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Phenotypic Plasticity in Embryonic Development of Reptiles: Recent Research and Research Opportunities in China

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Abstract Adaptive developmental plasticity can enable an organism to modify its phenotype rapidly, in response to local (and perhaps, unpredictable) conditions, by altering reaction norms during development. Previous studies on this topic have been dominated by western scientists, employing western study systems and approaches. Recently, the expansion of Chinese ecological research has seen a broadening of studies taxonomically (phylogenetically). Here, we briefly summarize research that has been conducted on developmental plasticity in Chinese reptiles over the past two decades, and suggest productive directions for future studies in this field. There are exciting research opportunities in this field in China, and we call for increased collaboration between western and eastern scientists to elucidate the role of developmental plasticity in evolutionary responses of organisms to environmental changes. As human activities increase the intensity and frequency of such changes, the need to understand responses of biological systems becomes an increasingly urgent priority.

Keywords developmental plasticity, embryonic reptile, ecological adaptation, environmental change, China

1. Introduction

Variation in phenotypic traits among individuals is the core material upon which natural selection can operate, and ultimately generate evolutionary change. Early paradigms that attributed phenotypic variation largely to underlying genetic variation have now been replaced by more complex views that allow a major role for non-genetic causes of variations, such as developmental plasticity (West-Eberhard, 2003). Natural selection is expected to fashion norms of reaction in the same way as it fashions genetically canalized traits, and thus many of the patterns we have seen in developmental plasticity likely are adaptive (e.g., Aubret *et al*., 2004). Adaptive developmental plasticity allows organisms to maximize their fitness by altering the reaction norms of phenotypes in direct response to various biotic and abiotic factors. Such plasticity thus may give the organism a "head start" on dealing with environmental changes (West-Eberhard, 2003; Bateson *et al*., 2004).

Developmental plasticity is widespread phylogenetically, but has attracted intensive studies in reptiles because these ectotherms experience a wide range of environmental conditions during the embryonic stage as well as later in life (Aubret *et al*., 2004; Shine, 2004). That exposure to (often unpredictable) variation in thermal, hydric and nutritional conditions plausibly has favoured an ability to respond to environmental factors through adaptive plasticity. Unlike birds and mammals where embryos develop under relatively constant conditions, embryonic development in reptiles often occurs under fluctuating conditions found within nests (oviparous species) or maternal uteri (viviparous species) (Ackerman and Lott, 2004). Such variation in environmental conditions, including both abiotic and biotic factors, may substantially affect the rates and trajectories of embryonic

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development, and thus, affect hatchling phenotypes in ways likely to affect survival and reproduction of offspring (Figure 1). The ways in which natural selection modifies phenotypic traits through developmental plasticity have emerged as an exciting field of study. For example, natural selection may function by modifying maternal behavior and physiology, thus affecting the conditions experienced by embryos. Nesting females can select nest-sites that provide abiotic conditions conducive to the production of offspring with high survival and reproductive success, which in turn improves their own (maternal) fitness (Figure 1). Additionally, natural selection may fine-tune developmental responses so that embryos can develop into high-quality offspring, even though they develop under the conditions that would greatly reduce viability in some ancestral species (Shine, 2004). Accordingly, we expect a complex evolutionary interplay between developmental plasticity in embryos and maternal traits that determine incubation parameters.

As in many other fields of science, Chinese research on developmental plasticity in reptiles has a long history, but is unfamiliar to most western scientists because of historical incidents and language obstacles. Until recently, most Chinese research was introduced to western science through publication in international journals, and collaboration between Chinese and western scientists. For example, in the first edited volume that reviewed the topic of egg incubation in reptiles (Deeming and Ferguson, 1991), the only studies that were cited were those from western countries (Europe, North America, and Australia). In a subsequent review on the same topic, however, 25 studies by Chinese scientists were cited (Deeming, 2004). This change is of course encouraging, but the opportunities have barely been tapped. China has an extensive reptilian biodiversity including some 160 species of lizards, 220 species of snakes, 38 species of turtles, and 3 species of crocodiles (Zhang *et al.*, 1998). These animals are geographically distributed from tropical to cold-temperate regions (10°–50° N), and from low to high elevations (-40−5300 m a.s.l.). Many of the Chinese taxa belong to phylogenetic lineages not represented, or poorly represented, in western countries. This diverse assemblage of species provides exciting opportunities to answer questions previously addressed only for geographically and phylogenetically limited subsets of taxa in western countries. Here, we summarize research on developmental plasticity in Chinese reptiles over the past two decades, followed by some suggestions for the direction of future studies in this field and for research opportunities in China.

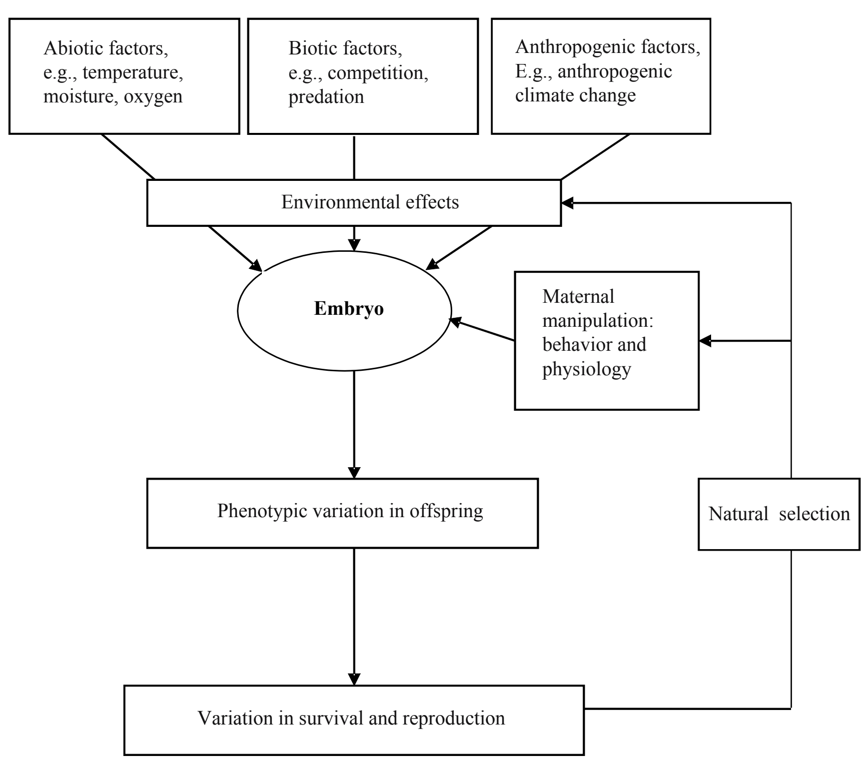

Figure 1 The causes, processes, and adaptive significance of developmental plasticity in embryonic reptiles.

2. Recent Development in Developmental Plasticity in Chinese Reptiles

Research on developmental plasticity in Chinese reptiles began in the 1980s. In the last decade, this research effort has increased considerably; we have been able to locate 93 papers addressing developmental plasticity in Chinese reptiles that have been published in Chinese or international journals [with 53 papers in English and 40 in Chinese with English abstract (Appendix I; see it below)]. Most of these studies are based on one of the following three topics.

2.1 Developmental plasticity in embryos Initially, studies on the effects of temperature and moisture on embryonic development and hatchling traits were based on experimental regimes that imposed constant conditions throughout incubation. That is, the treatments differed in mean conditions but did not incorporate thermal or hydric fluctuations. Such studies on about 20 species of Chinese reptiles (including lizards, snakes, turtles and alligators) showed that incubation temperature had substantial effects on embryonic development and hatchling phenotypes. Hatchlings from eggs incubated at moderate temperatures were generally larger, had better functional performance, and grew faster than those from extreme low and high incubation temperatures (e.g., Lin and Ji, 1998; Ji *et al.*, 2003; Du *et al.*, 2010a; Cao *et al.*, 2012). Hatchling sex is dependent on incubation temperatures and thermal environments experienced by gravid females in some oviparous and viviparous lizards (Zhu *et al.*, 2006; Zhang *et al.*, 2010; Ding *et al.*, 2012). However, moisture had much less effect on hatchling traits either in squamates or turtles (e.g., Ji and Du, 2001; Zhao *et al.*, 2009; Zhao *et al.*, 2013). Building upon these studies, Chinese ecologists increasingly began to design more naturalistic experiments, whereby developmental plasticity was examined under the conditions designed to mimic natural environments experienced by eggs. For example, phenotypic effects of incubation were explored by using different methods including in field nests, artificial nests and programmable incubators with fluctuating temperatures (e.g., He *et al.*, 2002; Du and Feng, 2008). In addition to confirming the findings of western ecologists that thermal fluctuation in natural nests may induce significant phenotypic variation in hatchlings (Deeming, 2004), these studies further revealed that the influence of thermal variance may differ with changing mean temperature.

2.2 Physiological basis of developmental plasticity Traditional egg incubation experiments were performed according to a "black box" approach, simply manipulating the embryo's environment and evaluating effects on the hatchlings. Such experiments reveal little about the mechanism of developmental plasticity. Chinese researchers have conducted experiments on a range of species to investigate the mechanisms of phenotypic variation in response to the environment. Several of these studies have suggested that the variation in hatchling size induced by incubation temperature is related to the efficiency of energy conversion from embryos to hatchlings (e.g., Ji *et al.*, 2001). Similarly, incubation period is shorter in high-latitude populations than low-latitude populations in some wide-ranging lizards (Du *et al.*, 2010b; Sun *et al.*, 2012). The physiological pathways to shorten incubation period in high-latitude populations may differ among species: early hatching is achieved by advanced embryonic development prior to oviposition in some species, but by faster developmental rates of embryos during incubation in others (Sun *et al.*, 2012). Within a species, geographic variation in incubation period also may result from more than one mechanism to accelerate rates of embryonic development: for example, through an increase in heart mass (and thus, stroke volume) in one population, and through an increase in heart rate in another (Du *et al.*, 2010b).

2.3 Adaptive significance of developmental plasticity Western scientists have proposed several hypotheses about the evolutionary role of developmental plasticity in reptilian biology. Recently, Chinese herpetologists have conducted empirical tests of major predictions from those published hypotheses by western scientists, using local species as their test subjects. For example, Shine's (1995) "maternal manipulation hypothesis" for the evolution of reptilian viviparity predicted that gravid females would maintain body temperatures different from those available in external nests, and that incubation at those modified conditions would enhance offspring fitness. Ji and his students (Ji *et al.*, 2007; Li *et al.*, 2009) tested these predictions using several Chinese lizard species from warm to frigid regions. Their results supported the principal predictions from the maternal manipulation hypothesis: that is, females adjust their thermoregulatory tactics during pregnancy, and the phenotypic traits forged by maternal thermoregulation are likely to enhance offspring fitness.

3. Future Research Opportunities in China

The interplay between maternal control of incubation conditions and reaction norms for embryogenesis provides a robust model system to explore the ways in which organisms can utilize developmental plasticity to respond to new environmental challenges. Reptiles provide excellent model systems in this respect. Much has been learnt, but many gaps remain. We suggest that the following topics are likely to attract significant research from Chinese ecologists in the near future.

3.1 Developmental plasticity in response to environmental factors other than only temperature and moisture Identifying the effects of abiotic and biotic factors other than temperature and moisture on embryonic development would help us understand developmental plasticity. For example, the availability of oxygen can strongly affect the development of reptilian embryos, but this topic has not received much attention due to the logistical difficulty of measuring respiratory gases in nests (Ackerman and Lott, 2004). Several reptile species in China are distributed across a wide range of elevations and thus experience different levels of oxygen availability during the embryonic stage. Thus, these animals can provide ideal model systems to identify how reptilian embryos respond to the variation in oxygen supply. In addition to abiotic factors, biotic variables such as food availability and predation also may affect embryonic development by influencing maternal behavior (e.g., nest selection and thermoregulation) and physiology (e.g., energy allocation to egg yolk). Although the effects of these biotic factors on embryonic development have rarely been studied, they would be of great interest. Recent scientific concern about the effects of anthropogenic changes (e.g., climate warming and habitat loss) focuses attention on issues such as how reptilian embryos respond to such changes, and what is the role of developmental plasticity in such responses?

Cultural differences between China and western societies may influence research directions and opportunities, in complex and often indirect ways. For example, Chinese people have traditionally treated almost all reptiles (from lizards to crocodiles) as valuable food, medicine or pets (Zhang *et al.*, 1998). As a result, artificial breeding of reptiles is a booming business, especially in recent years by providing a mass market for reptile products to improve economic conditions. That commercial breeding has not only reduced the pressure of human utilization on natural resources, but also resulted in many species being translocated to areas of China far away from their natural range. For example, some northern species have been brought to southern China for raising and breeding, because of advantages of accelerated development achieved under warmer conditions. The numbers of animals produced in these commercial farms are massive, not only making it easy to obtain study animals and eggs in numbers that would be logistically prohibitive in most other countries, but also providing natural experiments to identify how reptilian embryos respond to climate warming. In addition, increasingly rapid changes in China have stimulated major shifts in the locations and sizes of towns and cities, and prompted several major attempts at habitat restoration over large spatial scales. Such intensive habitat manipulations provide opportunities to determine the role of developmental plasticity of reptiles in response to habitat changes.

3.2 The mechanisms underlying developmental plasticity Another gap in our understanding involves the mechanisms by which abiotic conditions in nests influence the developmental biology of reptilian embryos. Mechanisms of developmental plasticity have remained poorly explored, largely because of logistical constraints. Until recently, technological difficulties precluded extensive studies on how embryos respond to environmental changes. Recent methodological advances in non-invasive heart rate monitoring have provided an opportunity to explore these proximate mechanisms. Studies using this new technology have indicated that lizard embryos may adopt different developmental pathways to achieve similar adaptive endpoints (Du *et al.*, 2010b). More researches using different systems worldwide (including China) obviously are needed, at the molecular level as well as at the whole-organism level. Such studies, equipped with the theory and technology of ecological genomics, would considerably expand our understanding of this topic.

3.3 Correlation between phenotypes and fitness Understanding the links between a hatchling's phenotype and its fitness is key to understanding the role of developmental plasticity in adaptation. Many studies have demonstrated that environmental conditions experienced by embryos can induce significant phenotypic variations in hatchling traits (e.g., body size and locomotor performance) that are plausibly related to offspring fitness, but these studies have rarely gone on further to actually demonstrate any such relationship (Warner and Andrews, 2002). Long-term fieldwork to address the effects of developmental plasticity – and on the ways that reproducing females manipulate the incubation conditions experienced by their embryos – on offspring fitness is a high priority.

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