



Metabolic expenditure and feeding performance in hatchling yellow pond turtles (*Mauremys mutica*) from different incubation temperatures

Kun-Ming Cheng^{a,1}, Lin Zhang^{a,1}, Jie Wang^a, Chun-Xia Xu^b, Hong-Liang Lu^{a,*}

^a Key Laboratory of Hangzhou City for Ecosystem Protection and Restoration, School of Life and Environmental Sciences, Hangzhou Normal University, Hangzhou, 310036, PR China

^b Key Laboratory of Animal Ecology and Conservation Biology, Institute of Zoology, Chinese Academy of Sciences, Beijing, 100101, PR China

ARTICLE INFO

Keywords:

Asian yellow pond turtle
Growth rate
Metabolic expenditure
Digestive efficiency
Physiological performance

ABSTRACT

Growth rate variation of organisms might stem from a series of physiological changes induced by different environmental conditions. Hatchling turtles from different incubation temperatures frequently exhibited diverse growth rates. However, the physiological mechanisms underlying this variation remain largely unclear. Here, we investigated the metabolic rate and feeding performance of hatchling Asian yellow pond turtles (*Mauremys mutica*) from eggs incubated at two different temperatures (26 and 30 °C) to evaluate the role of differences in metabolic expenditure, food intake and digestive efficiency on growth rate variation. Hatchlings from the cooler temperature had a greater growth rate and metabolic rate, tended to eat more food but showed a lower digestive efficiency of energy (DEE) than those from the warmer temperature. Accordingly, the difference in energy acquisition acts as a potential source for growth rate variation of hatchling turtles from different incubation temperatures, and increased energy intake (rather than enhanced digestive efficiency and reduced metabolic expenditure of other physiological processes) might be associated with the higher growth rate of cooler-incubated hatchling *M. mutica*.

1. Introduction

Growth rate is a key life history trait, and much research effort has been devoted to explore potential factors influencing animal growth rate (Angilletta, 2004; Dmitriew, 2011). In oviparous species, the temperature experienced by post-oviposition embryos can have a marked impact on many aspects of hatchling phenotypes, such as body size, locomotor performance, growth and survival (Deeming, 2004; Booth, 2006; Du et al., 2010; Li et al., 2013). However, incubation temperature can exhibit inconsistent effects on post-hatching growth in different turtle species. For example, relatively lower incubation temperatures produce faster-growing hatchlings in *Pelodiscus sinensis* (Du and Ji, 2003) and *Mauremys mutica* (Du et al., 2010), whereas higher (*Malaclemys terrapin*, Roosenburg and Kelley, 1996; *Chrysemys picta*, Janzen and Morjan, 2002; *Mauremys reevesii*, Du et al., 2007) or intermediate temperatures (*Chelydra serpentina*, Bohn and Brooks, 1994; *Gopherus agassizii*, Spotila et al., 1994) produce faster-growing hatchlings in others.

The between-sex differences in physiology have frequently been used to explain such variation in growth rate of turtles from different

incubation temperatures (Rhen and Lang, 1995; Du et al., 2007). Especially in species with temperature-dependent sex determination, more males (or females) produced from low (or high) temperatures may show a faster growth rate than those of an opposite sex from high (or low) temperatures (Janzen and Morjan, 2002; Booth, 2006; Du et al., 2007, 2010). In fact, inter-individual or between-treatment (including between-sex) differences in growth rate might ultimately stem from some physiological changes induced by different environmental conditions (Davidowitz and Nijhout, 2004; Ibarrola et al., 2017). However, the physiological mechanism underlying growth rate variation in turtles has rarely been explored.

Energy acquisition and expenditure should be the determinants of somatic growth rate of organisms (Brunel et al., 2013). Differences in related physiological processes (such as maintenance metabolism, food intake and assimilation) potentially contribute to growth rate variation (Niewiarowski, 2001; Zhang et al., 2009). For example, higher food intake, or greater food conversion and assimilation efficiency have been associated with higher growth rate in some species of fish (Present and Conover, 1992; Billerbeck et al., 2000; Imsland et al., 2000; Jonassen et al., 2000). Additionally, reduced metabolic expenditure of some

* Corresponding author.

E-mail address: honglianglu@outlook.com (H.-L. Lu).

¹ These authors contributed equally to this work.

physiological processes (maintenance, activity, etc.) also potentially enhances the growth rates of fish (Álvarez and Nicieza, 2005; Seppänen et al., 2010). In commercial aquaculture, to enhance the growth rate of farm-raised animals is an essential issue for improving the culture efficiency. Accordingly, the knowledge of physiological changes influencing growth rate of farm-raised animals is highly needed, which can provide valuable guidelines in aquaculture practice.

The Asian yellow pond turtle, *M. mutica*, is a freshwater species that is widely distributed in East Asia, including east part of China, Japan and Vietnam (Zhao and Adler, 1993; Chen et al., 2011; Zhao et al., 2015). Due to human over-exploitation for food, pets and traditional medicine, and habitat loss, wild populations of this species have declined dramatically in past decades (Fong et al., 2007). Artificial culture has currently become an important measure to meet commercial demand and to strengthen the conservation of turtle species (Fong et al., 2007). Previous studies have indicated that hatchlings from different incubation temperatures have different growth rates in *M. mutica* (Zhu et al., 2006; Du et al., 2010). However, whether incubation-related growth rate variation partially results from the differences in metabolic and digestive physiology is unclear.

In this study, we compared the metabolic rate, food intake and digestive efficiency of energy (DEE) of hatchling *M. mutica* from eggs incubated at two different temperatures to investigate the physiological mechanisms underlying growth rate variation. Specifically, we aimed to test: (1) whether individuals from different incubation treatments differed in metabolic rate, food intake, and DEE; (2) if so, whether these observed variations could explain the difference in growth rate. Based on previous results in other species, we predicted that hatchlings from cooler incubation temperature would have a greater growth rate, higher food intake and DEE, but lower metabolic rate than those from warmer incubation temperature.

2. Materials and methods

In mid-June 2014, a total of 32 fertilized eggs (mean mass: 10.26 g \pm 0.19 SE) were collected from more than 18 clutches at a private hatchery in Haining (30°19'N, 120°25'E; Zhejiang, eastern China). Eggs were transferred to our laboratory at Hangzhou Normal University, where they were numbered individually and incubated in 4 covered plastic containers (25 \times 20 \times 10 cm³, 8 eggs in each container) filled with moist vermiculite (-220 kPa, Du et al., 2010). Containers were placed inside two artificial climate incubators (Ningbo Life Science and Technology Ltd., China; 2 containers in each incubator) that were set at 26 and 30 (\pm 1) °C, respectively. The two temperatures fall within the range of incubation temperatures suitable for embryonic development in this species, and produce hatchlings with different growth rates (Du et al., 2010; Wu et al., 2014). Normally, turtle eggs are incubated under thermally fluctuated conditions in the farms. However, the effect of temperature fluctuation on post-hatching growth rate of turtles remains unclear. Therefore, we conducted the experiment that only involved constant temperatures in the current study. Containers were weighed every five days and, if necessary, rehydrated the vermiculite with distilled water to maintain a constant water potential of the substrate. Eggs from a single clutch were evenly split into the two temperature treatments to minimize clutch effects.

Twenty-nine eggs (14 at 26 °C and 15 at 30 °C) were hatched. Some newly hatched turtles still carried an external yolk sac, and they were individually housed in 33 \times 23 \times 20 cm³ containers with a layer of moist vermiculite until the yolk sac was absorbed within 1–2 days. After yolk sac absorption, each hatchling was weighed, and then housed in the container with 3-cm depth of water, that placed in two temperature-controlled rooms at 26 and 30 °C (the suitable rearing temperature for this species ranges from 25 to 32 °C). Turtles from the same incubation temperature were randomly assigned into different rearing temperatures. Pieces of tile were placed in the containers to provide shelter for turtles, and fluorescent lights that fixed at the top of rooms provided a

12 h:12 h light/dark cycle. Hatchling turtles typically do not feed in the first few days after hatching. Turtles were fed an excess amount of fish meat daily (provided between 08:00–09:00, and uneaten fish meat was removed about 2 h later) from the 4th day (most individuals began feeding on the 3rd or 4th day). All turtles were re-weighed twice on the 30th and 60th days after hatching. The specific growth rate (SGR) for each individual was calculated as $SGR = (\ln W_t - \ln W_0)/T \times 100\%$, where W_0 = initial wet body mass, W_t = final wet body mass.

The metabolic rate of each hatchling was assessed at two test temperatures (26 and 30 °C, with a rest for 48 h between test temperatures) on the 4th, 30th and 60th days after hatching, respectively. All trials were conducted in the aforementioned temperature-controlled rooms. The carbon dioxide production (V_{CO_2}) of each turtle was determined using an open-flow respirometry system (Qubit Systems, Kingston, ON, Canada) between 14:00–18:00. Turtles were housed individually in a 220 mL acrylic metabolic chamber. The air at a rate of 200 mL/min flowed sequentially through a Decarbite filter, metabolic chamber and desiccant, and then entered the CO₂ analyzer. CO₂ production was recorded continuously for at least 30 min using Logger Pro 3.7 software (Vernier, Inc., Beaverton, OR, USA) when turtles were resting. The metabolic measures performed here did not exclude the effect of post-prandial state on CO₂ production. Therefore, the metabolic rate that measured in this study actually reflected metabolic expenditure for maintenance, food digestion and some other processes, and it would be related to routine (or standard) metabolic rate (Valverde et al., 2009).

From the 10th day, turtle feeding performance was also assessed in aforementioned temperature-controlled rooms. During the measurement of feeding performance, pre-weighed fish meat (ca. 5% of animal mass) was provided to each turtle daily between 08:00–09:00, and the residual food was collected 2 h later. Turtle faeces were collected every 3 h from 09:00 to 21:00 using a spoon, and the water was filtered every morning to collect the faeces that produced during the night. Trials lasted for 30 days to allow the accumulation of sufficient faeces for accurate calorimetry. Faeces and residual fish meat were dried to constant mass at 65 °C and weighed. The energy densities of these samples were determined in a Parr 6300 automatic adiabatic calorimeter (Parr instrument company, Moline, Illinois, USA). The digestive efficiency of energy (DEE) was calculated as $DEE = (I - F)/I \times 100\%$, where I = total energy consumed, and F = energy in faeces (Zhang et al., 2009). All turtles appeared to be healthy, and no deaths occurred during the experiment and the month after our measurements.

Prior to statistical analyses, all data were tested for normality using Kolmogorov-Smirnov tests, and for homogeneity of variances using Bartlett's test. Preliminary analyses showed no significant container effects on all hatchling traits (body mass, metabolic rate, daily food intake and DEE) examined in this study [mixed model analysis of variance (ANOVA) with the container identity as the random factor, all $P > 0.05$], so this factor was excluded in subsequent analyses. Linear regression, student's t -test, one- (or two-) way ANOVA, repeated-measures ANOVA and one-way analysis of covariance (ANCOVA) were used to analyze the corresponding data that met the assumptions for parametric analyses.

3. Results

There was no difference in egg size (mass) between incubation treatments ($t = 0.17$, $df = 30$, $P = 0.864$). Incubation temperature did not affect the body size of hatchlings (ANCOVA with egg mass as the covariate, $F_{1, 26} = 0.56$, $P = 0.461$). Repeated measures ANOVA revealed that the body mass of turtles under different treatments gained significantly in the first two months after hatching ($F_{2, 50} = 768.70$, $P < 0.001$); and both incubation ($F_{2, 50} = 4.78$, $P = 0.013$) and rearing temperature ($F_{2, 50} = 56.27$, $P < 0.001$) had significant impacts on the increase in body mass. Overall, turtles that reared in the warmer environment grew faster than those in the cooler environment (repeated measures ANOVA with SGR as the independent variable, $F_{1, 25} = 39.90$,

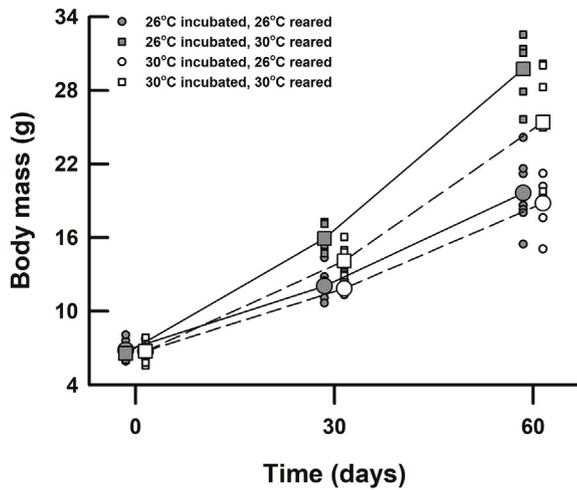


Fig. 1. Post-hatching growth of *Mauremys mutica* hatchlings from different incubation temperatures and at different rearing temperatures. Enlarged symbols (and lines) showed the mean values.

$P < 0.001$), and turtles from eggs incubated at 26 °C gained mass more quickly than those at 30 °C in the first month ($F_{1, 25} = 4.38, P = 0.047$), despite such effect vanishing in the second month ($F_{1, 25} = 0.98, P = 0.332$) (Fig. 1).

Turtles from eggs incubated at 26 °C appeared to have a higher metabolic rate than those at 30 °C (4-day age, $F_{1, 25} = 5.01, P = 0.034$; 60-day age, $F_{1, 25} = 7.67, P = 0.010$; despite no difference at 30-day age, $F_{1, 25} = 2.73, P = 0.111$), and turtles tested at 30 °C had a higher metabolic rate than those tested at 26 °C (all $P < 0.05$) (Fig. 2). However, no significant effects of rearing temperature on turtle metabolic rate were observed in this study (all $P > 0.079$).

Incubation temperature had a significant effect on turtle daily food intake ($F_{1, 25} = 4.99, P = 0.035$) and DEE ($F_{1, 25} = 21.48, P < 0.001$). Overall, turtles from eggs incubated at 26 °C had a greater daily food intake, but lower DEE than those from 30 °C (Fig. 3). Rearing temperature (daily food intake, $F_{1, 25} = 3.70, P = 0.066$; DEE, $F_{1, 25} = 0.09, P = 0.765$) and its interaction with incubation temperature (daily food intake, $F_{1, 25} = 0.61, P = 0.443$; DEE, $F_{1, 25} = 2.61, P = 0.118$) had no significant effects on daily food intake and DEE.

4. Discussion

As reported for numerous other turtle species (Rhen and Lang, 1995;

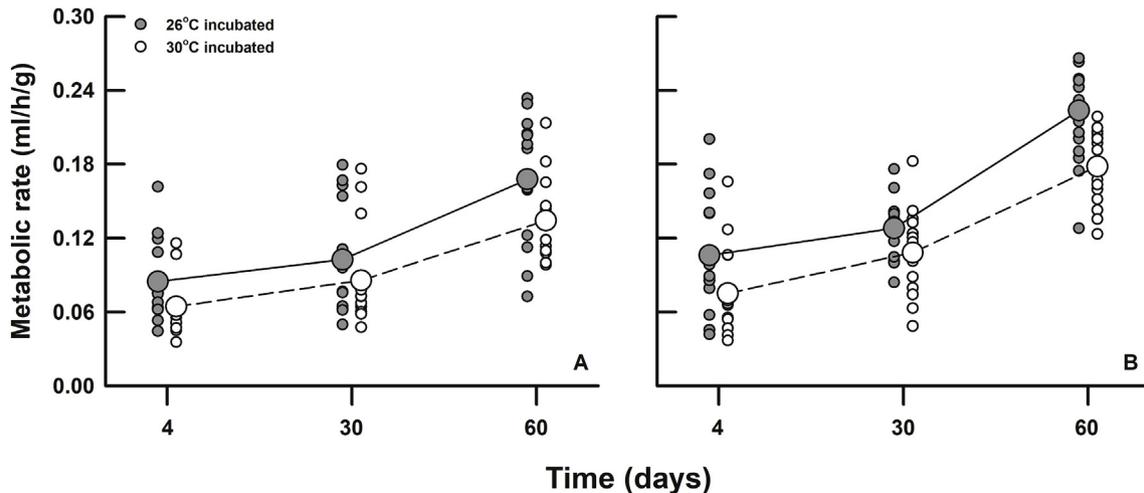


Fig. 2. Metabolic rates that tested at 26 °C (A) and 30 °C (B) of *Mauremys mutica* hatchlings from different incubation temperatures. Enlarged symbols (and lines) showed the mean values.

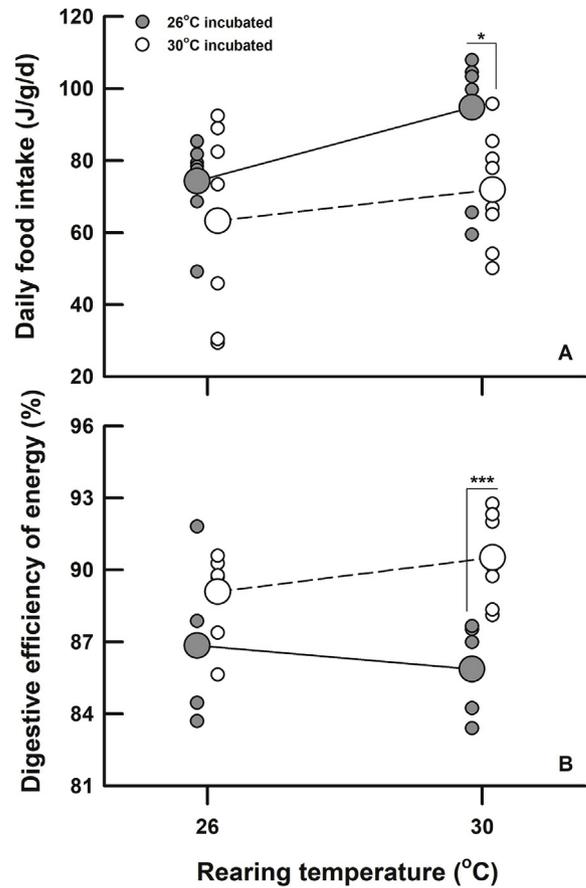


Fig. 3. Daily food intake (A) and digestive efficiency (B) of energy of *Mauremys mutica* hatchlings from different incubation temperatures and at different rearing temperatures. Enlarged symbols (and lines) showed the mean values. The asterisks indicate significant differences (* $P < 0.05$, *** $P < 0.001$).

Du and Ji, 2003; Ji et al., 2003; Booth et al., 2004; Du et al., 2007), incubation temperature had a significant effect on post-hatching growth in *M. mutica*. Eggs incubated at a cooler temperature (26 °C) produced faster-growing hatchling turtles than those from a warmer temperature (30 °C), which was consistent with a previous study on this species (Du et al., 2010). In other species, faster-growing individuals can be produced from eggs incubated at high (Roosenburg and Kelley, 1996;

Janzen and Morjan, 2002; Du et al., 2007) or intermediate temperatures (Bobynd and Brooks, 1994).

Between-treatment differences in turtle growth rate can be attributable to various physiological modifications (Jonassen et al., 2000; Lindgern and Laurila, 2005, 2009). Here, we would focus on the contributions of differences in metabolic expenditure, feeding and digestive performance to growth rate variation of hatchling *M. mutica* in later discussion.

Compared with turtles from eggs incubated at warmer temperatures, turtles from eggs incubated at cooler temperatures showed a higher metabolic rate, probably reflecting a greater amount of energy that was used for routine physiological processes (including maintenance, food digestion, etc.). Metabolic expenditure of animals can potentially influence the rate of growth (Lindgern and Laurila, 2009; Hu et al., 2019). Here, our study appeared to show a positive relationship between growth rate and metabolic rate, which was inconsistent with the prediction that higher growth rate could be a result of reduced maintenance metabolism (Angilletta, 2001; Niewiarowski, 2001; Steyermark, 2002; Álvarez and Nicieza, 2005). A negative relationship between growth rate and (routine or standard) metabolic rate normally occurs under the scenario when the amount of allocatable resources toward growth, maintenance and other processes are similar between individuals (or between populations). However, if inter-individual (or inter-population) variation in food acquisition is large, that trend could be reversed (van Noordwijk and de Jong, 1986). Under identical laboratory conditions, turtles from eggs incubated at 26 °C tended to acquire more food than those from 30 °C. A greater food intake might elevate metabolic costs due to requiring relatively more energy for food digestion (Valverde et al., 2009). Meanwhile, it meant more energy acquisition, which allowed turtles to allocate more energy towards growth. Based on the above assumptions, it might be plausible to produce a positive relationship between growth rate and metabolic rate in this study. In fact, increased growth rate would elevate energy expenditure due to tissue production (Wieser, 1994; Pörtner et al., 2005; Lindgern and Laurila, 2009). A positive relationship between growth rate and metabolic rate was also found in other species (Billerbeck et al., 2000; Arnott et al., 2006). For example, high-latitude Atlantic silversides (*Menidia menidia*) grow faster and have higher routine metabolic rates than low-latitude individuals (Billerbeck et al., 2000).

Our results showed that turtles from a cooler incubation environment ate and consumed more food than those from a warmer incubation environment overall. Actually, there was a difference under different rearing temperatures. In this study, a significantly greater food intake and higher growth rate for cooler-incubated turtles was found under the rearing temperature of 30 °C, but not under 26 °C (Figs. 1 and 3). These findings were not contradictory, but were consistent with our prediction, implying that growth rate variation for turtles from different incubation treatments might result from the difference in food and energy intake.

Interestingly, the digestive efficiency of turtles from warmer incubation environment was higher than that of turtles from cooler incubation environment overall and under the rearing temperature of 30 °C. It might be a compensatory response for slow-growing turtles from warmer incubation environment. After deducting faecal energy, the amount of energy acquired from food for turtles from cooler incubation environment was still greater than that for turtles from warmer incubation environment (approximately 15% and 20% more than warmer-incubated turtles at test temperatures of 26 and 30 °C, respectively).

Accordingly, greater growth rates for turtles from cooler incubation environment might be largely due to more food and energy intake, rather than lower metabolic expenditure for other physiological processes or higher food digestive efficiency. Such a situation also occurs in some species of fish and amphibians (Present and Conover, 1992; Billerbeck et al., 2000; Qian et al., 2002; Martins et al., 2005; Mas-

Muñoz et al., 2011). Physiological mechanisms underlying growth rate variation may vary in different species. Greater growth rates associated with increased food digestive efficiency have been documented in other fish and amphibians (Immsland et al., 2000; Jonassen et al., 2000; Lindgern and Laurila, 2005).

In summary, significant effects of incubation temperature on growth rate, metabolic expenditure, feeding and digestive performance were exhibited in hatchling *M. mutica*. Relatively more food intake was thought to be the major contributor to faster early-stage growth for turtles from cooler incubation environment than those from warmer incubation environment, although sometimes the positive correlation between growth rate and food intake could be modified (Martins et al., 2005; Mas-Muñoz et al., 2011). Lower metabolic expenditure and higher digestive efficiency are the contributing factors for higher growth rates in some species of fish and amphibians (Jonassen et al., 2000; Steyermark, 2002; Álvarez and Nicieza, 2005; Lindgern and Laurila, 2005). Contrary to those findings, the between-treatment differences in metabolic expenditure and digestive efficiency did not appear to be correlated with growth rate variation in *M. mutica*.

Declaration of competing interest

All of the authors declare that they have no conflicts of interest.

Acknowledgments

This work was supported by grants from the Natural Science Foundation of Zhejiang Province, China (Y3110276, LY15C030006). The experimental procedures complied with the current laws on animal welfare and research in China.

Appendix A. Supplementary data

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.aquaculture.2019.734627>.

References

- Álvarez, D., Nicieza, A.G., 2005. Is metabolic rate a reliable predictor of growth and survival of brown trout (*Salmo trutta*) in the wild? *Can. J. Fish. Aquat. Sci.* 62, 643–649.
- Angilletta, M.J., 2001. Variation in metabolic rate between populations of a geographically widespread lizard. *Physiol. Biochem. Zool.* 74, 11–21.
- Angilletta, M.J., 2004. Temperature, growth rate, and body size in ectotherms: fitting pieces of a life-history puzzle. *Integr. Comp. Biol.* 44, 498–509.
- Arnott, S.A., Chiba, S., Conover, D.O., 2006. Evolution of intrinsic growth rate: metabolic costs drive trade-offs between growth and swimming performance in *menidia menidia*. *Evolution* 60, 1269–1278.
- Billerbeck, J.M., Schultz, E.T., Conover, D.O., 2000. Adaptive variation in energy acquisition and allocation among latitudinal populations of the Atlantic silverside. *Oecologia* 122, 210–219.
- Bobynd, M.L., Brooks, R.J., 1994. Interclutch and interpopulation variation in the effects of incubation condition on sex, survival and growth of hatchling turtles (*Chelydra serpentina*). *J. Zool.* 233, 233–257.
- Booth, D.T., 2006. Influence of incubation temperature on hatchling phenotype in reptiles. *Physiol. Biochem. Zool.* 79, 274–281.
- Booth, D.T., Burgess, L., McCosker, J., Lanyon, J., 2004. The influence of incubation temperature on post-hatching fitness characteristics of turtles. *Int. Congr. Ser.* 1275, 226–233.
- Brunel, T., Ernande, B., Mollet, F.M., Rijnsdorp, A.D., 2013. Estimating age at maturation and energy-based life-history traits from individual growth trajectories with non-linear mixed-effects models. *Oecologia* 172, 631–643.
- Chen, Y., Zhao, B., Sun, B.-J., Wang, Y., Du, W.-G., 2011. Between-population variation in body size and growth rate of hatchling Asian yellow pond turtles, *Mauremys mutica*. *Herpetol. J.* 21, 113–116.
- Davidowitz, G., Nijhout, H.F., 2004. The physiological basis of reaction norms: the interaction among growth rate, the duration of growth and body size. *Integr. Comp. Biol.* 44, 443–449.
- Deeming, D.C., 2004. Post-hatching phenotypic effects of incubation on reptiles. In: Deeming, D.C. (Ed.), *Reptilian Incubation: Environment, Evolution and Behaviour*. Nottingham University Press, Nottingham, pp. 229–251.
- Dmitriew, C.M., 2011. The evolution of growth trajectories: what limits growth rate? *Biol. Rev.* 86, 97–116.
- Du, W.-G., Hu, L.-J., Lu, J.-L., Zhu, L.-J., 2007. Effects of incubation temperature on

- embryonic development rate, sex ratio and post-hatching growth in the Chinese three-keeled pond turtle, *Chinemys reevesii*. *Aquaculture* 272, 747–753.
- Du, W.-G., Ji, X., 2003. The effects of incubation thermal environments on size, locomotor performance and early growth of hatchling soft-shelled turtles, *Pelodiscus sinensis*. *J. Therm. Biol.* 28, 279–286.
- Du, W.-G., Wang, L., Shen, J.-W., 2010. Optimal temperatures for egg incubation in two Geomydid turtles: *Ocadia sinensis* and *Mauremys mutica*. *Aquaculture* 305, 138–142.
- Fong, J.J., Parham, J.F., Shi, H.-T., Stuart, B.L., Carter, L.C., 2007. A genetic survey of heavily exploited, endangered turtles: caveats on the conservation value of trade animals. *Anim. Conserv.* 10, 452–460.
- Hu, Y.-C., Lu, H.-L., Cheng, K.-M., Luo, L.-G., Zeng, Z.-G., 2019. Thermal dependence of feeding performance and resting metabolic expenditure in different altitudinal populations of toad-headed lizards. *J. Therm. Biol.* 80, 16–20.
- Ibarrola, I., Hilton, Z., Ragg, N.L.C., 2017. Physiological basis of inter-population, inter-familial and intra-familial differences in growth rate in the green-lipped mussel, *Perna canaliculus*. *Aquaculture* 479, 544–555.
- Imsland, A.K., Foss, A., Naevdal, G., Cross, T., Bonga, S.W., Ham, E.V., Stefánsson, S.O., 2000. Countergradient variation in growth and food conversion efficiency of juvenile turbot. *J. Fish Biol.* 57, 1213–1226.
- Janzen, F.J., Morjan, C.L., 2002. Egg size, incubation temperature, and posthatching growth in painted turtles (*Chrysemys picta*). *J. Herpetol.* 36, 308–311.
- Ji, X., Chen, F., Du, W.-G., Chen, H.-L., 2003. Incubation temperature affects hatchling growth but not sexual phenotype in the Chinese soft-shelled turtle, *Pelodiscus sinensis* (Trionychidae). *J. Zool.* 261, 409–416.
- Jonassen, T.M., Imsland, A.K., Fitzgerald, R., Bonga, S.W., Ham, E.V., Nævdal, G., Stefánsson, M.O., Stefánsson, S.O., 2000. Geographic variation in growth and food conversion efficiency of juvenile Atlantic halibut related to latitude. *J. Fish Biol.* 56, 279–294.
- Li, H., Zhou, Z.-S., Wu, T., Wu, Y.-Q., Ji, X., 2013. Do fluctuations in incubation temperature affect hatchling quality in the Chinese soft-shelled turtle *Pelodiscus sinensis*? *Aquaculture* 406–407, 91–96.
- Lindgren, B., Laurila, A., 2005. Proximate causes of adaptive growth rates: growth efficiency variation among latitudinal populations of *Rana temporaria*. *J. Evol. Biol.* 18, 820–828.
- Lindgren, B., Laurila, A., 2009. Physiological variation along a geographical gradient: is growth rate correlated with routine metabolic rate in *Rana temporaria* tadpoles? *Biol. J. Linn. Soc.* 98, 217–224.
- Martins, C.I., Schrama, J.W., Verreth, J.A.J., 2005. The consistency of individual differences in growth, feed efficiency and feeding behaviour in African catfish *Clarias gariepinus* (Burchell 1822) housed individually. *Aquacult. Res.* 36, 1509–1516.
- Mas-Muñoz, J., Komen, H., Schneider, O., Visch, S.W., Schrama, J.W., 2011. Feeding behaviour, swimming activity and boldness explain variation in feed intake and growth of sole (*Solea solea*) reared in captivity. *PLoS One* 6, e21393.
- Niewiarowski, P.H., 2001. Energy budgets, growth rates, and thermal constraints: toward an integrative approach to the study of life-history variation. *Am. Nat.* 157, 421–433.
- Pörtner, H.O., Storch, D., Heilmayer, O., 2005. Constraints and trade-offs in climate-dependent adaptation: energy budgets and growth in a latitudinal cline. *Sci. Mar.* 69 (Suppl. 1.), 271–285.
- Present, T.M.C., Conover, D.O., 1992. Physiological basis of latitudinal growth differences in *Menidia menidia*: variation in consumption or efficiency? *Funct. Ecol.* 6, 23–31.
- Qian, X., Cui, Y., Xie, S., Lei, W., Zhu, X., Xiong, B., Yang, Y., 2002. Individual variations in growth, food intake and activity in juvenile Chinese sturgeon *Acipenser sinensis* Gray. *J. Appl. Ichthyol.* 18, 695–698.
- Rhen, T., Lang, J.W., 1995. Phenotypic plasticity for growth in the common snapping turtle: effects of incubation temperature, clutch and their interaction. *Am. Nat.* 146, 726–747.
- Roosenburg, W., Kelley, K.C., 1996. The effect of egg size and incubation temperature on growth in the turtle, *Malaclemys terrapin*. *J. Herpetol.* 30, 198–204.
- Seppänen, E., Tiira, K., Huuskonen, H., Piironen, J., 2010. Metabolic rate, growth and aggressiveness in three Atlantic salmon *Salmo salar* populations. *J. Fish Biol.* 74, 562–575.
- Spotila, J.R., Zimmerman, L.C., Binckley, C.A., Grumbles, J.S., Rostal, D.C., List, A.J., Beyer, E.C., Phillips, K.M., Kemp, S.J., 1994. Effects of incubation conditions on sex determination, hatching success, and growth of hatchling desert tortoises *Gopherus agassizii*. *Herpetol. Monogr.* 8, 103–116.
- Steyermark, A.C., 2002. A high standard metabolic rate constrains juvenile growth. *Zoology* 105, 147–151.
- van Noordwijk, A.J., de Jong, G., 1986. Acquisition and allocation of resources: their influence on variation in life history tactics. *Am. Nat.* 128, 137–142.
- Valverde, J.C., Hernández, M.D., Aguado-Giménez, F., García, B.G., 2009. Oxygen consumption in spider crab (*Maja brachydactyla*): effect of weight, temperature, sex, feeding and daily light–dark cycle. *Aquaculture* 298, 131–138.
- Wieser, W., 1994. Costs of growth in cells and organisms: general rules and comparative aspects. *Biol. Rev.* 68, 1–33.
- Wu, M.-X., Zhao, B., Zhang, W., Lu, H.-L., 2014. Effects of incubation temperature on embryonic development and hatchling traits in the Asian yellow pond turtle, *Mauremys mutica*. *Acta Ecol. Sin.* 34, 5398–5404.
- Zhang, Y.-P., Du, W.-G., Shen, J.-W., Shu, L., 2009. Low optimal temperatures for food conversion and growth in the big-headed turtle, *Platysternon megacephalum*. *Aquaculture* 295, 106–109.
- Zhao, E., Adler, K., 1993. *Herpetology of China*. SSAR, Oxford, OH.
- Zhao, B., Chen, Y., Lu, H.-L., Zeng, Z.-G., Du, W.-G., 2015. Latitudinal differences in temperature effects on the embryonic development and hatchling phenotypes of the Asian yellow pond turtle, *Mauremys mutica*. *Biol. J. Linn. Soc.* 114, 35–43.
- Zhu, X.-P., Wei, C.-Q., Zhao, W.-H., Du, H.-J., Chen, Y.-L., Gui, J.-F., 2006. Effects of incubation temperatures on embryonic development in the Asian yellow pond turtle. *Aquaculture* 259, 243–248.