 0.944$).

The effects of food level and faeces on growth rate and survivorship

The effects of faeces and foodlevel on growth rate were significant (faeces, $F_{1,101} = 17.727$, $p < 0.001$; food level, $F_{1,101} = 15.694$, $p < 0.001$; Table 1, Fig. 1d), revealed that growth rate at a high food level and presence of faeces was significantly larger than those at a low food level (both $p < 0.008$) and absence of faeces (both $p < 0.007$). However, there was not a significant interaction between food level and faeces ($F_{1,101} = 0.034$, $p = 0.854$).

Survivorship was positively influenced by only food level ($F_{1,116} = 6.332$, $p = 0.013$), especially in the presence of faeces ($p = 0.050$, Table 1, Fig. 2). The effects of faeces on

Table 1. Two-way ANOVAs table of the effects of faeces and food level on metamorphic traits in a *Rana chensinensis* population

Response variable	Source of variation	df	MS	F-value	P-value
Length of larval period	Faeces	1	1.917	0.171	0.680
	Food level	1	89.091	7.936	0.006
	Faeces × Food level	1	9.427	0.840	0.362
	Error	101	11.227		
Body mass	Faeces	1	0.045	15.332	< 0.001
	Food level	1	0.028	9.481	0.003
	Faeces × Food level	1	0.000015	0.005	0.944
	Error	101	0.003		
SVL	Faeces	1	1.758	1.436	0.234
	Food level	1	4.54	3.708	0.057
	Faeces × Food level	1	1.33	1.087	0.300
	Error	101	1.224		
Growth rate	Faeces	1	5.703	17.727	< 0.001
	Food level	1	5.049	15.694	< 0.001
	Faeces × Food level	1	0.011	0.034	0.854
	Error	101	0.322		
Survival	Faeces	1	0.075	0.704	0.403
	Food level	1	0.675	6.332	0.013
	Faeces × Food level	1	0.008	0.078	0.780
	Error	116	0.107		

survivorship was not significant ($F_{1,116}$ = 0.704, p = 0.403), revealing that presence of faeces does not increase mortality. The interaction of food level and faeces was not statistically significant ($F_{1,116}$ = 0.078, p = 0.780).

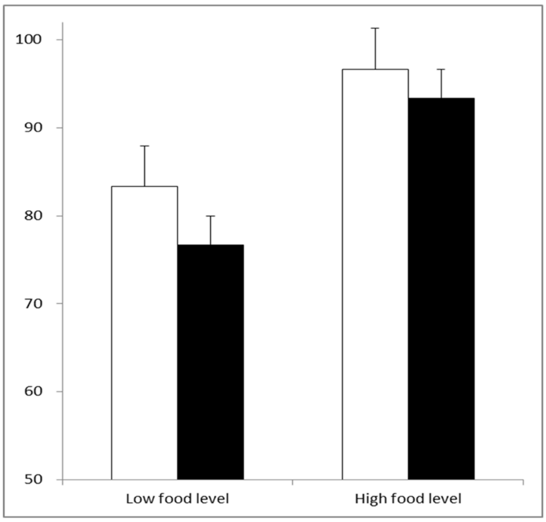

Figure 2. Influences of faecal material and food level on survival of the Chinese brown frog *Rana chensinensis* at forelimb emergence (Gosner stage 42; open columns, absence of faecal material; black columns, presence of faecal material).

DISCUSSION

Many environmental factors including temperature, food availability, pond desiccation and predation risk may influence growth and development of larval anurans (reviewed by Laurila et al., 2001; Neptune & Bouchard, 2020; Youngquist & Boone, 2021). In most cases, the effect of enhanced growth conditions is faster development (reviewed by Álvarez & Nicieza, 2002; Rowland et al., 2016). Our results showed clearly that food level influences the length of larval period of Chinese brown frog tadpoles, suggesting that delayed metamorphosis is caused by low food level. In fact, retardation is due to low food level, indicative of a function of effective energy. Our data showed that Chinese brown frog tadpoles in the presence of faeces were on average larger in body size than those in the absence of faeces. Further, our results have found evidence for positive effect on tadpole growth rate. Thus, we found no evidence for Richards' hypothesis, but it conformed to the inverse of Richards' hypothesis.

Two possible mechanisms could explain such a faeces effect independent of food levels. First, the present study indicated the inhibited growth of faeces may be weak, which could be due to: (1) a single tadpole housed individually in relatively large beakers, indicating that the uncrowded tadpoles may be expected to produce fewer growth-inhibiting algae than the crowded ones in presence of aggressive interactions between individuals (Richards, 1958); (2) algae may suffer inhibition during early development of Chinese brown frog tadpoles because their effects on growth were correlated negatively with tadpole size (Beebee, 1991; Beebee & Wong, 1992; Baker & Beebee, 2000); or (3) single species of anuran larvae produce fewer growth-inhibiting algae of tadpole (e.g. *Prototheca* algae) in their faeces than those raised with two or more species (Griffiths et al., 1993; Bardsley & Beebee, 2001). Therefore, the Chinese brown frog tadpoles that feed their own or congener faeces probably produce a small quantity of protothecan cells in their faeces. Biesterfeld et al. (1993) suggested that Anurofeca is a natural endocommensal of tadpoles, which only inhibits larval growth when they are present in a stressful environment, such as high density or high temperatures (Hailey et al., 2007).

A second possibility is that the results can be explained in terms of the nutritional value of the faeces. In this study, Chinese brown frog tadpoles, dawdling like micro automatic vacuum sweeps, absorb excrement with cells and food particles. In fact, compared with the wild ponds, even with the high food level in the laboratory the tadpoles cannot meet their nutritional needs because tadpoles can feed on a multitude of food sources in the wild ponds (Yu, personal observation). Here, the nutritional value of the faeces could be due to: (1) cellulose digested by organisms in the tadpole digestive tract becoming available only after the faeces have been passed, as found in some rodents (Gromko et al., 1973); or (2) it may increase intestinal microbial diversities and alter intestinal microbiota profile of larvae by means of feeding on congener faeces (Zhang et al., 2023); or (3) organisms associated with the faeces have nutritional value in themselves. Steinwascher (1978) suggested that faeces provide a ready particulate food resource for tadpoles although it seems to be a relatively low-quality food. Moreover, previous studies had demonstrated that faeces still contain a low quantity of plant material (Gromko et al., 1973). Our results showed that faeces had a significant acceleration of tadpole growth to obtain large metamorphic size. This result was consistent with Gromko et al. (1973), suggesting that it seems possible that faeces consist of a routine larval food source and are fed as a portion of the routine diet. Further, several studies revealed that there is no evidence of waterborne growth inhibitors or lack of such agents when two amphibian larvae coexist in a pond (Morin & Johnson, 1988; Petranka, 1989; Biesterfeldt et al., 1993). As a result, we suggest that faeces consist of a routine larval diet and are fed as part of the routine food source.

It had been verified that food availability plays fundamental roles in age at metamorphosis (Leips & Travis, 1994; Rowland et al., 2016). Some experimental studies have demonstrated that high food level with a large proportion of protein can generate a double action, accelerating both growth and development (Nathan & James, 1972; Steinwascher & Travis, 1983; Pandian & Marian, 1985; Yu et al., 2016a; 2016c; Yu & Han, 2020). For example, Pandian & Marian (1985) found that a richer and more nutritious food promote larval growth, resulting in shorter larval growth time and larger metamorphic size. Moreover, Wilbur & Collins (1973) model suggested that if the environmental conditions are optimal (such as adequate food), reduce the density and/or competition effects, and the larvae optimise their metamorphosis time and individual size to enter the terrestrial habitat. But limiting food before reaching the minimum size for metamorphosis will lead prolonged metamorphosis. In this study, our results revealed that *R. chensinensis* tadpoles reared at level of high food have a shorter larval developmental time and larger metamorphic size than those reared at the level of low food. Additionally, Beebee (1991) found that growth inhibition is relieved when larvae feed on high food levels.

In conclusion, we find no evidence for the suggestion that faeces are apparent growth-inhibiting factors, which failed to obey Richards' hypothesis. Interestingly, we found faeces can accelerate growth, obtain large metamorphic size and high survival of *R. chensinensis*, as well as food level, suggesting this novel mechanism is selected for where coprophagy is likely to prove profitable, irrespective of the abundance of alternative food.

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