

A Review for Life-history Traits Variation in Frogs Especially for Anurans in China

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Abstract Environmental variation can promote differentiation in life-history traits in species of anurans. Increased environmental stress usually results in larger age at sexual maturity, older mean age, longer longevity, slower growth, larger body size, and a shift in reproductive allocation from offspring quantity to quality, and a stronger trade-off between offspring size and number. However, previous studies have suggested that there are inconsistent geographical variations in life-history traits among anuran species in China. Hence, we here review the intraspecific patterns and differences in life-history traits (i.e., egg size, clutch size, testes size, sperm length, age at sexual maturity, longevity, body size and sexual size dimorphism) among different populations within species along geographical gradients for anurans in China in recent years. We also provide future directions for studying difference in sperm performance between longer and shorter sperm within a species through transplant experiments and the relationships between metabolic rate and brain size and life-history.

Keywords anurans, age at sexual maturity, body size, longevity, reproductive investment, sexual size dimorphism

1. Introduction

A central aim in an organism's life-history study is to explain its lifetime pattern of growth, development, reproductive investment and survival with different stages of life-history (Figure 1; Roff, 2002; Lange *et al.*, 2016; Ellen *et al.*, 2016; Ramírez-Bautista *et al.*, 2016; Tejada *et al.*, 2016; Qin *et al.*, 2018; Wu *et al.*, 2018). Because of the physical and physiological constraints and the common dependence on limited resources in nature, trade-offs have played a key role in the development of life-history theory (Stearns, 1989; Lu *et al.*, 2011). In particular, investment in one life-history trait is often traded off against investment in

other traits because the trade-offs represent the costs paid in the occurrence of fitness (Roff, 2002). There are evidences that environmental factors (e.g., temperature, rainfall, food supply) and genetic factor affect variation in life-history traits (e.g., age structure, body size and reproductive investment) in organisms across broad environmental ranges (Berven, 1982; Liao *et al.*, 2011a, 2013a; Liao and Lu, 2012; Huang *et al.*, 2014; Lu *et al.*, 2014a; Bülbül *et al.*, 2016; Feilich, 2016; Portik and Blackburn, 2016; De Melo and Masunari, 2017; Martínez-Caballero *et al.*, 2017; Yang *et al.*, 2018).

The evolution of life-history traits have been reviewed in a number of taxa (fishes: Roff, 1993; amphibians: Bull and Shine, 1979; Morrison and Hero, 2003; reptiles: Fitch, 1985; Niewiarowski, 1994; birds: Linden and Møller, 1989). In recent years a number of studies have addressed the variations in life-history traits in anurans of China in order to know about energetic allocation between reproductive investment and survival (Liao and Lu, 2011a,b,c; Mi *et al.*, 2012; Chen *et al.*, 2011a,b,

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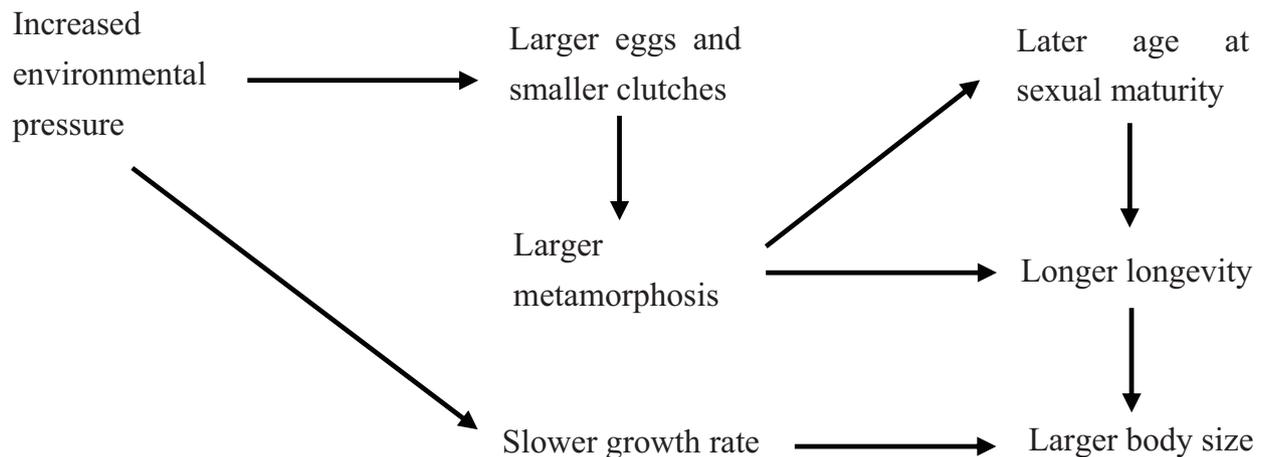


Figure 1 Environmental changes shape variation in life history traits in organisms.

2012, 2013a,b; Liao *et al.*, 2013b, 2014, 2016; Liu *et al.*, 2018). Although the increasing evidences suggest that environmental stress shape in changes in body size, growth rate, reproductive allocation from offspring quantity to quality (Liao *et al.*, 2014, 2015), no review, however, has been carried out on variation in life histories in anurans in China. Herein, we summarize the patterns in life-history variations of Chinese anurans in China based on the basis of published papers for the last 30 years. These life-history traits of anurans mainly include clutch/egg size, testes size/sperm traits, age at sexual maturity, longevity, growth rates, body size, and sexual size dimorphism.

2. Clutch size and Egg Size

Clutch size has been regarded as a trait that individuals from populations have evolved through time to adapt to local environment (Fitch, 1985; Wang *et al.*, 2017). Temperature, rainfall and adult activity period may indirectly affect clutch size due to food variation and energy required for reproduction (Bull and Shine, 1979; Heatwole and Taylor, 1987). Egg size is regarded as an attribute that affects the size, shape, growth and development rates during embryonic development, thereby influencing the survival of offspring (Kaplan and King, 1997).

Anurans can mediate clutch size, egg size and the relationship between egg size and clutch size when experiencing different environments. For instance, an increase in egg size is observed in high altitude/latitude with decreasing length of the growth season due to adaptive beneficial effects on larval and metamorphic performance in frogs (*Rana chensinensis*: Lu, 1994;

Rhacophorus omeimontis: Liao and Lu, 2011a; *Rana kukunoris*; Chen *et al.*, 2013b; Yu *et al.*, 2018a; *Bufo andrewsi*: Liao *et al.*, 2014; Liao *et al.*, 2016; *Polypedates megacephalus*: Zhao *et al.*, 2017). In particular, larger eggs contain a higher amount of yolk (Komoroski *et al.*, 1998), which is assumed to be advantageous under the high energetic requirements in harsh and unpredictable environmental conditions. In addition, clutch size increase with altitude in *R. kukunoris* and *P. megacephalus* (Chen *et al.*, 2013b; Zhao *et al.*, 2017), but not in *B. andrewsi* (Liao *et al.*, 2014; Liao *et al.*, 2016) and *Rh. Omeimontis* (Liao and Lu, 2011a). Life-history theory states that investment in larger eggs comes at a cost of decreasing egg numbers to improve the relative fitness of both the females and the juvenile in harsh environments (Roff, 2002). Consequently, there should be a trade-off between egg size and clutch size in species including *B. andrewsi*, *Rh. Omeimontis* and *R. chensinensis* (Lu, 1994; Liao and Lu, 2011a; Liao *et al.*, 2014, 2016). However, no trade-off exists between them in *R. kukunoris* and *P. megacephalus* (Chen *et al.*, 2013a,b; Zhao *et al.*, 2017).

Larger females often produce larger clutches (Roff, 2002). For most species of anurans, clutch size increase with maternal body size (Liao and Lu, 2009; Liao *et al.*, 2011b, 2016; Lu *et al.*, 2016; Zhao *et al.*, 2017; Yu *et al.*, 2018a). As females at high altitudes are usually larger, it would follow that high-altitude females lay larger clutches (Liao *et al.*, 2014). However, this is not always the case. High-altitude females have been found to produce relatively smaller clutches and larger eggs than their lowland counterparts (Kozłowska, 1971; Berven, 1982). Relatively smaller clutches and larger eggs in the high-altitude and -latitude populations can ensure that each egg is adequately provisioned in the face of cold climate and

short duration of development (Berven, 1982). Smaller clutches and larger eggs in the high-altitude have been observed in *B. andrewsi* and *Rh. omeimontis* (Liao and Lu, 2011a; Liao *et al.*, 2014).

However, for *P. megacephalus*, relatively clutch size and egg size from the highest-altitude population was larger than those from the lowest-altitude population (Zhao *et al.*, 2017). Females living at higher altitudes produce larger eggs, but without a concomitant increase in female body size or clutch size in *R. kukunoris* (Chen *et al.*, 2013b). By contrast, females with a concomitant increase in body size produce larger eggs and more offspring in low-altitude or/and latitude populations than females in high-altitude and -latitudes do (Yu *et al.*, 2018a).

3. Testes size and Sperm Traits

Temperature gradients and seasonality often affect activity periods, thereby limiting the time for development, resource acquisition, and breeding activity (Endler, 1977). Hence, activity period is often also associated with relatively larger clutches produced in a given season (Morrison and Hero, 2003). Similarly, variation in the activity period is also likely to influence male reproductive investments. For instance, direct fitness consequences have been caused by the ability to produce vast amounts of high-quality sperm within the constraints of energy uptake and allocation (reviewed in Simmons, 2001; Fitzpatrick and Lüpold, 2014; Lüpold *et al.*, 2017; Liao *et al.*, 2018). Sperm and testes are at the intersection of resource ecology, life-history selection, reproductive physiology, and sexual selection (Jin *et al.*, 2016a). As a result, studies on variations in testes size and sperm traits in frogs can reveal important information about adaptation and possible constraints in the reproductive investments.

Relative testis mass increases with altitude but not latitude or longitude across 25 populations of *Fejervarya limnocharis* along a 1550 km latitudinal and 1400 m altitudinal transect in China (Jin *et al.*, 2016a), indicating that environmental variation may underlie local adaptations to reproductive investments. Meanwhile, relative testes size from the high-altitude population is larger than that of the low-altitude population in *P. megacephalus* (Chen *et al.*, 2016). By contrast, it is reported that relative testis mass decreases with latitude and/or altitude in other frog species (*Rana temporaria*: Hettyey *et al.*, 2005; *R. kukunoris*: Chen *et al.*, 2014; *Hyla gongshanensis jingdongensis*; Jin *et al.*, 2016b;

Scutigera boulengeri: Zhang *et al.*, 2018). This is thought to be driven by an increasingly short breeding season, declining levels of male–male competition for mates, or more limited resources to be invested in reproduction (Hettyey *et al.*, 2005; Chen *et al.*, 2014). However, the relative testis size do not increase with altitude despite an increasing male bias in the operational sex ratio (OSR) in high altitude is recorded in the Yunnan pond frog (*Dianrana pleuraden*) along an altitudinal gradient (Mai *et al.*, 2017). Moreover, the relative testis mass do not increase with altitude and the OSR in the swelled vent frog *Feirana quadranus* (Tang *et al.*, 2018). For some species of anurans, testes mass is positively correlated with body size (Hettyey *et al.*, 2005; Chen *et al.*, 2014; Jin *et al.*, 2016a,b; Mai *et al.*, 2017).

Sperm length increases with altitude across *F. limnocharis* populations (Jin *et al.*, 2016a). It is possible that the variation in sperm length reflects differential selection or constraints associated with effects of temperature on sperm motility and longevity (e.g., Alavi and Cosson, 2005). Alternatively, sperm length might parallel variation in egg size if larger eggs need greater force by sperm for penetration and longer sperm can generate more powerful propulsion (Katz and Drobnis, 1990). However, sperm length does not increase with altitude in *D. pleuraden* (Mai *et al.*, 2017) and *P. megacephalus* (Chen *et al.*, 2016). Although the relative testis size has a positive effect on sperm length in some frogs (Jin *et al.*, 2016a; Liao *et al.*, 2018), which suggests that the intensity of sperm competition can account for the variation in sperm length (Immler *et al.*, 2011), it cannot explain a significant portion of sperm length in other (Hettyey and Roberts, 2007; Mi *et al.*, 2012; Mai *et al.*, 2017).

4. Age and Growth Rate

Age at sexual maturity is determined by juvenile growth rates and body size of mature individuals (Ryser, 1996). Because sexual maturity is dependent on body size, species with faster growth rates can reach the minimum size required for reproduction sooner compared to those with slower growth rates, and thus can begin breeding at a younger age (Morrison and Hero, 2003). For most species of anurans examined China, females have larger age at sexual maturity and mean age than males (Li *et al.*, 2010; Liao and Lu, 2010a,b; Liao *et al.*, 2010; Chen *et al.*, 2011a, 2012; Mi, 2015). Females displaying delayed reproduction can achieve larger body sizes than males, which results in greater survivorship of parents

and the production of larger clutches, or larger offspring which may have higher survival rates than smaller offspring (Berven, 1982; Begon *et al.*, 1990). However, both females and males have same age at sexual maturity (Liao, 2011; Liao *et al.*, 2011b; Chen *et al.*, 2011b; Huang *et al.*, 2013). In addition, longevity in females is longer than males in most anurans species (Lu *et al.*, 2006; Liao and Lu, 2010a,b,c; Chen *et al.*, 2011a, 2012; Mao *et al.*, 2012; Mi, 2015; Liao *et al.*, 2016).

As species at higher latitude and/or altitude experience shorter growing seasons than those at lower latitudes and/or altitudes, it takes longer time to reach the minimum size required for sexual maturity, and the age at sexual maturity is larger (Berven, 1982). For anurans, it is generally found that the oldest age at sexual maturity and average age exists in species at high latitude and/or altitude in both sexes (Table 1; Ma *et al.*, 2009a; Chen *et al.*, 2011a; Liao and Lu, 2011c; Liao and Lu, 2012; Liao *et al.*, 2016). However, average age of males and females does not differ among populations (Liao *et al.*, 2010; Liao and Lu, 2010c). Moreover, Zhang and Lu (2012) found that age at sexual maturity, average age and longevity all increase with altitude but not with latitude in amphibian groups using the meta-analyses.

Among anurans species, body size and age exhibit a positive relationship in both sex, and females often display a larger growth rate than males (Li *et al.*, 2010; Liao and Lu, 2010a, 2011a, 2012; Liao *et al.*, 2010; Chen *et al.*, 2012; Lou *et al.*, 2012). The relationship between body size and age, and growth rate changes with environmental conditions among populations. For instance, *Nanorana parkeri* from high-altitude populations exhibit lower growth rate than frogs from low-altitude populations (Ma *et al.*, 2009b). For *R. nigromaculata*, age is non-significantly correlated with body size for both sexes in the high-altitude population, and for males in the low-altitude population. For both *R. nigromaculata* populations, individuals from high altitude show a higher growth rate than that from low altitude (Liao *et al.*, 2010). For *B. andrewsi*, growth is more rapid in females compared to males for shorter growth seasons, while males have higher growth rates than females in longer growth seasons (Liao *et al.*, 2016). In addition, growth rates in male *Odorrana grahami* from the lowest altitude are the highest, whereas growth rates of females at high altitudes are the highest (Li *et al.*, 2013). For male *Rh. omeimontis*, the growth rates decrease with increasing altitudes, while females from the high altitude site exhibit higher growth rates than

their conspecifics from low-altitude sites (Liao and Lu, 2011c). Hence, anuran species and individuals from high-latitude and/or -altitude populations grow slower and consequently tend to have older age and larger body when breeding for the first time compared to those species and individuals found in tropical lowlands (Morrison and Hero, 2003).

5. Body Size

Body size of anurans is an important life-history trait that determines fitness and thus experiences the natural selection (Liao and Lu, 2012). In particular, females have larger age at sexual maturity, mean age, and longevity than males, thereby larger body in anuran species (Lu *et al.*, 2006; Ma *et al.*, 2009b; Li *et al.*, 2010, 2013; Chen *et al.*, 2012; Liao and Lu, 2012; Liao *et al.*, 2016). The effects of cold temperatures on anuran larval and juvenile growth and development rates have follow-on effects on the timing of maturity and subsequently, the body size of adults (Berven, 1982). As a result of these effects, high-altitude and -latitude anurans should be generally larger than the low-altitude and tropical individuals. Body size variation across an environmental gradient has been formulated as the Bergmann's rule: the tendency for animals to be larger in colder climates (Bergmann, 1847). There are evidences that individuals from higher altitudes are larger in body size than their lower-altitude conspecifics, conforming to the Bergmann's rule (Table 1; Lu *et al.*, 2006; Ma *et al.*, 2009b; Liao *et al.*, 2010; Liao and Lu, 2010b,c, 2012; Liu *et al.*, 2012). However, body size from low altitude and/or latitude is larger than high altitude and/or latitude for three anuran species, and the data conforms to the converse to Bergmann's rule (Ma *et al.*, 2009a; Liao *et al.*, 2010; Liu *et al.*, 2018a). In addition, variations in body size do not change consistently with altitude and/or latitude for some species, which is disagreement with the Bergmann's rule (Table 1; Liao and Lu, 2011c; Lou *et al.*, 2012; Li *et al.*, 2013; Feng *et al.*, 2015; Liao *et al.*, 2016; Jin *et al.*, 2017). Liao and Lu (2012) inferred that the relative effects of annual growth rate and longevity related to local environments will determine which cline rule a species will exhibit. In the Bergmann's rule case, later sexual maturity and longer longevity should play a larger role in enlarging body in contrast with slower growth in decreasing it. By contrast, in the converse to Bergmann's cline, growth rate is contained so much that any prolonged time spent in growing will fail to compensate the effect of slow growth on body size.

Table 1 The relationship between life-history traits and altitude or latitude within each species where applicable.

Species	Age at sexual maturity		Mean age		Longevity		Body size		Clutch size	Egg size	Testes size	Sperm size
	males	females	males	females	males	females	males	females				
<i>Amolops mantzorum</i>	unchangeable	increased	unchangeable	unchangeable	increased	increased	increased	increased	unchangeable	unchangeable	unchangeable	unchangeable
<i>Rhacophorus omeimontis</i>	increased	increased	increased	increased	increased	increased	unchangeable	unchangeable	decreased	increased	unchangeable	unchangeable
<i>Bufo andrewsi</i>	increased	increased	increased	increased	increased	increased	increased	increased	decreased	increased	unchangeable	unchangeable
<i>Fejervarya limnocharis</i>	unchangeable	unchangeable	unchangeable	unchangeable	unchangeable	unchangeable	unchangeable	unchangeable	unchangeable	unchangeable	increased	increased
<i>Rana nigromaculata</i>	unchangeable	unchangeable	unchangeable	unchangeable	unchangeable	unchangeable	decreased	decreased	unchangeable	unchangeable	unchangeable	unchangeable
<i>Pelophylax pleuraden</i>							unchangeable	unchangeable	unchangeable	unchangeable	unchangeable	unchangeable
<i>Rana chensinensis</i>	increased	increased	increased	increased	increased	increased	increased	increased	decreased	increased	unchangeable	unchangeable
<i>Nanorana parkeri</i>	increased	increased	increased	increased	increased	increased	decreased	decreased				
<i>Hyla annectans chuanxiensis</i>	increased	unchangeable	increased	increased	increased	increased	unchangeable	increased				
<i>Polypedates megacephalus</i>	unchangeable		unchangeable		increased		unchangeable	unchangeable	decreased	increased		
<i>Hyla gongshanensis jingdongensis</i>											decreased	unchangeable
<i>Rana kukunoris</i>	unchangeable	increased	unchangeable	unchangeable	increased	unchangeable	increased	unchangeable	unchangeable	increased	decreased	unchangeable
<i>Feirana quadranus</i>											unchangeable	unchangeable
<i>Scutiger boulengeri</i>											decreased	decreased

6. Sexual Size Dimorphism

Sexual size dimorphism (SSD) has been commonly regarded as an outcome of sex-specific patterns of sexual and natural selection (Fairbairn, 1997; Liao *et al.*, 2013c; Zhang and Lu, 2013; Zhao *et al.*, 2016; Rohner *et al.*, 2016). According to the Rensch's rule, SSD decreases when females are the larger sex, and increases with increasing body size when males are the larger sex (Rensch, 1950). The evolution of SSD and the Rensch's rule can be proposed by sexual selection and fecundity selection (Fairbairn, 1997; Liao *et al.*, 2013c). SSD in anurans is widespread (Shine, 1979; Wells, 2007), and females are the larger sex in 90% of species (Shine, 1979). The fecundity selection on large females can result in female-biased SSD in anurans (Monnet and Cherry, 2002; Han and Fu, 2013). Not surprisingly, interspecific studies of anurans have shown that the variations of SSD do not obey the Rensch's rule, but rather its inverse (Han and Fu, 2013; De Lisle and Rowe, 2013; Liao *et al.*, 2013c).

Intraspecific tests of variations in SSD and the Rensch's rule among populations in frogs have been reported in recent years. For example, using data on body size and age in 27 populations of *R. chensinensis* and body size from 40 populations and age from 31 populations in *F. limnochari* covering the full known size range of the species, the level of SSD increased with increasing mean size, supporting the inverse of Rensch's rule (Liao and Chen, 2012; Liao, 2013). The fecundity selection hypothesis assuming increased reproductive output in large females can explain the occurrence of the inverse of Rensch's rule. Most variations in SSD can be also explained in terms of differences in age between the sexes (Liao and Lu, 2012; Liao, 2013). For *B. andrewsi*, the degree of SSD increased with increased female size, following the inverse of Rensch's rule. Selection for large males and differences in age between the sexes is unlikely to be an important source of variations in SSD. However, fecundity selection is likely to explain the observed inverse of Rensch's rule (Liao *et al.*, 2015). In addition, Lu *et al.* (2014b) also found that pattern of SSD variation supports the inverse Rensch's rule in two frog species. However, variations in SSD of *R. kukunoris* support neither the Rensch's rule nor its inverse (Feng *et al.*, 2015).

7. Future Directions

Variations in life-history traits of organisms are affected

by ultimate (genetic) factors, environmental factors, metabolic acceleration and brains (Berven, 1982; Lüpold *et al.*, 2016; Pontzer *et al.*, 2016). Three aspects need to be addressed in future study. Firstly, it would be interesting and feasible to test the adaptive significance experimentally using transplant experiments by collecting frogs in high- and low-altitude populations. In particular, it would be possible to address whether sperm performance between longer and shorter sperm (from different altitudes) differ within a species (given there is sexual selection on sperm length). Meanwhile, because phenotypic variation in a trait results from either environment change during development or genetic adaptation to local environment, it is important to test the relative effect of the two factors for research on geographical variation in larval development rates. Secondly, the trade-off can provide the costs paid in the currency of fitness when a beneficial variation in one trait is associated with a detrimental variation in another (Stearns, 1989). Although brain size is positively correlated with age at sexual maturity and longevity (Barton and Capellini, 2011; Street *et al.*, 2017; Yu *et al.*, 2018b), it would be possible to address whether the other organs (i.e., heart, lungs, livers, gut, skin, and kidneys) correlate with life-history traits among populations within species or between species in order to test the energy trade-off hypothesis. Thirdly, Pontzer *et al.* (2016) found that the humans experience acceleration in metabolic rate, providing energy for larger brains and faster reproduction without sacrificing maintenance and longevity. Hence, it would be possible to test the hypothesis that for anurans an increased metabolic rate, along with variations in energy allocation, is crucial in the evolution of enlarged brains and life-history traits.

8. Conclusions

Environmental changes along geographical gradients can promote life-history traits differentiation in anurans. Life-history theory suggests that increased environmental stress results in a shift in reproductive allocation from offspring quantity (clutch size and testes mass) to quality (egg size and sperm length) and a stronger trade-off between offspring quantity and offspring quality. High-altitude/latitude individuals have higher investments per offspring to compensate for the increased mortality rates of their offspring than their low-altitude/latitude counterparts. The trade-off between offspring quantity and quality occurs due to resource limitation. Also, environmental changes shape variations in age at sexual

maturity, mean age, longevity, growth rate, body size and SSD. Growth rate and longevity determine whether body size variation follows the Bergmann's rule among populations along geographical gradients. Moreover, variation in SSD and Rensch's rule among populations or species of anurans are mainly determined by differences in age between males and females, sexual selection and fecundity selection.

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