

The Seasonal Acclimatisation of Locomotion in a Terrestrial Reptile, *Plestiodon chinensis* (Scincidae)

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Abstract Studies of the seasonal acclimatisation of behavioural and physiological processes usually focus on aquatic or semi-aquatic ectotherms and focus less effort on terrestrial ectotherms that experience more thermally heterogeneous environments. We conducted comparative studies and thermal acclimation experiments on the locomotion of the Chinese skink (*Plestiodon chinensis*) to test whether seasonal acclimatisation in locomotion exists in these terrestrial ectothermic vertebrates, and whether seasonal acclimatisation is predominantly induced by thermal environments. In natural populations, skinks ran faster during the summer season than during the spring season at high-test temperatures ranging from 27°C to 36°C but not at low-test temperatures ranging from 18°C to 24°C. In contrast, the thermal acclimation experiments showed that the cold-acclimated skinks ran faster than the warm-acclimated skinks at the low-test temperatures but not at high-test temperatures. Therefore, the seasonal acclimatisation occurs to *P. chinensis*, and may be induced by temperature as well as other factors like food availability, as indicated by the seasonal variation in the thermal dependence of locomotion, and the discrepancy between seasonal acclimatisation and thermal acclimation on locomotion.

Keywords Lizard, temperature, terrestrial ectotherms, thermal acclimation

1. Introduction

Phenotypic plasticity enables an organism to manipulate behavioural and physiological processes in response to environmental variation and thus plays an important role in species' adaptation to fluctuating environments (Gotthard and Nylin, 1995; Weinig, 2000). Acclimatisation is one form of phenotypic plasticity which means any facultative modification in functional performance in response to changes in an environmental variable in the field, while acclimation is defined as such plasticity induced by experimental treatments in the laboratory (Wilson and Franklin, 2002). In response to a long-term or chronic change of natural environments

such as seasonal thermal variation, the organism may attain selective advantages by acclimatisation when facing environmentally restrictive effects on functional performance (Schmidt-Nielsen, 1990; Wilson and Franklin, 2002).

As one of the most important ecological factors, temperature has pervasive effects on virtually every aspect of an organism at levels of organisation from the gene to the whole organism. The thermal acclimation of organisms has thus been the main topics of evolutionary and ecological physiology for the last few decades (e.g., Feder and Hofmann, 1999; Johnston and Temple, 2002; Seebacher and James, 2008). Animals may alter their own functional performance through acclimation or acclimatisation to cope with temperature change (Guderley and St Pierre, 2002; Johnston and Temple, 2002). Given that global climate change is unequivocal and imposes significant effects on many aspects of wild animals and plants from metabolism to population

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dynamics (Dillon *et al.*, 2010; Root *et al.*, 2003), an understanding of the acclimatory response of an organism to a changing environment would not only elucidate the processes of adaptation but also provide important implications for the conservation of biodiversity in response to ongoing climate change.

Locomotion has decisive effects on foraging, escaping from predators and even reproductive success and is thus tightly related to the Darwinian fitness of animals (e.g., Le Galliard *et al.*, 2004). Locomotion and its determinants have attracted great scientific attention with a number of studies of diverse groups of ectotherms ranging from insects to reptiles (e.g., Huey *et al.*, 1984; Rice and Westneat, 2005; Husak *et al.*, 2006; Strobbe *et al.*, 2009). In several lineages of ectothermic vertebrates, locomotion has been proved to be sensitive to temperature (Angilletta *et al.*, 2002) and shows acclimation or acclimatisation in response to thermal environmental changes (Navas *et al.*, 1999; Wilson *et al.*, 2000). Nonetheless, the evidence for the acclimation or acclimatisation of locomotion mainly comes from aquatic or semi-aquatic ectotherms with little opportunity for behavioural thermoregulation in aquatic homogeneous thermal environments (e.g., Wilson *et al.*, 2000; Johnston and Temple, 2002). In contrast to aquatic ectotherms, most terrestrial ectotherms experience thermally heterogeneous environments (from daily to seasonal) and may be able to maintain ideal body temperatures through behavioural thermoregulation (e.g., Avery, 1982; Huey *et al.*, 1989; Row and Blouin-Demers, 2006). Consequently, these animals are thought to have low capabilities of acclimation or acclimatisation in physiological and biochemical processes (Scheiner, 1993; Seebacher and James, 2008).

However, terrestrial ectothermic vertebrates show significant seasonal variation in body temperatures despite rigorous behavioural thermoregulation (e.g., Stevenson, 1985; Ji *et al.*, 1996). In addition, the terrestrial ectothermic vertebrates are also exposed to other seasonally varied factors, such as food conditions, humidity and photoperiod, which may also induce seasonal variation in performance or physiology (e.g., Adolph and Porter, 1993; Lima and Bednekoff, 1999; Madsen and Shine, 2000; Yom-Tov and Geffen, 2006; Sun *et al.*, 2011). Therefore, it would be necessary and interesting to understand how acclimatisation works in terrestrial ectotherms to enhance physiological performance and hence fitness in a seasonally fluctuating environment.

The Chinese skink (*Plestiodon chinensis*) is a medium-sized terrestrial lizard [adult snout-vent length (SVL) is

88 mm–132 mm] mainly observed in southern China and Vietnam (Zhao and Adler, 1993; Zhao *et al.*, 1999). We collected skinks from a wild population in eastern China during the spring and summer to identify the seasonal acclimatisation of locomotion in terrestrial reptiles. Acclimation experiments under thermal environments that mimicked spring and summer were then conducted to test the hypothesis that seasonal acclimatisation is predominantly induced by thermal environments.

2. Materials and Methods

2.1 Seasonal variation in environmental factors In 2009, a total of ten temperature loggers (iButton thermochron, DS 1921; Dallas Semiconductor, USA) were set up randomly in both shady and sunny spots in the natural habitat of the skinks in Quzhou of Zhejiang, China to record the thermal environments hourly in spring (April) and summer (July). We also collected data on sunshine hours and precipitation from local Bureau of Meteorology. The sunshine hours are average 7.9 h/day in July, but only 3.9 h/day in April. The average precipitation is less in July (136 mm) than in April (210 mm). Photoperiod is longer in July (13.9L: 10.1D) than in April (12.8L: 11.2D) on average. In addition, food is more abundant for the skinks in their natural habitat in July than in April (Sun *et al.*, 2011).

2.2 Animal collection and acclimation treatments In April and July of 2010, we collected 11 (6 males and 5 non-gravid females) and 13 (7 males and 6 non-gravid females) adult skinks with intact tails, respectively, to study the seasonal acclimatisation of locomotion. All skinks were measured for SVL (± 0.1 mm), and body mass (± 0.01 g), and then locomotion were determined (see below for the details). Additionally, 22 adult skinks (13 males and 9 non-gravid females) with intact tails were collected in April and used in the acclimation experiment. The skinks were also measured for SVL, body mass before housed individually in plastic cages (300 mm \times 200 mm \times 185 mm). The cages were lined with paper, halved PVC pipes were provided for shelters, and water and food (*Tenebrio molitor* larvae) were provided *ad libitum*. A heating bulb was hung at one end of each cage to provide basking opportunities for the skinks. The two acclimation treatments mimicked the thermal environments of spring and summer based on the 2009 ambient temperature records (see Figure 1 for details). In the cold-acclimated treatment (mimicked spring, 5 males and 4 females), the skinks were kept at a room temperature of 16°C with a basking opportunity of 5 h

per day (from 10:30–15:30). In the warm-acclimated treatment (mimicked summer, 8 males and 5 females), the skinks were kept at a room temperature of 28°C with a basking opportunity of 10 h per day (from 08:00–18:00). The cloacal temperatures of the skinks were measured hourly from 07:00 to 20:00 on the 20th day of the acclimation experiments by inserting a calibrated UNT-T325 electronic thermal meter ($\pm 0.1^\circ\text{C}$, UNI-Trend Technology, Shanghai, China) at a depth of about 10 mm in cloacae. The acclimation treatments lasted for 30 days, and the locomotion of the skinks were subsequently measured. Independent samples were used in each season, after the experiment, the skinks were released to sites where they were collected. All experimental procedures were approved by the Animal Care and Ethics Committee at the Institute of Zoology, Chinese Academy of Science.

2.3 Locomotion The locomotion of the skinks was measured at seven temperatures (18°C, 21°C, 24°C, 27°C, 30°C, 33°C, 36°C). Each skink was tested at one temperature per day, and the order of test temperatures was random. The skinks were placed in an incubator (KB240, Binder, Germany) set at one of test temperatures for 2 h prior to each trial. We sampled the cloacal temperatures of several skinks to confirm the consistence between body temperature and test temperature before initiating the measurement of locomotion. The locomotion trials were conducted in a custom-made runway (1800 mm \times 150 mm \times 200 mm) with transparent glass on the front side to allow the video camera to capture the skink's locomotion. The skinks were introduced from one end of the runway and ran through 1500 mm (6 intervals of 250 mm) under vigorous stimulation (by tapping the tail of skinks with a painting brush). The locomotion of the skinks was captured using a digital video camera (SONY, DCR-SR220E), and the recorded videos were analysed by Windows Movie Maker (Microsoft Corp., USA) for the sprint speed in the fastest 250 mm interval. Each skink was tested three times with a 1 h interval at each temperature; the testing sequence for all individual skinks was the same in each trial. The sprint speed was calculated as the mean of the fastest speed for the three measurements because there was no among-measurement difference in the fastest speed ($P > 0.15$ in all treatments at any temperature). All the locomotion measurements were conducted from 09:00 to 12:00, and after measurements the skinks were transferred back to the cages where food and water were available *ad libitum* until 20:00.

2.4 Statistical analysis We analysed the normality of

variance distributions with the Kolmogorov-Smirnov test and the homogeneity of variances with Levene's test. One-way ANOVAs were used to analyse between-treatment or between-sex difference in the body size of skinks. Repeated measures ANOVAs were utilised to analyse body temperature variations of the skinks in the acclimation treatments over time; while the locomotion variations were analyzed in the same way with test temperature as the repeated measures and treatment as the factor. A Tukey's *post-hoc* multiple-comparison was used to distinguish the mean traits values.

3. Results

3.1 Thermal environment In the natural habitat where *P. chinensis* was collected, the mean ambient temperature was 21.1°C (13.5°C–33.0°C) in the spring and 31.9°C (25.0°C–37.3°C) in the summer (Figure 1a). During the acclimation experiments, the mean ambient temperature in the cold-acclimated treatment was 19.1°C (15.3°C–32.0°C) and 30.9°C (26.5°C–36.9°C) in the warm-acclimated treatment (Figure 1b).

3.2 Body size and temperature of lizards The body size of skinks did not differ between spring and summer [SVL: 113.8 \pm 2.9 mm ($n = 11$) vs. 111.0 \pm 1.1 mm ($n = 13$), $F_{1,22} = 0.980$, $P = 0.333$; body mass: 39.54 \pm 3.15 g ($n = 11$) vs. 32.88 \pm 1.45 g ($n = 13$), $F_{1,22} = 4.094$, $P = 0.056$], nor between cold- and warm-acclimated treatments [SVL: 111.8 \pm 3.3 mm ($n = 9$) vs. 112.8 \pm 2.8 mm ($n = 13$), $F_{1,20} = 0.071$, $P = 0.792$; body mass: 35.53 \pm 2.93 g ($n = 9$) vs. 36.66 \pm 2.87 g ($n = 13$), $F_{1,20} = 2.250$, $P = 0.149$]. Body size did not differ between sexes (for SVL and body mass, all $P > 0.160$).

The body temperatures of *P. chinensis* in the acclimation treatments corresponded with the thermal environments in treatments. The mean body temperature in the cold-acclimated treatment was 21.6°C (16.8°C–31.2°C) and 32.3°C (25.9°C–37.0°C) in the warm-acclimated treatment (Figure 2). The body temperatures of *P. chinensis* were significantly higher in the warm-acclimated treatment than in the cold-acclimated treatment ($F_{1,30} = 2442.9$, $P < 0.001$).

3.3 Locomotion Sprint speed was significantly affected by test temperatures ($F_{6,132} = 101.81$, $P < 0.001$), and was generally higher in summer than in spring ($F_{1,22} = 5.35$, $P = 0.030$), but did not differ between sexes ($F_{1,22} = 1.37$, $P = 0.256$). A significant interaction between test temperatures and season groups indicated that the seasonal variation in sprint speed depended on the test

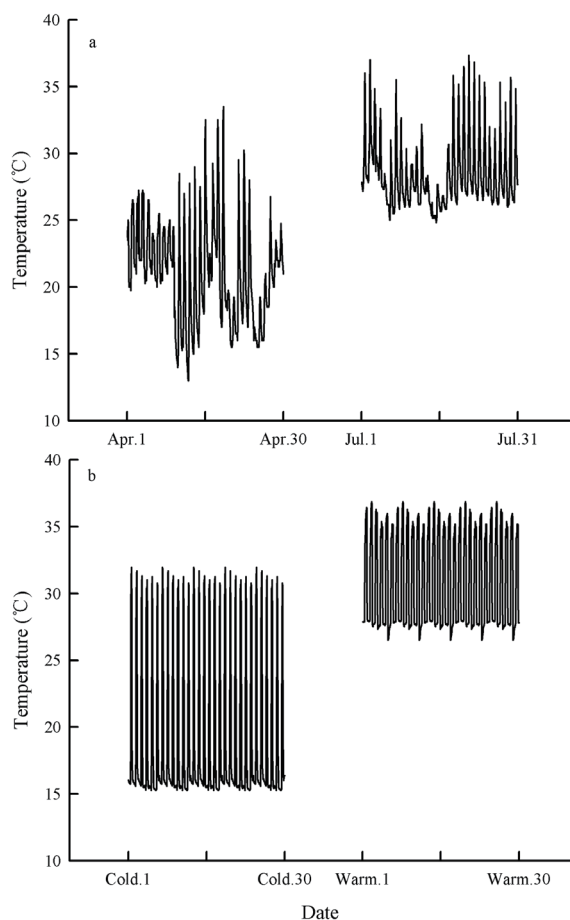


Figure 1 The thermal environment in the natural habitat and thermal acclimation treatments: (a) the thermal environments in spring (April) and summer (July), and (b) the thermal environments in cold- and warm-acclimated treatments. Temperatures were recorded hourly in the natural habitat of the skinks in spring (April) and summer (July). The two acclimation treatments mimicked the thermal environments of spring and summer. The mean ambient temperature was 21.1°C (13.5°C–33.0°C) in the spring and 31.9°C (25.0°C–37.3°C) in the summer. The mean ambient temperature in the cold-acclimated treatment was 19.1°C (15.3°C–32.0°C) and 30.9°C (26.5°C–36.9°C) in the warm-acclimated treatment.

temperatures ($F_{6, 132} = 3.90$, $P = 0.001$). Sprint speed was higher for skinks in the summer treatment than for skinks in the spring treatment at high-test temperatures (27°C, 30°C, 33°C, 36°C) ($F_{1, 22} = 8.00$, $P = 0.010$) but did not differ at low-test temperatures (18°C, 21°C, 24°C) ($F_{1, 22} = 0.26$, $P = 0.614$) (Figure 3a).

Sprint speed of skinks in the acclimation experiments did not differ between the cold- and warm-acclimated treatments ($F_{1, 20} = 0.36$, $P = 0.56$), or between sexes ($F_{1, 20} = 0.03$, $P = 0.873$). However, the sprint speed was significantly affected by test temperatures ($F_{6, 120} = 68.20$, $P < 0.001$) and the interaction between test temperature and treatment ($F_{6, 120} = 6.71$, $P < 0.001$). The sprint

speed of the skinks in the cold-acclimated treatment was significantly higher than the skinks in the warm-acclimated treatment at low-test temperatures ($F_{1, 20} = 15.25$, $P = 0.001$) but did not show between-treatment differences at high-test temperatures ($F_{1, 20} = 1.05$, $P = 0.318$) (Figure 3b).

4. Discussion

Similar to many other diurnal lizards, *P. chinensis* lives in an open and warm environment and rigorously regulates body temperature when surrounding heating sources are available to achieve optimal temperatures for physiological and behavioural functions (Ji *et al.*, 1995; Shu *et al.*, 2010). In spite of the significant role of behavioural thermoregulation in the thermal adaptation of this species, our results suggest that *P. chinensis* may also use acclimation as an adaptive strategy to respond to environmental variation, as indicated by the seasonal acclimatisation and thermal acclimation of locomotion in this species. Therefore, the acclimation of functional performance which is originally thought to mainly occur in aquatic and semi-aquatic animals (Scheiner, 1993; Wilson *et al.*, 2000; Johnston and Temple, 2002) may also exist in terrestrial species.

Acclimation responses to temperature have been clearly demonstrated in a diversity of species in the laboratory (see review by Angilletta, 2009). Our thermal acclimation experiments indicated that the cold-acclimated *P. chinensis* ran faster than the warm-acclimated *P. chinensis* at low-test temperatures but not

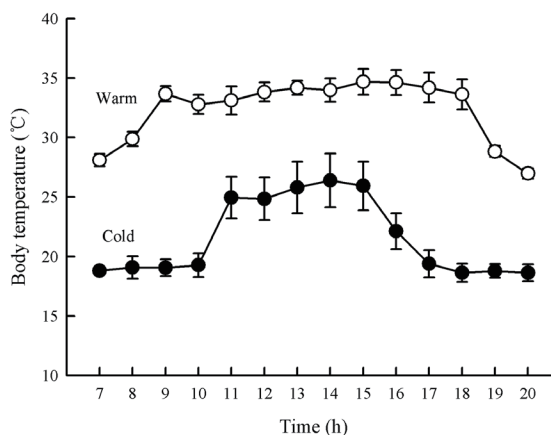


Figure 2 The body temperatures of *Plestiodon chinensis* exposed to different thermal acclimation treatments. The cloacal temperatures of the skinks were measured hourly from 07:00 to 20:00 on the 20th day of the acclimation experiments. The mean body temperature in the cold-acclimated treatment was 21.6°C (16.8°C–31.2°C) and 32.3°C (25.9°C–37.0°C) in the warm-acclimated treatment.

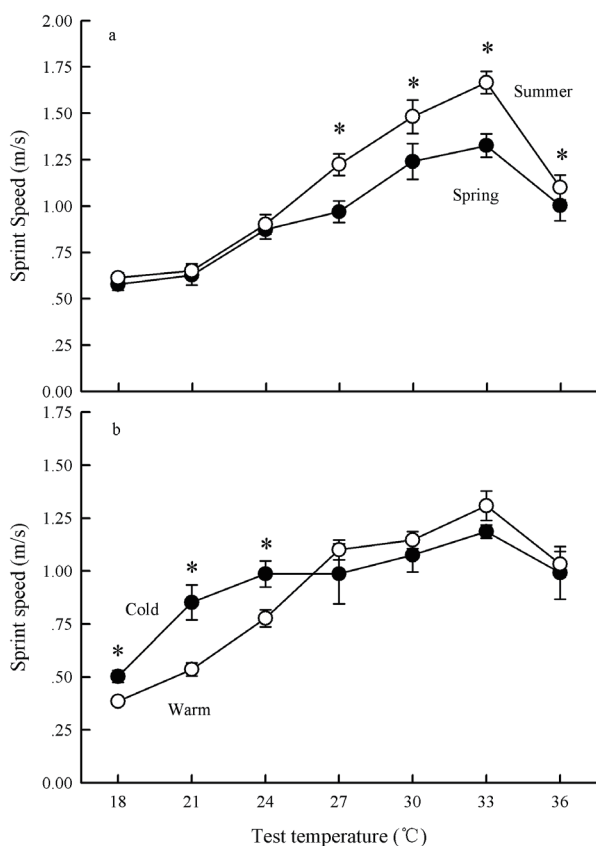


Figure 3 *Plestiodon chinensis* locomotions at different test temperatures ranging from 18°C to 36°C: (a) individuals from field populations during spring and summer, and (b) individuals from the cold- and warm-acclimated treatments. The asterisks indicate significant differences between acclimation (acclimatisation) groups. Each skink was tested at one temperature per day, and three times within a 1 h interval in each trial. *P. chinensis* ran faster during summer than during spring at high-test temperatures but not at low-test temperatures. In contrast, the cold-adapted *P. chinensis* ran faster than the warm-adapted *P. chinensis* at low test temperatures but not at the high test temperatures. The sample size for spring was 11, summer was 13, cold-acclimated treatment was 9 and warm-acclimated treatment was 13.

at high-test temperatures. The thermal acclimation of locomotion is largely consistent with previous studies on other ectotherms, such as fish and amphibians (e.g., Fry and Hart, 1948; Wilson *et al.*, 2000; Carey and Franklin, 2009). The results partially support the beneficial acclimation hypothesis that an acclimatory response to a particular environment (low temperatures in this case) confers a physiological performance advantage or fitness promotion on an individual organism in that environment over another organism that has no acclimation or is acclimated to another environment (Leroi *et al.*, 1994; Wilson and Franklin, 2002). However, this pattern of thermal acclimation was not observed in seasonal acclimatisation of the natural population.

Instead, *P. chinensis* from the summer population ran faster than *P. chinensis* from the spring population at high-test temperatures from 27°C to 36°C but not at low-test temperatures from 18°C to 24°C, which seems to be consistent with the prediction of beneficial acclimation hypothesis (high temperatures in this case).

This discrepancy between seasonal acclimatisation and thermal acclimation suggests that the seasonal acclimatisation in response to other factors masks thermal acclimation in the skink. These environmental factors may be abiotic (e.g., water and sunlight) or biotic (e.g., food and predation). For example, the lower food availability and temperatures (leading to inefficient food assimilation; Ji *et al.*, 1995) observed in spring than in summer may result in the poor condition of the energetic state of *P. chinensis* in this season. As a result, the decrease in energetic expenditure available for locomotion due to energy limitation may affect the physiological properties of muscle and therefore locomotion (Shu *et al.*, 2010). Therefore, the seasonal acclimatisation in locomotion may be relevant for the effect of body temperature and other environmental factors (e.g. food availability) on energetic metabolism (Johnston *et al.*, 1985; Rall and Woledge, 1990), yet the underlying mechanisms of this physiological process remain unknown.

In summary, our study indicated that the acclimatisation in nature could be a result of combined effects of many environmental factors and is more complex than the acclimation in response to a single environmental factor demonstrated in the laboratory. Disentangling the causes of and identifying the ecological significance of acclimatisation responses in nature would be a significant challenge for eco-physiologists to increase our knowledge of animal physiological adaptations in response to environmental changes. However, the ecological processes and significance of acclimation have received much less attention, while physiologists keep their focus on the biochemical and molecular bases of acclimation (Somero, 2005).

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