

Björn Lardner · Jon Loman

## Growth or reproduction? Resource allocation by female frogs *Rana temporaria*

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**Abstract** The decision how to allocate marginal resources to reproduction and growth can have important effects on associated life-history parameters as well as on population dynamics. In addition to showing variation among individuals in a population, such allocation rules may be either condition-dependent or fixed in different individuals. While many studies on anuran amphibians have focused on egg numbers and egg sizes in females of different sizes, virtually no data exist on the relative allocation of marginal resources to growth versus reproduction. In the laboratory, we therefore offered female common frogs (*Rana temporaria*) low versus high food rations for a full reproductive cycle, and monitored their growth and later reproductive investment (egg number and egg size the following breeding season). Feeding rates had an effect both on female growth and on egg number and size. There was no trade-off found between the two forms of investment. A flexible allocation rule could not be supported as there was no significant effect of feeding rate on the relative allocation of resources to growth versus reproduction.

**Keywords** Acquisition · Anurans · Clutch size · Egg size · Feeding

### Introduction

Life history theory is concerned with the way individuals allocate resources to growth and reproduction (Roff 1992; Stearns 1992). It assumes that resources are limited and that there are physiological constraints on growth and reproduction. When growth is indeterminate, there is a choice between allocating marginal resources (or surplus energy; Kozłowski 1991) to growth or to reproduction or to some combination of the two (Kozłowski 1996; Heino

and Kaitala 1999). In such animals growth may, in turn, be considered an investment in future reproduction as large females frequently produce (or at least have the capacity to produce) more young than do small females. Which strategy is optimal may depend on several factors: size-dependent fecundity, size-dependent mortality, and the mortality risk associated with reproduction (Schaffer 1974; Cichon 1997). As an extreme option, if the marginal resources available are low and the mortality risk associated with reproduction is high, it may be beneficial to skip reproduction and allocate available resources to growth, allowing a higher fecundity for the following reproductive event (Loman 1978; Schwarzkopf 1993; Jokela 1997; Edwards et al. 2002). At the other extreme, if conditions suggest a low probability of surviving to later breeding seasons, all marginal resources should be invested in breeding in the present season (Schneider and Lubin 1997).

Among organisms with indeterminate growth, there have been numerous studies on the trade-off between offspring quality (egg size) and offspring quantity (egg number) in reptiles (Ji and Braña 2000) and amphibians (Jørgensen 1981; Cummins 1986; Tejedo 1992a). This subject has also received considerable theoretical interest (Smith and Fretwell 1974; Parker and Begon 1986; Winkler and Wallin 1987; Roff 1992; Stearns 1992; Bernardo 1996; Caley et al. 2001). There have also been many studies of the relation between present female size and egg size and egg number in reptiles (Brown and Shine 2002) and amphibians (van Gelder 1995).

In this perspective there have been surprisingly few studies devoted to the relation between investment in somatic growth versus reproduction in reptiles and amphibians.

This problem is important for an understanding of the population dynamics of amphibians. It is usually assumed, quite reasonably, that reproductive output increases if feeding conditions are good (Loman 1990). However, demonstrations of this for frogs are rare. The few we have found include a study by Girish and Saidapur (2000) on *Rana tigrina* and indirect evidence from a study by Ryser

B. Lardner · J. Loman (✉)  
Department of Animal Ecology, Lund University,  
223 62 Lund, Sweden  
e-mail: jon.loman@zoekol.lu.se  
Fax: +46-46-2224716

(1989) that suggests an effect of environmental conditions, e.g. food, on reproductive output in *Rana temporaria*.

In this study we conducted an experiment to study what effect resource availability has on investment in growth and reproduction in female frogs (*R. temporaria*). An experimental approach meant that the frogs actual feeding rate could be controlled, something that is difficult to achieve in nature. Also, it had the advantage of not confounding cause and effect. It is quite possible that frogs in good condition both feed at a high rate and grow (or reproduce) well because they are in good condition.

We also asked if all females aim at the same balance between growth and reproduction (i.e. the same allocation rule) or if there is a tendency that females investing heavily in growth reduce investment in reproduction, relative to other females. While an optimal trade-off should be realized within individuals, quality differences (genetic or phenotypic) among individuals (Gebhardt-Henrich et al. 1998) may mask a negative correlation within a population (van Noordwijk and de Jong 1986). Our experimental method enabled us to analyse this problem.

Studying allocation rules in organisms with no parental care has the advantage that compensatory feeding can not confound the relation between offspring size and fitness. Most anuran amphibians have no parental care, and offspring from all individuals which reproduce in a certain breeding pond will experience similar juvenile conditions. Hence the allocation rule of different females may directly affect their offsprings performance. There are two fundamentally different patterns to be expected (Jokela and Mutikainen 1995). First, the allocation rule of an individual female may be fixed, which may be genetically based or determined by growth during the pre-reproductive phase. Alternatively, the allocation rule is flexible, so that recent resource acquisition (for example, since the last reproduction event) determines the relative investment in growth relative to reproduction. We analysed this possibility.

To study these aspects we gave adult females different rations of food for a whole reproductive cycle (from one spring reproduction to the next spring reproduction) and monitored growth and reproductive parameters. Thus we attempted to answer three basic, but in amphibians nevertheless little studied questions:

1. Do females use marginal resources primarily for growth or for reproduction?
2. Is there a trade-off between investment in these two traits? and
3. Are allocation rules affected by resource availability?

## Materials and methods

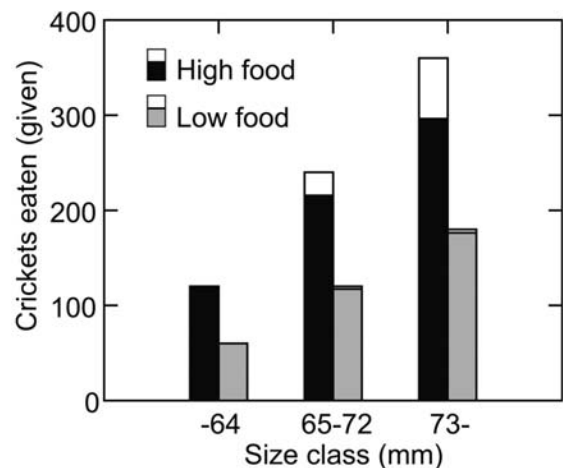
### Procedures

Frogs were collected from three ponds ( $n=2$ , 6 and 32 pairs respectively) in south-western Scania (southernmost Sweden) during the spring breeding period in 2000. The amplexus pairs were placed

in plastic aquaria with pond water. The pairs were allowed to breed in the aquaria (standing in the source pond), and the females were then brought into the laboratory. Females spawned from 3 to 9 April 2000. The spawn was measured 2 days after laying with regards to egg diameter and egg number. The females were weighed and their snout-urostyle length measured immediately after oviposition. Length and weight were combined to a composite measure of size, as the first principal component. This explained 97% of the variation in length and weight. The frogs were then kept individually in slightly tilted 20 l plastic aquaria, with some water in the lowermost end and a half clay pot as cover in the dry end. A coarse plastic net on the bottom prevented food animals from drowning. A window provided a natural light regime. The housing was unheated but moderately insulated which meant that average temperatures were natural but the daily fluctuations somewhat ameliorated.

After an initial phase of feeding frogs crickets ad libitum, we gave each frog either a standard low or a standard high food ration. Since frogs varied in size, we divided them into three size classes: up to 64 mm ( $n=22$ ), 65 to 72 mm ( $n=12$ ), and 73+ mm ( $n=6$ ). The average weight of frogs within each size class related as 1:2:3. Frogs in the lowest size class were given either one (low ration) or two (high ration) crickets every second day, while the corresponding rations for the other two size classes were two or four and three or six crickets. The crickets (obtained from a commercial breeder) varied somewhat in size, averaging 16 mm. We selected the crickets used on any given feeding day so that they were all of equal size, thus minimizing the differences among individual frogs. Frogs were kept and fed this way from 5 May to 11 September. In the low ration groups, almost all crickets were eaten. In the high ration groups, small frogs also consumed almost all crickets offered while medium and large frogs consumed on average 90% and 82% respectively of the crickets (Fig. 1). We again measured the snout-urostyle length and weight on 19 September. After the summer feeding period, we left the frogs in a natural light and temperature regime for another 2 weeks before moving them to a dark thermo-constant room at +3°C. During the non-feeding phase, frogs were kept in ventilated plastic boxes with moist *Sphagnum* moss.

Rather than trying to persuade the females to mate and breed in the laboratory the next spring, we chose to kill and dissect them to obtain data on reproductive effort. This approach was taken due to the difficulties we expected in inducing synchronous and reliable breeding under artificial conditions. Thus, on 20 March we measured female length, weight (excluding eggs), egg number and diameter.



**Fig. 1** Potential and realized feeding rate. The filled bars show the number of crickets offered and eaten by frogs in the different size and feeding classes. The open parts on top represent crickets offered but not eaten

## Reference frogs

As a check of the well-being of the experimental frogs, their growth was compared to that of wild frogs in the same area. These were captured, measured, marked, released and recaptured after 1 year as part of another study (Loman and Lardner, in preparation).

## Analyses and variables used

Within the three size classes, variation in frog size resulted in variation in feeding rate (food consumed per unit frog), in addition to variation imposed by our two feeding rations and variation in actual number of crickets consumed. Therefore, an index of feeding rate was constructed. This was the residual in a regression of number of crickets consumed per frog on frog weight in May (i.e. weight at the start of the controlled feeding). This index was used in the statistical analyses as the measure of resource acquisition rate.

Investment in growth was measured as the increase in size from 2000 to 2001, corrected for original size in 2000. This was done by including size in 2000 in a multiple regression together with feeding rate. Investment in reproduction was also analysed by multiple regressions including female size in 2000 together with feeding rate. This is better than correcting for the female size in the year of response (2001) since the latter approach confounds the effect of investment in reproduction with that of investment in the females own growth. Two separate measures of reproduction were used: egg size (diameter) and clutch size.

For the analysis of a trade-off, investment in growth was measured as size in 2001, corrected for size in 2000. Here, the correction was done by using the residuals from a regression of size in 2001 on size in 2000. For investment in reproduction, only one measure is used. This is an index of total clutch volume. It is computed as number of eggs  $\times$  egg diameter<sup>3</sup>. This index is computed for 2001 and is corrected for female size in 2000 by using the residual in a regression on size in 2000. This residual provides a measure of the reproductive investment of each female.

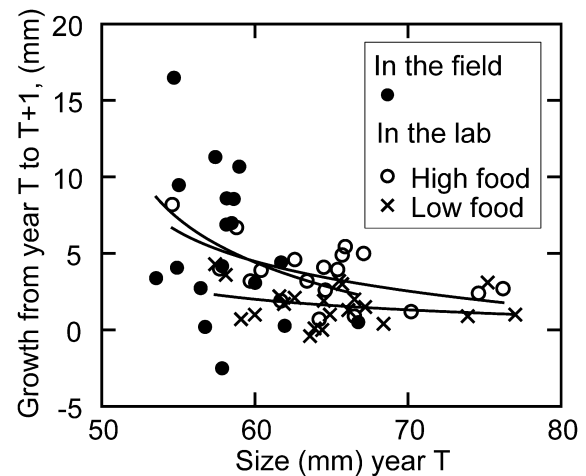
## Results

### Growth pattern

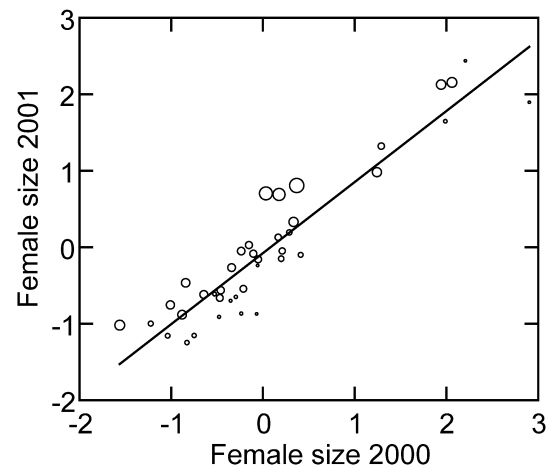
Frogs increased less in length the longer they were (Fig. 2,  $df=1, 37, F=5.83, P=0.021$ , the interaction with feeding rate was not significant). Length growth rates observed in the experiment were in the same range as those recorded in the wild in the same source area (Fig. 2). All increase in length took place before 19 September. Actually, between September 2000 and March 2001 the frogs decreased by an average of 0.7 mm (paired  $t$ -test,  $df=40, t=4.12, P<0.001$ ). There was no difference between frogs fed a high or a low food ration in this respect (ANOVA,  $df=1:39, F=0.934, P=0.34$ ).

### Investment in growth and eggs

Females with a high feeding rate grew more than those with a low feeding rate (Fig. 3, Table 1). There was also an effect on overall egg characters (size and number combined) from feeding rate (multivariate multiple regression,  $df=2, 36, Wilks\ lambda=0.33, P<0.001$ ). Analysing the two egg characters separately, large females and (independently of this) females with a high feeding rate



**Fig. 2** Annual growth in relation to body size in common frogs from the field (J. Loman and B. Lardner, unpublished data) and from this study. Logarithmic curve fits are shown



**Fig. 3** Effect of feeding rate on female growth. Female size indices are PCA scores based on female length and weight after breeding in 2000 and 2001 respectively. Size of symbols is proportional to female feeding rate, accounting for female weight and food ration. Notice that large symbols (females with high feeding rate) are generally above the overall growth regression line

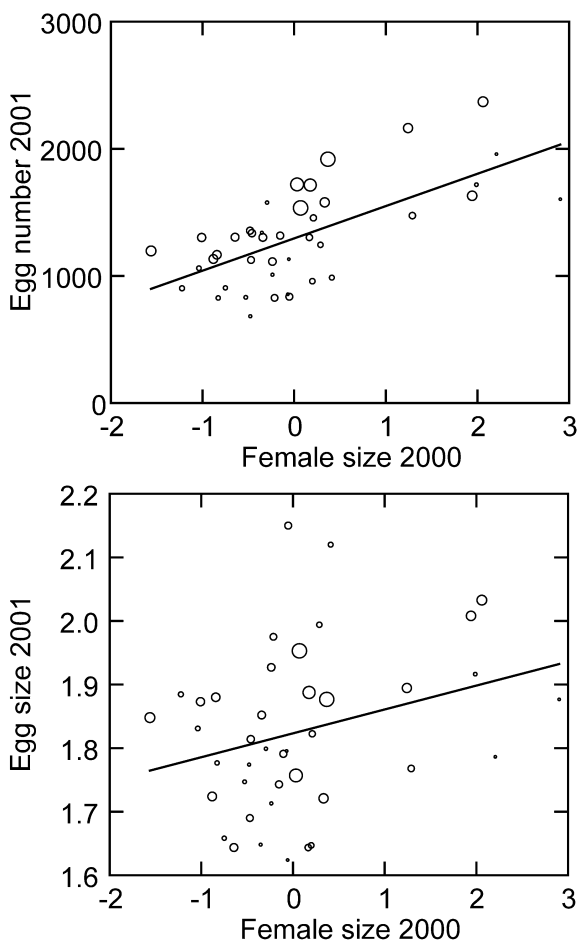
laid more eggs than small and low feeding rate ones (Fig. 4a, Table 1). There were corresponding effects on egg size (Fig. 4b, Table 1). Thus, marginal resources were invested in both growth and reproduction.

### Trade-off

After correcting for feeding rate (by including it as one of two factors in a multiple regression), there was no significant correlation between female growth and reproductive investment (egg volume) (Fig. 5,  $t=0.84, P=0.41$ ). The interaction feeding rate  $\times$  female residual growth (removed in the test above) in this multiple regression was not significant ( $t=0.51, P=0.62$ ), indicating that the allocation rule is not strongly affected by female condition.

**Table 1** Analysis of the effect of female size in 2000 and feeding rate on female size in 2001 (and thus growth), egg number and size. Female size is a PCA score based on female length and weight after breeding in year 2000. The test is a two-way multiple regression. The interactions, which were not significant, were removed before the final analysis, as given in the table

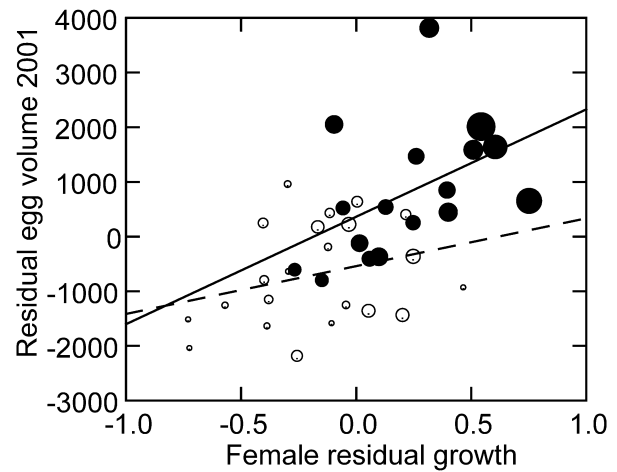
		Growth	Egg number	Egg size
Size	<i>df</i>	2, 37	2, 37	2, 37
	<i>t</i>	25.07	7.35	1.97
	<i>P</i>	< 0.001	< 0.001	0.056
Feeding rate	<i>t</i>	7.00	5.16	2.11
	<i>P</i>	< 0.001	< 0.001	0.042
Size×rate	<i>df</i>	3, 36	3, 36	3, 36
	<i>t</i>	1.29	0.016	0.34
	<i>P</i>	0.21	0.99	0.74



**Fig. 4a, b** Effect of feeding rate and female size on egg size and number. Female size and feeding rate values are calculated as in Fig. 3

## Discussion

The food rations we chose proved to be accurate for the desired effect. Medium-sized and large frogs in the high provision treatments did not eat all crickets. This shows that a higher ration would not have been meaningful. On



**Fig. 5** Analysis of possible trade-off between female growth and reproductive investment. Female residual growth is size (PCA based on length and weight) increase from 2000 to 2001 corrected for size in 2000. Residual egg volume is egg volume in 2001 corrected for female length in 2000. Size of symbols proportional to female feeding rate. Also, *filled* symbols are for females fed a high food ration and *open* symbols for females fed a low ration. To support the discussion, we also show linear regressions that are based on feeding rations (high and low) rather than actual feeding rates. The difference in slope between these two regressions is not significant ( $df=1, 35, F=0.98, P=0.33$ )

the other hand, even frogs on a low ration grew at a rate similar to what has been observed in nature.

Since the animals used were collected from different populations, it might be that their life-history traits to some extent differed due to their origin (Ryser 1996; Loman 2001). However, we here assume that the allocation rules and trade-off patterns that we focus on in this study should be qualitatively similar across populations and that effects of condition (food treatment) and frog size have greater effects on these patterns than does origin.

## Marginal resources: growth or reproduction?

Regardless of the rations provided, larger females produced more and larger eggs. Both effects have repeatedly been found for *R. temporaria* (Hönig 1966; Kosłowska 1971; Jörgensen 1981; Cummins 1986; Gibbons and McCarthy 1986; Kyriakopoulos-Sklavounou and Loubourdis 1990; Joly 1991) and also other frogs [*Bufo calamita* clutch size only (Tejedo 1992b); *Rana sylvatica* (Berven 1988); *Rana palustris* (Resetarits and Aldridge 1988); *Bufo bufo* (van Gelder 1995)], reptiles (Ji and Braña 2000; Brown and Shine 2002), gastropoda (Ito 1997) and fish (Grossman et al. 2002).

The experiment showed effects of feeding rate on both female growth and egg number and size. This confirms, for a frog, the assumption that feeding conditions for animals with indeterminate growth affects both the coming seasons reproduction and, through effects on growth, that of following seasons (Heino and Kaitala 1999).

A corresponding experiment by Girish and Saidapur (2000) also found an effect of feeding ration on repro-

ductive investment. In other taxa, similar studies have provided variable results. Doughty and Shine (1998) found that increased basking led to a higher feeding rate in a skink (*Eulamprus tymapanus*), which increased tail width (the tail is a storage organ). This in turn led to increased reproduction but not to body growth. In contrast, Reznick (1983) found that female guppies on a rich diet grew larger and invested more in reproduction than did females on a poorer diet.

### Capital or income breeding?

Recently, there has also been an interest in the question of Capital versus Income breeding (Jönsson 1997; Bonnet et al. 1998; Doughty and Shine 1998). Indeed, it is often not altogether clear if the organisms under study practise one of these, or a mix. The frogs in this study spawn in spring, after a 5- to 6-month inactive non-feeding period. However, the eggs laid are actually formed while the frogs are actively feeding and have already almost reached their final size by late summer (Jørgensen 1981). In this study, energy not canalized into growth or reproduction during summer was probably used to form fat bodies that provide the energy required to survive the winter (Seymour 1973) as there was no growth during this period. Thus, *R. temporaria* should probably be classified as an income breeder. To complicate things further, there is even the possibility that females do not spawn all (cf. Reyer et al. 1999) or any (Loman 1978) eggs, in effect turning the eggs into stored energy reserves. Since we have shown that marginal resources are allocated to both growth and reproduction, such reserves could therefore be seen as a potential for capital breeding in successive seasons.

### Trade-off and allocation rules

There was no sign of any trade-off between female growth and reproductive investment. A positive correlation is a commonly observed phenomenon in similar studies. While there might be a trade-off within an individual, quality differences in acquisition competence among individuals may mask a comparatively weak, negative trade-off pattern (van Noordwijk and de Jong 1986; Doughty and Shine 1997; Lardner 2000; Loman and Claesson 2003). While our analysis tried to overcome this by standardising food rations, and further corrected for the actual feeding rate (rendering a size-adjusted measure of resource acquisition), there was no sign of negative correlations among individuals having similar feeding rates. Thus, we believe that there is a correlation between the ability for fast growth and the ability to invest much in reproduction that off-sets the expression of a trade-off within the individual. Such a correlation could either have a genetic or a phenotypic background, the latter due to e.g. pathogen or parasite load, or due to beneficial early growth (a silver spoon effect; Grafen 1988; Kaplan 1998).

Note that a negative correlation between growth and fecundity has also been repeatedly documented (Stearns 1992). However, this refers to situations when effects of reproduction on later growth is measured, a different form of trade-off to the one studied here. Our study, outlined in Fig. 5, can be termed an analysis of income trade-off because it balances investment in growth and egg production in the same season, the summer of 2000. This assumes we can disregard the possibility that females store eggs as energy reserves, mentioned above. Other studies (Stearns 1992) can more aptly be termed capital trade-off, balancing investment in one season against investment in a future season (see references in Stearns 1992 and Worley et al. 2003). These two forms of trade-off can affect trade-off patterns found in various ways. Firstly, many animals making up the lower left part of the plot—those of low quality—are likely to be lost, truncating the plot at the time their choice is scored. This will reduce any tendency to a positive correlation in the plot. Secondly, in an income trade-off situation females are continuously monitoring their environment and allocate a proportion of their resources to either form of investment. In a capital trade-off situation, they must make an evaluation of the optimal amount of resource to invest in one form, and in the following season they suffer the consequences of this choice, investing what may be left into the other form. It is possible that these two situations also affect the patterns found. However, in either case an inverse correlation is a manifest expression of a trade-off. Lack of an inverse slope (as in the present study) does not prove there is none, only that all animals make the same decision or that other processes overrule the expression of the trade-off.

Had there been a statistical interaction between the effects of feeding rate and female growth rate, this would have been an indication of one form of a flexible allocation rule. This was tested, but no effect was found. For the test we use the most powerful data available: actual feeding rate. However, to make the concept mere easy to grasp intuitively, we offer an alternative illustration in Fig. 5, accounting not only for feeding rate (size of symbols) but also for food ration, high or low (filled and open symbols). If the slopes for frogs on high and low ration had been significantly different (which they clearly were not) this would have meant that the food ration given had affected the balance between the two forms of resource allocation, i.e. a flexible allocation rule. Thus, our data give no support for this.

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