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Locomotor costs of pregnancy in a viviparous toad-headed lizard, *Phrynocephalus vlangalii* (Agamidae)

Hong-Liang Lu¹, Chuan-Quan Jiang¹ & Xiang Ji²

¹Hangzhou Key Laboratory for Animal Adaptation and Evolution, School of Life Sciences, Hangzhou Normal University, Hangzhou 310036, Zhejiang, China

²Jiangsu Key Laboratory for Biodiversity and Biotechnology, College of Life Sciences, Nanjing Normal University, Nanjing 210023, Jiangsu, China

Locomotor impairment during pregnancy can be attributed to physical burden or physiological changes associated with pregnancy. However, the degree to which physical and physiological changes affect reproductive costs likely varies between species. Here, we used the Qinghai toad-headed lizard (*Phrynocephalus vlangalii*) as a model to assess locomotor costs during pregnancy and the relative impact of physical and physiological effects in pregnant viviparous lizards. The locomotor costs of pregnancy were pronounced: sprint speed decreased gradually throughout pregnancy, reached a minimum at parturition and increased slowly thereafter. The reduced speed in pregnant females was not related to relative litter mass. Compared with the locomotion of non-reproductive females or males, pregnant females exhibited lower speeds and shorter stride lengths. These results suggest that, despite having a physical effect on locomotor performance, physiological changes associated with pregnancy likely play a major role in locomotor impairment in pregnant *P. vlangalii*.

Key words: Agamidae, locomotor performance, *Phrynocephalus vlangalii*, physical burden, reproductive costs, stride length

INTRODUCTION

Reproduction entails several costs including probability of survival and reduced growth which can limit future reproductive success (Shine, 1980; Schwarzkopf, 1994; Cox & Calsbeek, 2010; Johnson et al., 2010). Reproductive costs are regarded as a crucial determinant of life history evolution (Stearns, 1992; Roff, 2002). One of the most apparent forms of reproductive costs is a change in locomotor ability, which has been documented in diverse taxa from insects to mammals (Bauwens & Thoen, 1981; Isaacs & Byrne, 1998; McLean & Speakman, 2000; Shine, 2003). For example, pregnant females exhibit lower locomotor speed and stamina in most reptiles studied thus far (Olsson et al., 2000; Goodman, 2006; Zani et al., 2008; Iraeta et al., 2010). This reduction in locomotor performance can be attributed to the physical burden of carrying the clutch and/or physiological changes associated with reproduction (Olsson et al. 2000; Shine, 2003; Goodman, 2006). In *Uta stansburiana*, locomotor impairment in gravid females is the result of physical burden, because locomotor stamina decreases with increasing burden until eggs are laid (Miles, 2000). However, in *Niveoscincus microlepidotus*, locomotor impairment during pregnancy is the result of physiological changes unrelated to physical burden (Olsson et al., 2000). Impaired locomotor performance in reproductive females is often multifactorial, especially for species where the physical and physiological effects are not mutually exclusive (Olsson et al., 2000; Goodman,

2006). A common approach to determining whether the impairment has a physical or physiological basis involves monitoring locomotor recovery following egg-laying or parturition, whereby immediate and gradual recovery of locomotor performance to pre-reproductive levels indicate a physical and a physiological impairment, respectively (Olsson et al., 2000).

The prolonged gestation period, complex placental structure and intimate maternal-fetal communication in viviparous species may lead to more pronounced endocrinological and physiological modifications during pregnancy than in oviparous species (Stewart & Thompson, 1994; Lourdais et al., 2004). Reduced locomotor speed in pregnant females is related to reproductive burden in some viviparous reptiles (Shine, 1980; Van Damme et al., 1989; Aubret et al., 2005), but not in others (Brodie, 1989; Wapstra & O'Reilly, 2001; Webb, 2004). Within-species inconsistencies (Le Galliard et al., 2003; Itonaga et al., 2012) may reflect differences in morphology and habitat use between different populations (see also Sinervo et al., 1991).

Locomotor costs of reproduction have been determined in many viviparous lizards, but most work has focused on species or populations from the temperate zone and low to medium elevation sites (Van Damme et al., 1989; Olsson et al., 2000; Wapstra & O'Reilly, 2001; Lin et al., 2008; Itonaga et al., 2012). Given that proportionally more viviparous species occur in high latitude and altitude regions (Tinkle & Gibbons, 1977), addressing reproductive costs and associated

physiological changes in these species is important for our overall understanding of life history variation. The cold and unpredictable environmental conditions at high latitude and altitudes result in short activity periods and high mortality rates in ectothermic animals, often favouring large offspring (Arribas & Galán, 2005; Wang et al., 2011; Roitberg et al., 2013; Sun et al., 2013; Li et al., 2014). Species affected by this fundamental tradeoff are excellent models to tease apart the complex relationship between the physiological and physical costs associated with locomotion during pregnancy.

Toad-headed lizards of the reproductively bimodal genus *Phrynocephalus* (Agamidae) are widely distributed in desert, arid and semiarid regions in central and western Asia and north to northwestern China, with all viviparous species restricted to the Qinghai-Tibet Plateau and adjacent areas (Zhao, 1999; Barabanov & Ananjeva, 2007). In this study we examined the effects of pregnancy on locomotor performance in the Qinghai toad-headed lizard *Phrynocephalus vlangalii*. This lizard is typically found in arid and semi-arid areas from 2200–4500 m above sea level (Zhao, 1999). Females give birth to young mostly between mid-July and early August (Zhang et al., 2005; Li et al., 2014; Wang et al., 2014). Our aims were to assess the locomotor costs of reproduction in a high-altitude viviparous lizard, and to identify potential causes of such costs.

MATERIALS AND METHODS

We collected adult *P. vlangalii* in June and July 2008 from a previously studied population in Daotanghe (36°26'N, 100°56'E), Qinghai, northwestern China. Lizards were transported to our laboratory in Hangzhou, where they were individually marked using paint, measured for snout-vent length (SVL) and weighed. We individually palpated females to evaluate reproductive condition. Between four and six lizards were randomly assigned to each 600x400x400 mm (length x width x height) communal cages containing fine sand (150 mm depth) and pieces of clay tiles. A 100 W light bulb (12 hours light: 12 hours dark) suspended above one end of each cage formed a supplementary heat source. All communal cages were placed in a room where ambient temperatures were never higher than 22°C. Lizards were fed mealworms (larvae of *Tenebrio molitor*) and house crickets (*Acheta domesticus*) every two to three days. We individually housed females in plastic cages (300x200x200 mm) with a substrate of fine sand (50 mm depth) soon after the first female gave birth, and checked these cages at least three times daily for newborns. Postpartum females and their neonates were measured and weighed less than 6 hours post-parturition. Relative litter mass (RLM) was calculated by dividing litter mass by postpartum female mass.

Twenty-five adult females (51.9–62.4 mm SVL) collected in June were used to evaluate temporal variation in locomotor performance (sprint speed) over a two-month period, one month before and one month after parturition. All trials were conducted in a room at 32±0.5°C, a temperature close to the mean level

(33°C) of thermal preference recorded in *P. vlangalii* (Shu et al., 2010). To minimise the possible influence of diel variation in locomotor performance, trials were conducted between 1400–1700 hours. Prior to each trial, lizards were kept in the room at 32°C for about 1 hour, and then chased with a paint brush down a 2 m racetrack with a substrate of fine sand (10 mm depth). Lizards were tested every five days, and each lizard was tested twice on each testing day with a minimum of 30 minutes of rest between the two trials. Locomotor performance was recorded with a NV-GS408 digital video camera (Panasonic, Japan). The tapes were later examined for running speed using MGI VideoWave III (MGI Software, Canada). Sprint speed was recorded as the fastest running speed over a distance of 25 cm.

An independent sample of 37 adults (61.6–77.5 mm SVL) collected in July were used to examine whether pregnant females differ from non-pregnant females or males in locomotor performance. Lizards were assigned to one of four groups: pregnant females ($n=10$), postpartum females ($n=9$), non-pregnant females ($n=8$) and males ($n=10$). The four groups did not differ from each other regarding mean SVL ($F_{3,33}=2.15$, $p=0.113$). Locomotor performance on a 2 m racetrack was recorded for each lizard in the room at 32°C with a PCO1200 high-speed digital camera (Cooke, USA; 200 frames per second). Each lizard was tested three to four times, with a minimum of 30 minutes of rest between trials. Video clips that included two to four consecutive strides at a steady speed were examined on a frame-by-frame basis using MaxTRAQ 2D software (Innovision Systems, USA). Sprint speed was again recorded as the fastest running speed over a distance of 25 cm. We defined a stride as the interval between successive footfalls of the right hind foot, and calculated stride length (distance traveled between successive footfalls), frequency (the reciprocal of the duration between successive footfalls) and speed (stride length multiplied by stride frequency) for each stride. Strides at steady-speeds of 0.5 m/s and 1.0 m/s (±10%) were selected for statistical analyses.

We used Statistica v.6.0 (StatSoft Inc., USA) to analyse data. Prior to all statistical analyses, data were tested for normality using the Kolmogorov-Smirnov test, and for

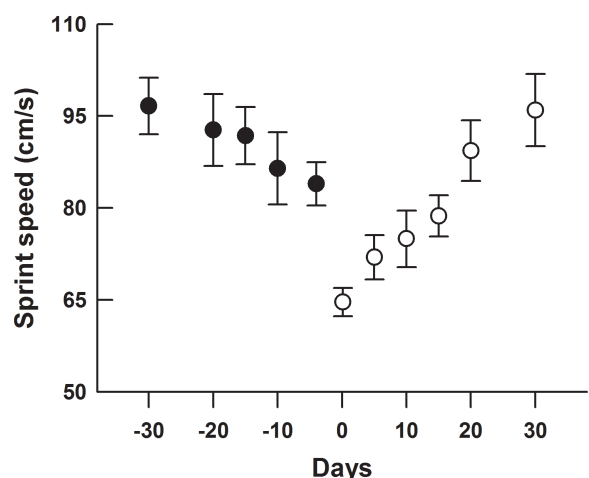


Fig. 1. Mean values (±SE) for sprint speed of female *P. vlangalii* during pregnancy and after parturition.

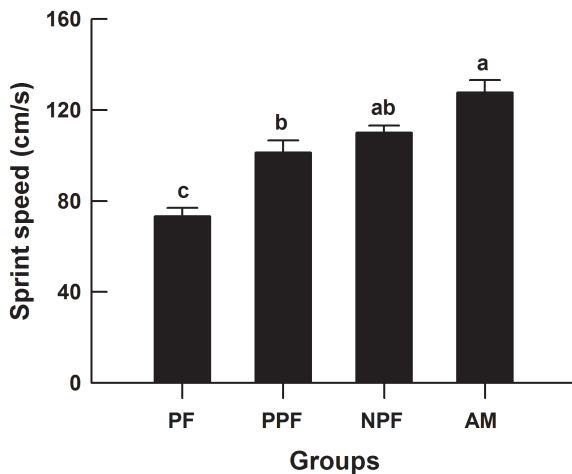


Fig. 2. Mean values (+SE) for sprint speed of pregnant females (PF), postpartum females (PPF), non-reproductive females (NPF) and adult males (AM). Means with different letters differ significantly (Tukey's *post hoc* test, $\alpha = 0.05$, $a > b > c$).

homogeneity of variances using Bartlett's test. We used linear regression, one-way analysis of variance (ANOVA), repeated-measures ANOVA and Tukey's *post hoc* test to analyse corresponding data. Descriptive statistics are presented as mean \pm standard error (SE), and the significance level is set at $\alpha = 0.05$.

RESULTS

Sprint speed was not related to body size (SVL, $p > 0.129$). Variation in sprint speed was very pronounced for pregnant females ($F_{10,150} = 4.97$, $p < 0.001$), with the mean value gradually decreasing as females neared parturition, followed by an increase thereafter (Fig. 1). There was no relationship between sprint speed and RLM (ranging from 0.10 to 0.55) before ($r^2 = 0.13$, $F_{1,19} = 2.91$, $p = 0.104$) and after ($r^2 = 0.02$, $F_{1,23} = 0.44$, $p = 0.512$) parturition.

Sprint speed differed among the three reproductive classes of females and males ($F_{3,33} = 29.43$, $p < 0.0001$). Pregnant females ran more slowly than all other animals (Fig. 2), and both stride length and frequency were affected by reproductive condition (stride length, $F_{3,33} = 19.22$, $p < 0.001$; stride frequency, $F_{3,33} = 10.86$, $p < 0.001$) and locomotor speed (stride length, $F_{1,33} = 153.64$, $p < 0.001$; stride frequency, $F_{1,33} = 399.21$, $p < 0.001$). Stride length and frequency at 1 m/s were greater than at 0.5 m/s in each group. Pregnant females took relatively shorter strides at higher frequency than males and postpartum females at 0.5 m/s or 1 m/s (Fig. 3). The reproductive condition \times locomotor speed interaction did not affect stride length ($F_{3,33} = 0.21$, $p = 0.887$) and frequency ($F_{3,33} = 0.33$, $p = 0.801$).

DISCUSSION

As observed for other lizards (Bauwens & Thoen, 1981; Sinervo et al., 1991; Olsson et al., 2000; Goodman, 2006; Lin et al., 2008), pregnancy impairs locomotor ability in *P. vlangalii*. The average maximal speed of pregnant females was reduced by 33% compared with non-

pregnant females (Fig. 2). This proportion is higher than the values reported for other viviparous lizards such as *Zootoca vivipara* (28%; Van Damme et al., 1989), *Lerista bougainvillii* (23%; Qualls & Shine, 1998), *Niveoscincus microlepidotus* (16%; Olsson et al., 2000), *N. ocellatus* (21% for a low-elevation population and 27% for a high-elevation population; Wapstra & O'Reilly, 2001) and *Eutropis multifasciata* (25%; Lin et al., 2008). The adverse impact of pregnancy on locomotor speed in *P. vlangalii* was not persistent, as females gradually recovered their locomotor abilities about one month after parturition (Fig. 1). Locomotor costs of reproduction vary considerably among lizard species and populations. Such variation can be explained by differences in reproductive effort, but also different physiological (e.g., reproductive status) and environmental conditions (e.g., habitat structure and predation risk) that may lead to inter- and intra-specific differences in locomotor performance (Qualls & Shine, 1997; Wapstra & O'Reilly, 2001; Itonaga et al., 2012).

Pregnant *P. vlangalii* had a shorter stride length than non-pregnant females as well as males, suggesting a physical effect of the clutch on locomotor performance in pregnant females. Maternal abdominal distension due to carrying the clutch may hinder axial bending and limb kinematics, and thus shorten stride length (Sinervo et al., 1991; Miles et al., 2000). To maintain the same speed as non-pregnant females, pregnant females must

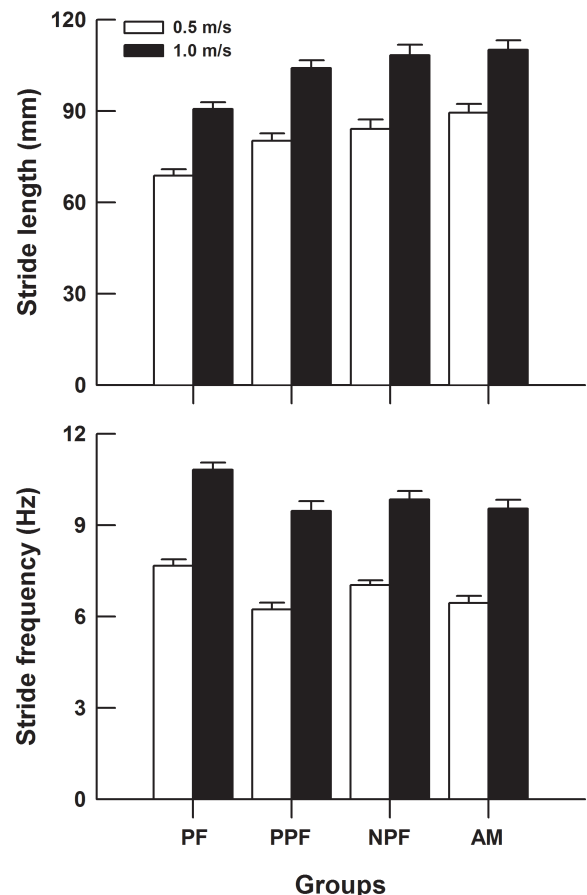


Fig. 3. Mean values (+SE) for stride length and frequency at 0.5 m/s and 1.0 m/s. PF: pregnant females; PPF: postpartum females; NPF: non-reproductive females; and AM: adult males.

increase stride frequency. Compared to non-pregnant females, the mean stride length of pregnant females was reduced by 18% at a speed of 0.5 m/s and 16% at 1.0 m/s, while the mean stride frequency was increased by 9% at 0.5 m/s and 10% at 1.0 m/s (Fig. 3). The additional mass of the clutch and increasing stride frequency will increase the energetic cost of locomotion (Miles et al., 2000). Increases in stride frequency tend to be limited by energetic constraints and cannot offset the adverse impact of reduced stride length. It is therefore difficult for pregnant females to attain the same speed as non-pregnant females. That this physical burden results in reduced locomotor performance in gravid or pregnant females has been documented in several other lizard species (Shine, 1980, 2003; Sinervo et al., 1991; Zani et al., 2008).

Our data also showed that (i) there was no significant correlation between locomotor speed and the magnitude of reproductive investment (relative litter mass); (ii) a minimum sprint speed occurred soon after parturition; and (iii) locomotor speed recovered relatively slowly (at least 3 weeks). These results are consistent with findings in the viviparous scincid lizard, *N. microlepidotum* (Olsson et al., 2000). Olsson et al. (2000) posited that physical effects on locomotor performance during gestation should dominate in oviparous species and that physiological effects be more pronounced in viviparous species. Impaired locomotor ability is often not related to RLM and recovers slowly in viviparous reptiles (Olsson et al., 2000; Wapstra & O'Reilly, 2001; Le Galliard et al., 2003; Webb, 2004). Conversely, a significant negative relationship between locomotor ability and physical burden, and rapid recovery for locomotor ability after (or even before) oviposition has been found in some oviparous species (Sinervo et al., 1991; Miles et al., 2000; Shine, 2003). A prolonged gestation period and intimate physiological connection between the mother and the embryos may cause palpable physiological effects (Stewart & Thompson, 1994). Physiological modifications, such as changes in hormone levels and metabolic rates, affect the sprinting ability of pregnant females (Dauphin-Villemant et al., 1990; Ladyman et al., 2003). Accordingly, locomotor impairment in pregnant *P. vlangalii* is primarily a physiological consequence of reproduction. Indeed, physiological changes associated with reproduction are sometimes regarded as the major cause of reduced locomotor performance during pregnancy in some oviparous lizards (Goodman, 2006). Interestingly, in different aspects of locomotor performance, factors contributing to the impairment may vary. For example, endurance impairment was more likely to be driven by the physical burden of reproduction, whereas speed impairment was more likely to be a physiological consequence of reproduction (Miles et al., 2000; Le Galliard et al., 2003; Zani et al., 2008).

Locomotor impairments may increase vulnerability of reproductive females to predation, and consequently increase mortality in nature (Shine, 1980; Bauwens & Thoen, 1981; Schwarzkopf & Shine, 1992; Miles et al., 2000). Gravid or pregnant females often change their anti-predator tactics to compensate for reduced

locomotor capacity (Cooper et al., 1990; Braña, 1993; Husak, 2006; Iraeta et al., 2010; Johnson et al., 2010; Miller et al., 2010). Lizards such as *Z. vivipara* (Bauwens & Thoen, 1981) and *Eumeces laticeps* (Cooper et al., 1990) become less active and rely more heavily on crypsis during pregnancy; female collared lizards (*Crotaphytus collaris*) tend to stay closer to refuges, but take a shorter flight distance when a predator approaches (Husak, 2006). Qinghai toad-headed lizards appear to also modify anti-predator behaviour under adverse environmental conditions. For example, they used a shorter approach distance and flight distance on cloudy days than on sunny days (Qi et al., 2012). Available data have allowed the hypothesis that locomotor costs in pregnant *P. vlangalii* could be compensated to some extent by behavioural modifications, but this idea requires to be tested in the field.

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REFERENCES

- Arribas, O.J. & Galán, P. (2005). Reproductive characteristics of the Pyrenean high-mountain lizards: *Iberolacerta aranica* (Arribas, 1993), *I. aurelioi* (Arribas, 1994) and *I. bonnali* (Lantz, 1927) *Animal Biology* 55, 163–190.
- Aubret, F., Bonnet, X., Shine, R. & Maumelat, S. (2005). Swimming and pregnancy in Tiger snakes, *Notechis scutatus*. *Amphibia-Reptilia* 26, 396–400.
- Barabanov, A.V. & Ananjeva, N.B. (2007). Catalogue of the available scientific species group names for lizards of the genus *Phrynocephalus* Kaup, 1825 (Reptilia, Sauria, Agamidae). *Zootaxa* 1399, 1–57.
- Bauwens, D. & Thoen, C. (1981). Escape tactics and vulnerability to predation associated with reproduction in the lizard *Lacerta vivipara*. *Journal of Animal Ecology* 50, 733–743.
- Braña, F. (1993). Shifts in body temperature and escape behaviour of female *Podarcis muralis* during pregnancy. *Oikos* 66, 216–222.
- Brodie, E.D. (1989). Behavioral modification as a means of reducing the cost of reproduction. *American Naturalist* 109, 225–238.
- Cooper, W.E., Vitt, L.J., Hedges, R. & Huey, R.B. (1990). Locomotor impairment and defense in pregnant lizards (*Eumeces laticeps*): behavior shift in activity may offset costs of reproduction in an active forager. *Behavioral Ecology and Sociobiology* 27, 153–157.
- Cox, R.M. & Calsbeek, R. (2010). Severe costs of reproduction persist in *Anolis* lizards despite the evolution of a single-egg clutch. *Evolution* 64, 1321–1330.
- Dauphin-Villemant, C., Le Boulenger, F., Xavier, F. & Vaudry, H. (1990). Adrenal activity in the female lizard *Lacerta vivipara* jacquin associated with breeding activities. *General and Comparative Endocrinology* 78, 399–413.

- Goodman, B.A. (2006). Costs of reproduction in a tropical invariant-clutch producing lizard (*Carlia rubrigularis*). *Journal of Zoology* 270, 236–243.
- Husak, J.F. (2006). Do female collared lizards change field use of maximal sprint speed capacity when gravid? *Oecologia* 150, 339–343.
- Iraeta, P., Salvador, A., Monasterio, C. & Díaz, J.A. (2010). Effects of gravidity on the locomotor performance and escape behaviour of two lizard populations: the importance of habitat structure. *Behaviour* 147, 133–150.
- Itonaga, K., Edwards, A., Wapstra, E. & Jones S.M. (2012). Interpopulational variation in costs of reproduction related to pregnancy in a viviparous lizard. *Ethology, Ecology and Evolution* 24, 367–376.
- Isaacs, R. & Byrne, D. (1998). Aerial distribution, flight behaviour and eggload: their inter-relationship during dispersal by the sweet potato whitefly. *Journal of Animal Ecology* 67, 741–750.
- Johnson, M.A., Caton, J.L., Cohen, R.E., Vandecar, J.R. & Wade, J. (2010). The burden of motherhood: the effect of reproductive load on female lizard locomotor, foraging, and social behavior. *Ethology* 116, 1217–1225.
- Ladyman, M., Bonnet, X., Lourdaïs, O., Bradshaw, D. & Naulleau, G. (2003). Gestation, thermoregulation, and metabolism in a viviparous snake, *Vipera aspis*: evidence for fecundity-independent costs. *Physiological and Biochemical Zoology* 76, 497–510.
- Le Galliard, J.F., Le Bris, M. & Clobert, J. (2003). Timing of locomotor impairment and shift in thermal preferences during gravidity in a viviparous lizard. *Functional Ecology* 17, 877–885.
- Lin, C.-X., Zhang, L. & Ji, X. (2008). Influence of pregnancy on locomotor and feeding performances of the skink, *Mabuya multifasciata*: Why do females shift thermal preferences when pregnant? *Zoology* 111, 188–195.
- Li, J.-Q., Zhou, R. & Liu, N.-F. (2014). Life-history variation among three populations of the toad-headed lizard *Phrynocephalus vlangalii* along an elevation gradient on the northeastern Tibetan Plateau. *Herpetological Journal* 24, 17–23.
- Lourdaïs, O., Brischoux, F., DeNardo, D. & Shine, R. (2004). Protein catabolism in pregnant snakes (*Epicrates cenchria maurus* Boidae) compromises musculature and performance after reproduction. *Journal of Comparative Physiology B* 174, 383–391.
- McLean, J. & Speakman, J. (2000). Morphological changes during postnatal growth and reproduction in the brown long-eared bat *Plecotus auritus*: implications for wing loading and predicted flight performance. *Journal of Natural History* 34, 773–791.
- Miles, D.B., Sinervo, B. & Frankino, W.A. (2000). Reproductive burden, locomotor performance, and the costs of reproduction in free ranging lizards. *Evolution* 54, 1386–1395.
- Miller, K.A., Hare, K.M. & Nelson, N.J. (2010). Do alternate escape tactics provide a means of compensation for impaired performance ability? *Biological Journal of the Linnean Society* 99, 241–249.
- Olsson, M., Shine, R. & Bak-Olsson, E. (2000). Locomotor impairment of gravid lizards: is the burden physical or physiological? *Journal of Evolutionary Biology* 13, 263–268.
- Qi, Y., Noble, D.W.A., Fu, J.-Z & Whiting, M.J. (2012). Spatial and social organization in a burrow-dwelling lizard (*Phrynocephalus vlangalii*) from China. *PLoS One* 7, e41130.
- Qualls, C.P. & Shine, R. (1997). Geographical variation in ‘costs of reproduction’ in the scincid lizard *Lampropholis guichenoti*. *Functional Ecology* 11, 757–763.
- Qualls, C.P. & Shine, R. (1998). Costs of reproduction in conspecific oviparous and viviparous lizards, *Lerista bougainvillii*. *Oikos* 82, 539–551.
- Roff, D.A. (2002). *Life history evolution*. Sunderland, MA: Sinauer Associates.
- Roitberg, E.S., Kuranova, V.N., Bulakhova, N.A., Orlova, V.F., et al. (2013). Variation of reproductive traits and female body size in the most widely-ranging terrestrial reptile: testing the effects of reproductive mode, lineage, and climate. *Evolutionary Biology* 40, 420–438.
- Schwarzkopf, L. (1994). Measuring trade-offs: a review of studies of costs of reproduction in lizard. In *Lizard Ecology: Historical and Experimental Perspectives*, 7–29. Vitt, L.J. & Pianka, E.R. (eds.). Princeton: Princeton University Press.
- Schwarzkopf, L. & Shine, R. (1992). Costs of reproduction in lizards: escape tactics and susceptibility to predation. *Behavioral Ecology and Sociobiology* 31, 17–25.
- Shine, R. (1980). Costs of reproduction in reptiles. *Oecologia* 46, 92–100.
- Shine, R. (2003). Effects of pregnancy on locomotor performance: an experimental study on lizards. *Oecologia* 136, 450–456.
- Shu, L., Zhang, Q.-L., Qu, Y.-F. & Ji, X. (2010). Thermal tolerance, selected body temperature and thermal dependence of food assimilation and locomotor performance in the Qinghai toad headed lizard, *Phrynocephalus vlangalii*. *Acta Ecologica Sinica* 30, 2036–2042.
- Sinervo, B., Hedges, R. & Adolph, S.C. (1991). Decreased sprint speed as a cost of reproduction in the lizard *Sceoloporus occidentalis*: variation among populations. *Journal of Experimental Biology* 155, 323–336.
- Stearns, S.C. (1992). *The Evolution of Life Histories*. Oxford: Oxford University Press.
- Stewart, J.R. & Thompson, M.B. (1994). Placental structure of the Australian lizard, *Niveoscincus metallicus*. *Journal of Morphology* 220, 223–236.
- Sun, B.-J., Li, S.-L., Xu, X.-F., Zhao, W.-G., et al. (2013). Different mechanisms lead to convergence of reproductive strategies in two lacertid lizards (*Takydromus wolteri* and *Eremias argus*). *Oecologia* 172, 645–652.
- Tinkle, D.W. & Gibbons, J.W. (1977). The distribution and evolution of viviparity in reptiles. *Miscellaneous Publications Museum of Zoology* 154, 1–55.
- Van Damme, R., Bauwens, D. & Verheyen, R.F. (1989). Effect of relative clutch mass on sprint speed in the lizard *Lacerta vivipara*. *Journal of Herpetology* 23, 459–461.
- Wang, Z., Lu, H.-L., Ma, L. & Ji, X. (2014). Viviparity in high-altitude *Phrynocephalus* lizards is adaptive because embryos cannot fully develop without maternal thermoregulation. *Oecologia* 174, 639–649.
- Wang, Z., Xia, Y. & Ji, X. (2011). Clutch frequency affects the offspring size-number trade-off in lizards. *PLoS One* 6, e16585.
- Wapstra, E. & O’Reilly, J.M. (2001). Potential ‘costs of reproduction’ in a skink: inter- and intrapopulational variation. *Austral Ecology* 26, 179–186.

- Webb, J.K. (2004). Pregnancy decreases swimming performance of female northern death adders (*Acanthopis praelongus*). *Copeia* 2004, 357–363
- Zani, P.A., Neuhaus, R.A., Jones, T.D. & Milgrom, J.E. (2008). Effects of reproductive burden on endurance performance in side-blotched lizards (*Uta Stansburiana*). *Journal of Herpetology* 42, 76–81.
- Zhang, X.-D., Ji, X., Luo, L.-G., Gao, J.-F. & Zhang, L. (2005). Sexual dimorphism and female reproduction in the Qinghai toad-headed lizard *Phrynocephalus vlangalii*. *Acta Zoologica Sinica* 51, 1006–1012.
- Zhao, K.-T. (1999). *Phrynocephalus* Kaup. In *Fauna Sinica, Reptilia*, Vol. 2 (Squamata: Lacertilia), 151–192. Zhao, E.-M., Zhao, K.-T. & Zhou, K.-Y. (eds.). Beijing: Science Press.

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