

An overview of geographic variation in the life history traits of the tropical agamid lizard, *Calotes versicolor*

Rajkumar S. Radder

Building A08, The School of Biological Sciences, University of Sydney, NSW 2006, Australia

Life history theory seeks to explain patterns of variation among geographically widespread populations of same species to understand their ecology and adaptations. To date, very few attempts have been made to review and compare life history traits of tropical reptiles, especially those that inhabit the Asian continent. Among tropical reptiles, the agamid lizard *Calotes versicolor* is widespread, extensively studied and thus ‘tailor made’ to understand geographic variation if any. Therefore, in this review, life history traits of *C. versicolor* are compared to understand variation in life history with reference to their geographical distribution. The examination of *C. versicolor* populations across its geographic range demonstrates considerable variation in some of the life history traits but not in all. For example, there is no sexual size dimorphism at hatching in one population but it is apparent in another. Body size, mass, reproductive output, influence of incubation thermal regimes on eggs and embryos differ between the populations. There is a trade-off between clutch size and egg size in one population but egg size is optimised in another. Lizards that belong to one population mature at a smaller size but at the same age compared to another population. Also, embryos exhibit high thermal tolerance in one population compared to another. These emergent life history patterns from the comparisons are discussed in light of traditional as well as recent views and theories of life history in reptiles.

Keywords: *Calotes versicolor*, geographic variation, life history, lizards, reptiles, reproduction.

EVERY organism can be truly represented only by its whole life history. An organism's life history is its lifetime pattern of growth, differentiation, development, storage and, especially, reproduction¹. Life history tactics are a series of co-adapted traits designed by natural selection to solve ecological problems. The life history of an organism is not immutable and fixed within the limits of the individual's genotype. However, life history traits can be modified by the environment an individual experiences during its life². Therefore, the observed life history of a

given organism represents the result of long-term evolutionary forces and also of the more immediate response of an organism to the environment it is and has been living¹. It is necessary to consider geographic differences among populations to understand the source of variation in life history traits because difference in life history characteristics of populations may provide insights into the ecology and adaptive value of particular traits³.

The typical approach of evaluating variation in life history is to compare two or more populations (or species or groups) and understand the differences between them with reference to their environments. Thus, not surprisingly, as in many animal taxa, reptiles have been the subjects of series of long-term field-based studies for such a purpose. These studies have explicitly demonstrated geographic variation in morphological, reproductive, behavioural and ecological characteristics among populations of different localities or habitats^{3–16}. Such studies not only provide strong experimental support to many of the life history views and predictions proposed by Begon *et al.*¹ and Stearns² but also enable us to understand the diversity of reptilian life histories.

Importance of understanding tropical reptilian life histories

Our understanding of reptilian life histories is based on the numerous medium and/or long-term field-based studies and a series of careful recent experimental approaches^{5,6,17–25}. But, by and large the above studies suggest that there is a high degree of phylogenetic conservatism and strong bias in our understanding of lizards' life histories^{3,26–29}. This is because conclusions are based on studies conducted on a few selected groups of lizards, particularly new world lizards (iguanids) and Australian skinks^{3,9,13}. However, their old world equivalents, the agamids, have rarely been the subject of such comparative studies. Remarkably, the greatest gap in our knowledge of geographical variation in reptilian life history patterns stems from the lack of data on tropical species – especially those that inhabit the Asian continent. Thus, independent datasets from species belonging to such lizard taxa are necessary to understand general patterns of co-variation among life histories.

e-mail: raju@mail.usyd.edu.au

***Calotes versicolor*: ‘Cinderella’ for life history comparisons**

The agamid lizard, *Calotes versicolor* is one among the few geographically widespread tropical lizards. French naturalist Francois M. Daudin first described this lizard in 1802. In earlier literature it is referred as *Agama versicolor*. It ranges from South-eastern Iran to Afghanistan and Nepal, India to Sri Lanka, Myanmar to Indo-China, Southern China to Peninsular Malaysia and Sumatra^{30–33}. Recent field surveys confirm its distribution stretching from Oman to the West^{34,35}, across Southern and South-east Asia to Indo-China to the East, the Maldives, Réunion, Mauritius, Seychelles and more recently it has been introduced to Florida in the United States of America^{36–42}. Due to its wide geographic distribution naturalist Pat Matyot recently referred to *C. versicolor* as a strong candidate for the status of most widespread non-gekkonid lizard in the world⁴¹. *C. versicolor* has several common names in its different geographic locations; ‘blood-sucker’ (India, Florida, US), ‘garden or garden fence lizard’ (Southern India), ‘garden girgit’ or ‘bush lizard’ (Punjab, India), ‘oriental lizard’ (China), ‘crested tree lizard’ (Seychelles) and ‘changeable lizard’ (Malaysia). Most of these common names have been derived from its morphology and habitat. In fact, the Latin-specific name ‘*versicolor*’ means variable colour since it changes colour rapidly to blend with its surroundings and hence known as ‘changeable’ lizard in Malaysia⁴³. However, a few of these common names are inappropriate and misleading. For instance, it is referred as ‘blood-sucker’ in several parts of India. But this lizard cannot suck anything, let alone blood.

Calotes versicolor belongs to genus *Calotes*, which is one of the most species-rich groups in Asia (represented by twenty species) and considered as an ecological equivalent of the iguanid *Anolis* with reference to its species richness^{43–46}. Thus, not surprisingly, among tropical agamids, *C. versicolor* has gained importance as a laboratory model system. To date *C. versicolor* is subject of >470 published research articles on a broad-spectrum biological studies (source: ISI Science Citation Index) making *C. versicolor* as a ‘Cinderella’ of tropical reptilian research.

Therefore, the main purpose of this article is to review and provide a comparative account of the life history of *C. versicolor* occupying different geographical regions in Asia. In the following sections, published information on life history traits is reviewed to examine variation if any, in (1) morphology and growth (i.e. body size and sexual size dimorphism with respect to ontogeny), (2) reproduction (clutch, egg and offspring traits and factors controlling clutch and offspring sizes), (3) development (factors influencing eggs and embryos during development), and (4) response of eggs and embryos to different incubation thermal regimes.

Methods adopted for comparison

Life history data for *C. versicolor* from the populations inhabiting different geographical regions were obtained and screened for suitability of comparisons. For comparative purpose, I have selected only published data sets that represent and include complete information regarding all life history stages (i.e. from eggs (embryos) to adult stage of life) for a given population. There are several studies reporting information on some of the selected life history traits in one or other stages of life history for *C. versicolor*^{33,43,47,48}. However, these represent either only part of the life history or information is not emanating from a single population. Hence, data and information from such studies were not used for comparison in order to avoid any misinterpretation that could arise due to confounding effects related to population or ontogenetic changes.

Life history of two exclusive *C. versicolor* populations has been studied in detail during last decade in India^{49–52} and China^{53,54}. The Indian population is from the surrounding areas of Dharwad (15°17'N and 75°3'E), Karnataka State, India. While the China population is from the surrounding areas of Tongshi (18°47'N, 109°30'E), Hainan, Southern China. The published life history data from the above studies were used for the present comparisons. Henceforth, these populations are referred to as ‘Dharwad’ and ‘Tongshi’ population for convenience. Information for some of the traits/indices is not available in the original publications and was derived using the available data. The derived traits are male–female Snout-vent length (SVL) ratio (commonly known as MFR), egg volume and developmental rate for the Tongshi population, and relative head size for the Dharwad population. The MFR for the Tongshi population was derived by calculating the ratio of average SVL of males divided by average SVL of females. The egg volume was derived by a formula for prolate spheroid $\frac{4}{3} \pi (\text{length}/2) (\text{width}/2)^2$ using egg length and width data. The embryonic developmental rate at various incubation thermal regimes for the Tongshi population was calculated by dividing the observed incubation period at different incubation regimes by the shortest observed incubation period and taking the inverse of this value following the procedure described for the species⁵¹. The relative head size for the Dharwad population was derived by using the formula $(\text{head length}/\text{SVL}) \times 100$ and $(\text{head width}/\text{SVL}) \times 100$ respectively.

Life history comparison is restricted to qualitative rather than quantitative methods for the following reasons: (a) the data is secondary – gathered from published literature representing large unequal sample sizes with respect to each population and (b) comparisons are based on many derived ratios and indices. However, the emerging life history differences are strong enough to allow interpretations and there is little chance of making misinterpretations for generalization due to the qualitative methods adopted.

Variation in morphology and ontogeny of sexual size dimorphism

At hatching

The difference in body mass at birth (hatching) is least between the two populations (Table 1). However, both male and female hatchlings of the Tongshi population are on an average 8% slower in linear growth (SVL) than those from the Dharwad population (Table 1). A difference of 0.03 units in MFR is evident between these populations (Table 1). The relative head length is comparable between the populations. But relative head width is less in the Tongshi population compared to that of the Dharwad population (Table 2). There is no sexual size dimorphism in majority of the morphological traits (i.e. SVL, head length and width) in the Dharwad population. Interestingly, despite reports of sexual dimorphism in head size for the Tongshi population⁵³, the average head length of males and females overlaps in the Tongshi population (Table 2).

During sub-adult stage of life

The above two populations differ greatly in MFR (Table 1). The MFR of the Tongshi population is higher (1.0 unit) than that of the Dharwad population. Lizards belonging to the Dharwad population are twice as heavy as those from the Tongshi population (Table 1). Sexual size dimorphism is not apparent in recorded morphological traits (i.e. SVL, body mass, head length and width) within a population, but there are differences in head length, width and relative head size between these two populations. The Dharwad population exhibits higher average values for head size parameters (Table 2). The average difference for head length and width is 5.02 mm and 4.07 mm respectively (Table 2). As a result, HL/SVL% and HW/SVL% are also greater for the Dharwad population by a unit of 7.41 and 5.77 respectively. Overall, these trends indicate

that lizards from the Dharwad population have larger heads than those from the Tongshi population.

During adult stage

Interestingly, MFR of adults is similar for both populations (Table 1). However, lizards from the Dharwad population are 14% larger in size (SVL) than those from the Tongshi population (Table 1). As a result, average body mass of the Dharwad population is greater than that of the Tongshi population (Table 1). Sexual size dimorphism in head size is evident in both the populations. However, both absolute and relative head size is greater for the Dharwad population (Table 2). Average relative head length (HL/SVL%) varies by 6.33 and 3.98 units for males and females respectively. Similarly relative head width (HW/SVL%) varies by a factor of 6.77 and 0.69 units between the Dharwad and Tongshi populations for males and females respectively.

Variation in reproductive traits

Female *C. versicolor* in the Dharwad population attains sexual maturity at ~85 mm SVL, while those in the Tongshi population mature at ~79 mm SVL. The maximum body size of gravid females recorded is 136 mm and 103 mm for the Dharwad and Tongshi population respectively (Table 3). The average body mass of gravid females from Dharwad is twice heavier than that of the Tongshi population (Table 3). Clutch size (eggs/reproductive episode) exhibits a marked difference between these two populations. *C. versicolor* in Dharwad have average 17.26 ± 0.40 eggs/clutch, while those of the Tongshi population produce an average of 9.0 ± 0.3 eggs per reproductive episode (Figure 1a). Apparently, the Dharwad population exhibits a greater range (26 eggs) for clutch size during a reproductive episode. But the range for the Tongshi popu-

Table 1. Summary (mean \pm SE) of morphological traits of *C. versicolor* from two geographic localities

Life history stage	Dharwad population*					Tongshi population**				
	<i>n</i>	SVL	Body mass	Tail length	MFR	<i>n</i>	SVL	Body mass	Tail length	MFR
Hatchlings										
Male	22	26.5 \pm 0.2	0.59 \pm 0.06	50.6 \pm 0.6	1.01	40	24.0 \pm 0.2	0.58 \pm 0.01	46.2 \pm 1.0	0.98
Female	16	26.2 \pm 0.2	0.56 \pm 0.02	49.8 \pm 0.6		33	24.6 \pm 0.2	0.57 \pm 0.01	44.9 \pm 1.0	
Sub-adults										
Male	17	71.9 \pm 1.2	13.62 \pm 0.91	182.3 \pm 3.9	0.99	16	75.6 \pm 0.7	7.8 \pm 0.4	232.1 \pm 3.3	1.09
Female	14	72.0 \pm 1.8	14.03 \pm 1.12	168.1 \pm 7.2		14	69.6 \pm 2.0	5.8 \pm 0.5	207.0 \pm 8.0	
Adults										
Male	48	106.6 \pm 1.7	43.94 \pm 1.63	238.3 \pm 3.9	1.02	117	90.1 \pm 0.5	16.0 \pm 0.4	272.8 \pm 1.7	1.01
Female	42	104.1 \pm 1.9	35.52 \pm 1.45	226.5 \pm 4.7		76	89.8 \pm 0.8	15.1 \pm 0.6	259.1 \pm 2.4	

Sources: *ref. 50, **ref. 53.

SVL = Snout-vent length, MFR = Male to female ratio. All length units are in millimeters and mass units are in grams. *n* = sample size.

Table 2. Comparative account of (mean \pm SE) head size in *C. versicolor* belonging to the Dharwad and Tongshi populations. All length units are in millimeters

Life history stage	Dharwad population*				Tongshi population**			
	Head length	Head width	HL/SVL (%)	HW/SVL (%)	Head length	Head width	HL/SVL (%)	HW/SVL (%)
Hatchlings								
Male	7.81 \pm 0.08	4.91 \pm 0.05	29.47	18.52	7.1 \pm 0.07	5.6 \pm 0.04	29.5	23.02
Female	7.62 \pm 0.12	4.76 \pm 0.10	29.08	18.16	7.1 \pm 0.05	5.5 \pm 0.004	28.7	22.5
Sub-adults								
Male	22.15 \pm 0.37	15.62 \pm 0.54	30.81	21.72	17.3 \pm 0.2	11.8 \pm 0.2	22.9	15.6
Female	21.75 \pm 0.41	15.42 \pm 0.47	30.21	21.41	16.2 \pm 0.4	11.1 \pm 0.3	23.3	16.0
Adults								
Male	32.12 \pm 0.75	24.70 \pm 0.77	29.19	23.17	20.5 \pm 0.1	14.8 \pm 0.1	22.8	16.4
Females	26.94 \pm 0.53	16.86 \pm 0.56	25.88	16.19	19.6 \pm 0.2	13.9 \pm 0.1	21.9	15.5

Sources: *ref. 50, **ref. 53.

Table 3. Comparative account of habitat, reproductive and morphological traits in female *C. versicolor* (length units are in millimeters and weight units are in grams, for SVL and body mass mean \pm SE, n = sample size)

Variable	Dharwad population*		Tongshi population**	
SVL	(n = 236)	102.8 \pm 0.8	(n = 65)	90.4 \pm 0.9
Size at maturity		86.00		78.9
Maximum adult size		136.00		103.8
Body mass	(n = 236)	35.17 \pm 0.81	(n = 20)	15.0 \pm 0.9
Mass at maturity		16.30		9.9
Maximum body mass		65.00		25.9
Habitat		Arboreal		Arboreal
Breeding timing		May–October		April–July
Reproductive mode		Oviparous/multi-clutched		Oviparous/multi-clutched
Breeding pattern		Seasonal		Seasonal
Age at maturity		<12 Months		< 12 Months

Sources: *refs 49–52, **refs 53, 54.

lation is comparatively less (11 eggs/reproductive episode). As a result, clutch mass (reproductive output) is greater for the Dharwad population compared to that of the Tongshi population (Figure 1 *b*). Interestingly, though clutch size varies between these populations, there is not much variation in the egg size (especially in parameters like egg length, width or volume, Figure 2 *a–c*). The range for above egg traits largely overlaps between the populations (Figure 2 *a–c*). Further, average egg mass of the Tongshi population is greater than that of the Dharwad population (Figure 1 *c*). The Dharwad population exhibits higher range (490 mg) with respect to average egg mass among clutches. While egg mass for the Tongshi population exhibits comparatively less variation (170 mg, Figure 1 *c*).

Variation in factors influencing clutch and egg sizes

In both populations, clutch size and mass are positively related to female body size (SVL), and no relationship is evident between egg mass and maternal SVL. The body

condition is positively related to clutch size in the Dharwad population but not in the Tongshi population. Average egg mass is not related to clutch size in the Tongshi population. But it is negatively related with clutch size in the Dharwad population. Further, average egg length, width and clutch size are not correlated in the Tongshi population but egg length and egg volume are negatively related with clutch size in the Dharwad population. Thus, there is no trade-off between clutch size and egg size in the Tongshi population indicating an egg size optimization. But trade-off between clutch size and egg size is evident in the Dharwad population.

Variation in the embryonic responses to incubation thermal regimes

The embryonic responses to incubation temperature regimes vary between populations as evident by the differences in developmental rates, duration of incubation, survival (hatching percentage) and other related traits (Figure 3, Table 4). In both populations, higher incubation tempera-

tures accelerate embryonic growth but there is temporal variation. For instance, eggs from the Tongshi population hatch 10 days earlier than those from the Dharwad population at $27 \pm 2^\circ\text{C}$. While, incubation duration largely

overlaps at 30°C for both the populations (Table 4, Figure 3). Further, at 33°C incubation regimes eggs from the Dharwad population hatch 6 days earlier compared to the Tongshi population (Table 4, Figure 3). Hatching success decreases with an increase in incubation temperature in both the populations (Table 4). However, hatching success reduces drastically (3.4% survival) at 33°C in the Tongshi population (Table 4). At similar thermal regimes, ~59% hatching success can be observed in the Dharwad popula-

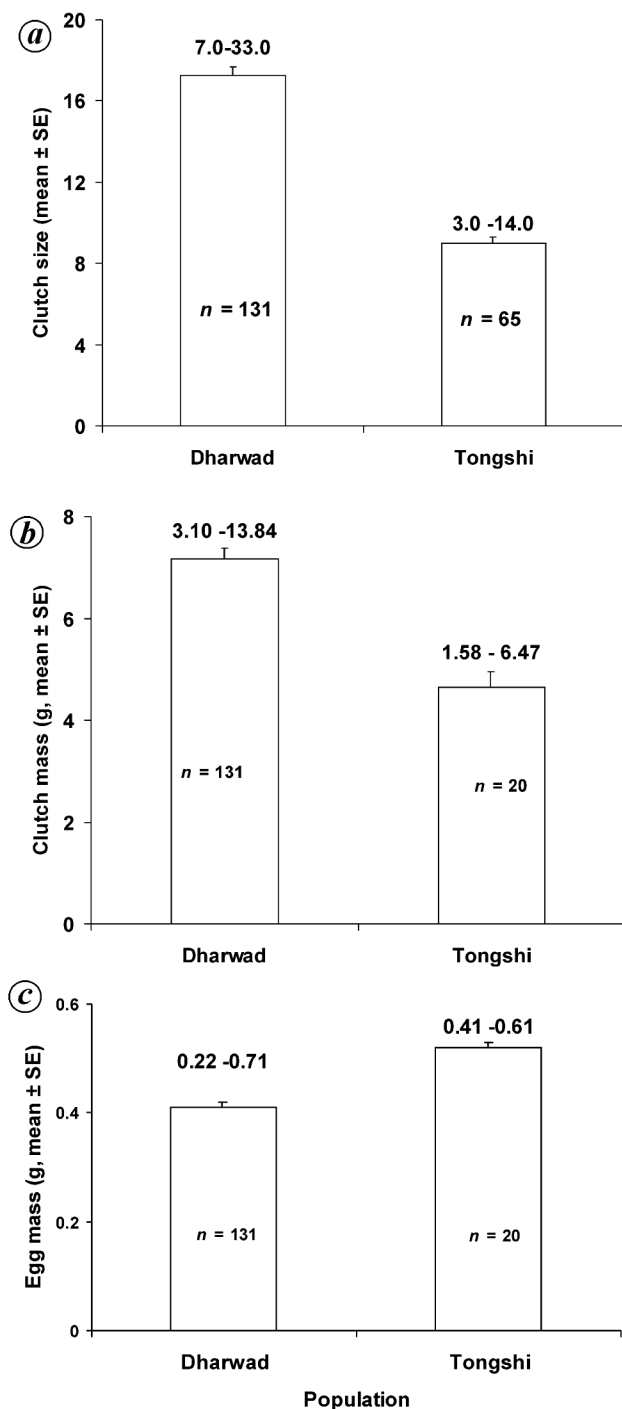


Figure 1. Summary of reproductive output in two populations of *C. versicolor*. Number inside the bars indicates sample size and those above the bar indicate range for respective population. Represented traits are: **a**, Number of eggs/reproductive episode (clutch size); **b**, Reproductive investment/episode (clutch mass); **c**, Partition of the reproductive investment (egg mass). Note a large difference (mean and range) in clutch size and mass, and an overlapping average egg mass between the populations (refs 49, 52, 53).

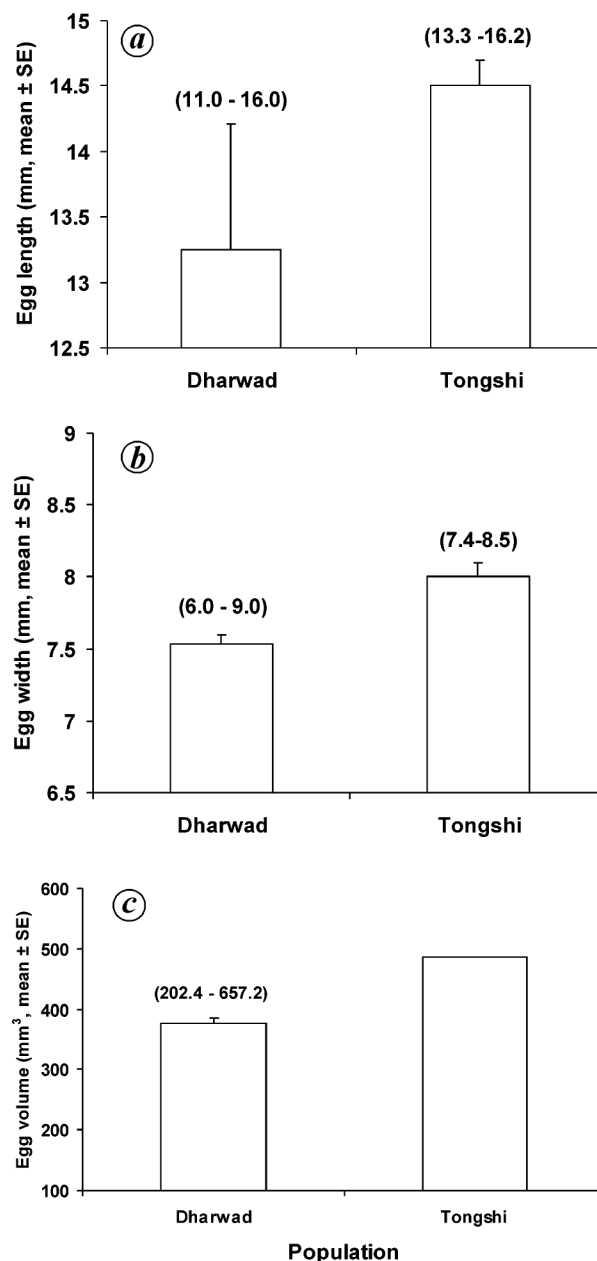


Figure 2. Summary of comparison of egg traits in two populations of *C. versicolor*. Represented traits are: **a**, egg length; **b**, egg width and **c**, egg volume. Note large range for all the traits in the Dharwad population indicating complex trade-offs. Small ranges for the Tongshi population indicate egg size optimisation ($n = 131$ and $n = 20$ clutches for the Dharwad and Tongshi population respectively, refs 49, 52, 53).

Table 4. Comparative account (mean \pm SE) of embryonic responses to incubation temperature regimes in two populations of *Calotes versicolor*. Number in parenthesis indicates number of eggs hatched/total eggs used for incubation

Variables	Dharwad population*				Tongshi population**		
	Incubation temperature ($^{\circ}$ C)				Incubation temperature ($^{\circ}$ C)		
	27 \pm 2	30 \pm 1	33 \pm 1	35 \pm 1	27 \pm 2	30 \pm 1	33 \pm 1
Incubation duration (days)	70.33 \pm 0.49	50.6 \pm 0.92	44.40 \pm 1.02	38.40 \pm 0.24	60.5 \pm 0.4	51.4 \pm 0.05	50.3
Hatching success (%)	93% (138/148)	89% (49/55)	59% (36/61)	53% (33/59)	80.6% (25/31)	67.9% (19/28)	3.4% (1/29)
Offspring SVL (mm)	26.2 \pm 0.2	24.7 \pm 0.6	26.0 \pm 0.5	24.8 \pm 0.1	24.6 \pm 0.2	24.3 \pm 0.2	23.4 \pm 0.5
Offspring body mass (mg)	563.0 \pm 17	466 \pm 32	495 \pm 89	481 \pm 30	553.3 \pm 14.0	555.3 \pm 17.3	630.4 \pm 29.8
Tail length (mm)	48.8 \pm 0.5	46.2 \pm 1.2	45.8 \pm 1.6	44.8 \pm 1.4	47.0 \pm 1.3	46.5 \pm 1.3	41.6 \pm 1.4

Sources: *refs 51, 52; **ref. 54.

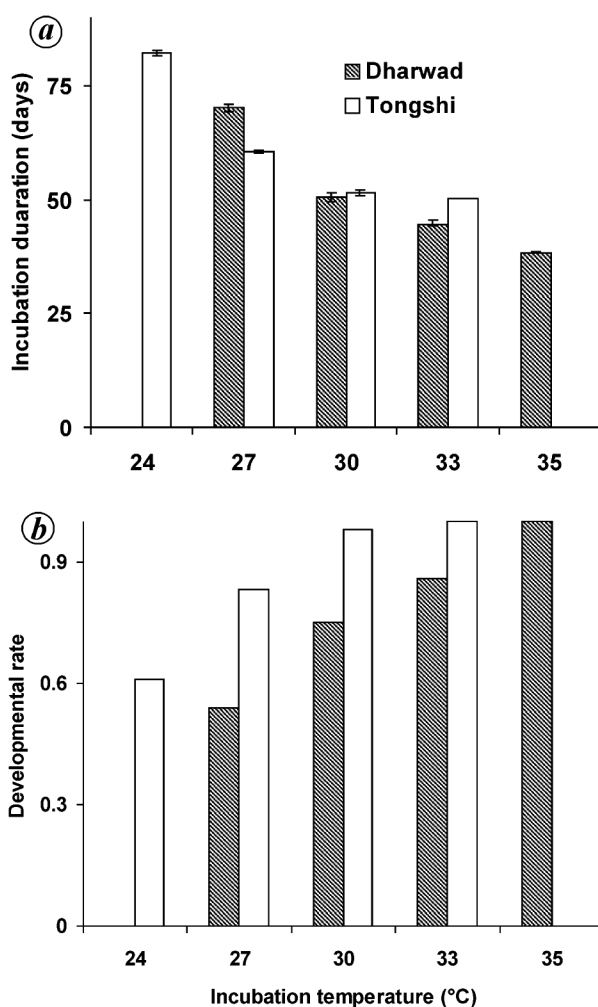


Figure 3. Summary of geographic difference in embryonic responses to incubation temperature regimes in *C. versicolor*. Note the variation in incubation duration (a) and developmental rate (b) between the populations (sample size is as in Table 4, refs 51, 54).

tion and indicates a high thermal tolerance. In the Dharwad population, eggs incubated at 35 $^{\circ}$ C usually produce small-sized hatchlings (SVL and tail length), whereas the

33 $^{\circ}$ C incubation temperature yields small-sized hatchlings in the Tongshi population (Table 4).

Several embryonic responses are comparable between the populations. For example, the optimal egg incubation temperature range is 25–30 $^{\circ}$ C. The eggs from both populations gain mass as incubation progresses due to the absorption of water. However, the timing of mass gain in response to incubation temperature varies between these two populations. The small size of hatchlings at high thermal incubation regimes is due to increase in the amount of un-utilized yolk left behind in the eggshells. Incubation temperatures do not have any significant effect on sex determination in both the populations. Thus, all incubation regimes yield approximately equal sex ratios.

Patterns emerging from the comparison of life history traits

Generally, life history traits differ considerably between geographically well-separated populations. The present comparison between two *C. versicolor* populations, with no continuous distribution between them, also revealed considerable variation in some of the life history traits but not in all. The following patterns can be recognized by the comparisons. There is no sexual size dimorphism at birth (hatching) in *C. versicolor* population of Dharwad, but between sex differences in head size is apparent in the Tongshi population. Surprisingly, though the average SVL, head length and width of the offspring overlaps between sexes in the Tongshi population, sexual size dimorphism in head size is documented in previous report⁵³. Further, this pattern does not persist during ontogeny in the Tongshi population, as SSD is not apparent in sub-adults. However, in both the populations, SSD in head size is reported once the lizards attain sexual maturity and persist throughout life. In many reptiles, the larger head of males has been suggested to play a role in intrasexual competition, territory defence, mate choice and intersexual dietary differences⁵⁵. In addition, it is suggested that the rate of increase in female body size after attaining

maturity is greater than the rate of increase in head size as a mechanism for increase in fecundity⁵⁶. Yet according to another prediction, head size may be phylogenetically conserved in certain taxa with no significant present functions⁵⁷. At this juncture, ecological advantage(s) of head size dimorphism is unclear for both the populations and warrant further investigations.

Calotes versicolor from the Dharwad and Tongshi populations differ in body size as well as mass. These differences are evident at hatching and become more pronounced during ontogeny. For instance, the average adult size in the Dharwad population is greater than that of the largest recorded individual from the Tongshi population. Also, there is a difference in body size at sexual maturation between the populations. Such differences may be attributable to several proximate factors/selective pressures acting on each population. Majority of the empirical studies on reptiles address the role of temperature as a proximate source for the variation in life histories^{25,58,59}. Based on such studies, Adolph and Porter⁵⁹ developed a model in which age and size at first reproduction can be predicted for lizards living in different thermal environments. In this model, they proposed that individuals of the species from the warmer populations mature early at relatively smaller sizes. Whereas, those from the cooler environments delay maturity due to reduced opportunity for growth, and hence mature at relatively larger size and older age. Thus, delay in maturity lead to large differences in body size between populations living at different climatic conditions. Majority of the empirical data on reptiles support this model-delay in maturity with the resultant larger size, a common pattern of cool-climate populations of geographically widespread species^{20,60–65}. However, one caveat of this model is that other proximal factors should be considered when applying it to a wide variety of taxa in order to explain delays in maturity, size and age⁶⁵.

The present observations on *C. versicolor* do not fit *in toto* with predictions of Adolph and Porter's model. The annual average temperature in surrounding areas of Tongshi hovers around 23°C^{53,54} and is comparatively cooler than that of the Dharwad region (average annual temperature 29°C). Interestingly, *C. versicolor* from the cooler climate (Tongshi) matures at a smaller size, but at the same age compared to the warmer (Dharwad) population. In such cases an alternative explanation to the predictions of Adolph and Porter's model is lizards may mature at the same age but at a smaller size than conspecifics from milder habitat^{66,67} since delaying maturity can be costly to individual fitness^{68,69}. In such scenarios, the ultimate factors governing maturation are likely to be future fecundity gains as a result of a delay in maturation. These views seem to hold true for *C. versicolor*.

The reproductive output varies between the Dharwad and Tongshi populations. This may be due to body size differences between the sites. However, the large difference in fecundity does not result in equally large difference in

egg size between the populations (i.e. in traits like egg length, width or volume). Traditionally, in squamate reptiles, variation in reproductive output in intra-specific comparison is attributed to variation in maternal size^{70,71}. In *C. versicolor* differences in clutch size can be attributable to longer maternal body size (SVL) in the Dharwad population. However, average egg sizes are comparable between these two populations. This surprising observation is contrary to traditional views. Recent observations in reptiles suggest that differences in some of the reproductive traits are not a simple direct consequence of body size, but are due to the variation in reproductive investment and resource limitation, etc.^{3,65,66}. In such cases, females from the cool sites are known to exhibit relatively higher reproductive investments compared to those from warm climatic conditions. However, deriving such conclusions based on the present observation is difficult for *C. versicolor* because of large variation associated with reproductive frequency (as it exhibits polyautochronic multi-clutched breeding pattern). Detailed empirical studies may clarify some of these issues in future.

The evolution of offspring size has received considerable attention in reptiles^{72–76}. It is often proposed that large offspring are associated with cooler climates and higher altitude in species occupying a wide geographic range^{65,66,77,78}. However, this is not always the case²². It is believed that in cold climate such a response may occur when potential for growth is low or when there is strong selection on offspring survival. In the present comparisons, large offspring (in terms of body mass and conditions) are from the warm climate. This supports the non-traditional view of Sinervo²² rather than above general trend in reptiles. One should note here that life history theory is primarily based on the assumption that organisms aim to maximize fitness within their lifetime. At the most basic level, the primary goal of any organism is to reproduce and maximum fitness is achieved when that organism produces the greatest number of successful offspring within its lifetime⁷⁵. Lifetime reproductive success, however, is limited by the physiology of the organism and the resources that are available in a given ecological setting.

The thermal regimes during incubation differentially influence some of the life history traits between the populations. For instance, embryos from the Dharwad population exhibit much higher thermal tolerance than those from the Tongshi population. The upper threshold of critical constant incubation temperature seems to be close to 33°C in the Tongshi population as hatching success is extremely low (only 3.4%) at this incubation temperature. In contrast, >50% hatching success was recorded at 35°C incubation temperature for the Dharwad population. Thus, 35°C is close to upper range of tolerance but not critical upper limit for the Dharwad population. The average maximum temperature recorded in surrounding areas of Dharwad over the past 8 years during breeding and egg incubation periods (May–January; 1996–2004) of *C. ver-*

versicolor is 37.2°C. It is 33°C at the Tongshi regions during the breeding period. Such differences in maximum ambient temperatures experienced by these two populations over generations may be a possible selective force responsible for the geographic differences in the upper thermal tolerance level of embryos. Interestingly, most of the previous work on geographic variation in lizard phenotypes is specifically focussed on post-hatching life. Only a few studies have addressed plastic responses acting during embryonic development⁹. However, developmental plasticity manifested during embryogenesis may contribute significantly to the observed patterns of geographic variations in phenotypic traits, since events early in development (especially during differentiation) potentially can have more impact on the final (adult) phenotype than the later events⁹. In general, the observations on embryonic responses in *C. versicolor* populations are consistent with long-term field studies that reveal geographic differences in developmental characteristics among population due to local environmental conditions^{4,71}.

Conclusion

The exclusive and detailed studies conducted at various life history stages of *C. versicolor* in the Dharwad and Tongshi regions provided a unique opportunity to compare and understand the geographic variation in life history traits of poorly studied tropical lizards. Species like *C. versicolor* that occupies a wide range of thermal environments over broad geographic regions can demonstrate variation in life history traits. The present observations and other circumstantial evidences in *C. versicolor* support this. For instance, in parts of North and South India females breed seasonally, while females in more Southern populations (i.e. in Sri Lanka) breed continuously³³, suggesting an extreme variation in this important life history mode.

Theoretical discussions generally partition contributions to geographic variation into genetic and environmental components. Geographic variation in life history between the populations is often assumed to reflect genetic divergence caused by natural selection. However, a significant proportion of the variation is attributed to proximate environmental conditions also^{79–81}. Then, is it right to refer this variation as ‘phenotypic plasticity’? According to the classical definition, phenotypic plasticity is ‘the property of a genotype to produce different phenotypes in response to different environmental conditions’⁸¹. A recent study on acrodont lizard molecular phylogenetics (representing many species of genus *Calotes*, including *Calotes versicolor*) suggests that the most agamid lizards belong to three distinct clades⁸². One clade is composed of all taxa occurring in Australia and New Guinea. A second clade is composed of taxa occurring from Tibet and Indian Subcontinent east through South and East Asia. A third clade is composed of taxa occurring from Africa east through

Arabia and West Asia to Tibet and the Indian Subcontinent. These three clades contain all agamid lizards except *Uromastix*, *Leiolepis* and *Hydrosaurus*. A hypothesis of agamid lizards rafting with Gondwanan plates is tested in the above study and reveals that African/West Asian clade is of African or Indian origin, and the South Asian clade is either of Indian or Southeast Asian origin⁸². At present, this is the available information for relatedness between the Tongshi and Dharwad populations. Furthermore, while the distinction between genotype and phenotype is in principle very clear, several complicating factors immediately ensue. For example, genotype can be modified by environmental action as in the case of DNA methylation patterns⁸¹. More intuitively, since environments are constantly changed by the organisms that live in them, the genetic constitution of a population influences the environment itself⁸¹. Thus, at this stage, I prepare to call it ‘geographic variation’ rather than phenotypic plasticity. Perhaps common garden or transplant experiments are necessary to gain a better understanding of the relative contributions of genotype versus environment to the observed geographic variation.

1. Begon, M., Harper, J. L. and Townsend, C. R., Life history variation. *Ecology Individuals, Populations and Communities*, Blackwell Scientific Publications, Massachusetts, 1990, 2nd edn, pp. 473–509.
2. Stearns, S. C., Life history tactics: a review of the ideas. *Q. Rev. Biol.*, 1976, **51**, 3–47.
3. Wapstra, E. and Swain, R., Geographic and annual variation in life-history traits in a temperate zone Australian skink. *J. Herpetol.*, 2001, **35**, 194–203.
4. Tinkle, D. W. and Ballinger, R. E., *Sceloporus undulatus*: a study on the interspecific comparative demography of a lizard. *Ecology*, 1972, **53**, 570–584.
5. Ballinger, R. E., Comparative demography of two viviparous lizards (*Sceloporus jarrovi* and *Sceloporus poinsetti*). *Ecology*, 1973, **54**, 269–283.
6. Ballinger, R. E., Life history variations. In *Lizard Ecology: Studies of a Model Organism* (eds Huey, R. B., Pianka, E. R. and Schoener, T. W.), Harvard University Press, Cambridge MA, 1983, pp. 241–260.
7. Vitt, L. J., Diversity of reproductive strategies among Brazilian lizards and snakes: The significance of lineage and adaptation. In *Reproductive Biology of South American Vertebrates* (ed. Hamlet, W. C.), Springer Verlag, New York, 1992, pp. 135–149.
8. Andrews, R. M., Geographic variation in field body temperature of *Sceloporus* lizards. *J. Therm. Biol.*, 1998, **23**, 329–334.
9. Qualls, F. J. and Shine, R., Geographic variation in lizard phenotypes: importance of the incubation environment. *Biol. J. Linn. Soc.*, 1998, **64**, 477–491.
10. Vitt, L. J., Zani, P. A., Avila-Pires, T. C. S. and Esposito, M. C., Geographical ecology of the gymnophthalmid lizard *Neusticurus ecleopus* in the Amazon rainforest. *Can. J. Zool.*, 1998, **76**, 1671–1680.
11. Angilletta, M., Variation in metabolic rate between populations of a geographically widespread lizard. *Physiol. Biochem. Zool.*, 2001, **74**, 11–21.
12. Downes, S. and Adams, M., Geographic variation in antisnake tactics: the evolution of scent-mediated behavior in a lizard. *Evolution*, 2001, **55**, 605–615.

13. Smith, S. A., Austin, C. C. and Shine, R., A phylogenetic analysis of variation in reproductive mode within an Australian lizard (*Saiphos equalis*, Scincidae). *Biol. J. Linn. Soc.*, 2001, **74**, 131–139.
14. Ji, X., Huang, H., Hu, X. and Du, W., Geographic variation in female reproductive characteristics and egg incubation of *Eumeces chinensis*. *Ying Yong Sheng Tai Xue Bao*, 2002, **13**, 680–684.
15. Macedonia, J. M., Echternacht, A. C. and Walguarnery, J. W., Color variation, habitat light, and background contrast in *Anolis carolinensis* along a geographical transect in Florida. *J. Herpetol.*, 2003, **37**, 467–478.
16. Mesquita, D. O. and Colli, G. R., Geographical variation in the ecology of populations of some Brazilian species of *Cnemidophorus* (Squamata, Teiidae). *Copeia*, 2000, **2000**, 285–298.
17. Parker, W. S. and Pianka, E. R., Comparative ecology of populations of the lizard *Uta stansburiana*. *Copeia*, 1975, **1975**, 615–632.
18. Dunham, A. E., Demography and life history variation among populations of the iguanid lizard *Urosaurus ornatus*: implications for the study of life history phenomena in lizards. *Herpetologica*, 1982, **38**, 201–221.
19. Jones, S. M. and Ballinger, R. E., Comparative life histories of *Holbrookia maculata* and *Sceloporus undulatus* in Western Nebraska. *Ecology*, 1987, **68**, 1828–1838.
20. Jones, S. M., Ballinger, R. E. and Porter, W. P., Physiological and environmental sources of variation in reproduction: prairie lizards in a food rich environment. *Oikos*, 1987, **48**, 325–335.
21. Tinkle, D. W., Dunham, A. E. and Congdon, J. D., Life history and demographic variation in the lizard *Sceloporus graciosus*: a long term study. *Ecology*, 1993, **74**, 2413–2429.
22. Sinervo, B., Evolution of thermal physiology and growth rate between populations of the Western fence lizard (*Sceloporus occidentalis*). *Oecologia*, 1990, **83**, 228–237.
23. Sinervo, B., The evolution of maternal investment in lizards: an experimental and comparative analysis of egg size and its effects on offspring performance. *Evolution*, 1990, **44**, 279–294.
24. Sinervo, B., Doughty, P., Huey, R. B. and Zamudio, K., Allometric engineering: a causal analysis of natural selection on offspring size. *Science*, 1992, **258**, 1927–1930.
25. Ferguson, G. W. and Talent, L. G., Life-history traits of the lizard *Sceloporus undulatus* from two populations raised in a common laboratory environment. *Oecologia*, 1993, **93**, 88–94.
26. Stearns, S. C., The effects of size and phylogeny on patterns of covariation in the life history traits of lizards and snakes. *Am. Nat.*, 1984, **123**, 56–72.
27. Dunham, A. E. and Miles, D. B., Patterns of covariation in life history traits of squamate reptiles: effects of size and phylogeny reconsidered. *Am. Nat.*, 1985, **126**, 231–257.
28. Dunham, A. E. and Miles, D. B., Life history traits of lizards and snakes. *Am. Nat.*, 1985, **125**, 480–484.
29. Bauwens, D. and Diaz-Uriarte, R., Covariation of life-history traits in lacertid lizards: a comparative study. *Am. Nat.*, 1997, **149**, 91–111.
30. Günther, A. C. L. G., *The Reptiles of British India*, Robert Hardwick for Ray Society, London, 1864.
31. Boulenger, G. A., A vertebrate fauna of the Malay Peninsula from the Isthmus of Kra to Singapore, including the adjacent islands. *Reptilia and Batrachia*, Taylor and Francis, London, 1912.
32. Smith, M. A., *The Fauna of British India including Ceylon and Burma. Reptilia and Amphibia*, Taylor and Francis, London, 1935, vol. 2.
33. Erdelen, W., The genus *Calotes* (Sauria: Agamidae) in Sri Lanka: clutch size and reproductive seasonality of *Calotes versicolor* preliminary results. *Spixiana*, 1986, **9**, 111–115.
34. Loman, J., *Calotes versicolor*, Salalah, southern Oman, 1997, [<http://www.biol.lu.se/zoekolog>].
35. Seuffer, H., Kowalski, T. and Zilger, H. J., Herpetologische Impressionen einer Reise in den Oman. *Herpetofauna Weinstadt*, 1999, **21**, 24–34.
36. Stuart, B. L., Amphibians and reptiles of Laos. *Duckworth, Salter Khounboline*, 1999, 43–67.
37. Hasen Didi, N. T., Observations on the nesting of a garden lizard (*Calotes versicolor*) in the Maldives. *Hamadryad*, 1993, **18**, 42.
38. Permalnai ck, L., Didgen, J. C., Hoarau, Z., Deveau, G. and Elma, G., *Les plus belles balades à la Réunion. Les Créations du Péllican*, Lyon, 1993.
39. Staub, F., *Fauna of Mauritius and Associated Flora*, Précigraph Ltd, Mauritius, 1993.
40. Blanchard, F., *Guide des milieux naturels: La Réunion, Maurice*, Rodrigues, Ulmer, Paris, 2000.
41. Matyot, P., The establishment of the crested tree lizard, *Calotes versicolor* (Daudin, 1802) (Squamata: Agamidae) in Seychelles. [http://www.phelsumania.com/public/articles/biogeography_calote_s.html].
42. Enge, K. E. and Krysko, K. L., A new exotic species in Florida, the bloodsucker lizard, *Calotes versicolor* (Daudin, 1802) (Sauria: Agamidae). *Biol. Sci.*, 2004, **67**, 226–230.
43. Diong, C. H., Chou, L. M. and Lim, K. K. P., *Calotes versicolor*, the changeable lizard. *Nature Malaysian*, 1994, **19**, 46–54.
44. Schmidt, K. P. and Inger, R. F., Knaurs Tierreich in Farben. Reptilien. *Droemersch Verlaganstalt, Munchen*, 1957, 312.
45. Bellairs, A., Die Reptilien. *Enzyklopadie der Natur 11*, Editions Recontre, Lausanne, 1971, p. 767.
46. Erdelen, W., Population dynamics and dispersal in three species of agamid lizards in Sri Lanka: *Calotes calotes*, *Calotes versicolor* and *Calotes nigrilabris*. *J. Herpetol.*, 1988, **22**, 42–52.
47. Pandha, S. K. and Thapliyal, J. P., Egg laying and development in the garden lizard, *Calotes versicolor*. *Copeia*, 1967, **1967**, 121–125.
48. Indurkar, S. S. and Sabnis, J. H., Observations on the breeding biology of the garden lizard, *Calotes versicolor*. *Indian J. Anim. Res.*, 1977, **11**, 7–11.
49. Shanbhag, B. A., Radder, R. S. and Saidapur, S. K., Maternal size determines clutch mass, whereas breeding timing influences clutch and egg sizes in the tropical lizard, *Calotes versicolor* (Agamidae). *Copeia*, 2000, **2000**, 1062–1067.
50. Radder, R. S., Shanbhag, B. A. and Saidapur, S. K., Ontogeny of sexual size dimorphism in the tropical garden lizard, *Calotes versicolor* (Daud.). *J. Herpetol.*, 2001, **35**, 156–160.
51. Radder, R. S., Shanbhag, B. A. and Saidapur, S. K., Influence of incubation temperature and substrates on eggs and embryos of the garden lizard, *Calotes versicolor* (Daud.). *Amp. Rep.*, 2002, **23**, 71–82.
52. Radder, R. S. and Shanbhag, B. A., Factors influencing offspring traits in the oviparous multi-clutched lizard, *Calotes versicolor* (Agamidae). *J. Biosci.*, 2004, **29**, 105–110.
53. Ji, X., Qiu, Q-B. and Diong, C. H., Sexual dimorphism and female reproductive characteristics in the oriental garden lizard, *Calotes versicolor*, from Hainan, Southern China. *J. Herpetol.*, 2002, **36**, 1–8.
54. Ji, X., Qiu, Q-B. and Diong, C. H., Influence of incubation temperature on hatching success, energy expenditure for embryonic development, and size and morphology of hatchlings in the oriental garden lizard, *Calotes versicolor* (Agamidae). *J. Exp. Zool.*, 2002, **292**, 649–659.
55. Hews, D. K., Size and scaling of sexually-selected traits in the lizard, *Uta palmeri*. *J. Zool.*, 1996, **238**, 743–757.
56. Cooper, W. E. and Vitt, L. J., Sexual dimorphism of head and body size in an iguanid lizard: paradoxical results. *Am. Nat.*, 1989, **133**, 729–735.
57. Harvey, P. H. and Pagel, M. D., *The Comparative Method in Evolutionary Biology*, Oxford University Press, Oxford, 1991.
58. Adolph, S. C. and Porter, W. P., Temperature, activity, and lizard life histories. *Am. Nat.*, 1993, **142**, 273–295.
59. Adolph, S. C. and Porter, W. P., Growth, seasonality, and lizard life histories: age and size at maturity. *Oikos*, 1996, **77**, 267–278.

60. Andrews, R. M., Patterns of growth in reptiles. In *Biology of the Reptilia* (eds Gans, C. and Pough, F. H.), Academic Press, New York, 1982, vol. 12, pp. 273–320.
61. Bruce, R. C. and Hairston, N. G. Sr., Life history correlates of body size differences between two populations of the salamander, *Desmognathus monticola*. *J. Herpetol.*, 1990, **24**, 124–134.
62. Shine, R. and Charnov, E. L., Patterns of survival, growth, and maturation in snakes and lizards. *Am. Nat.*, 1992, **139**, 1257–1269.
63. Niewiarowski, P. H., Effects of supplemental feeding and thermal environment on growth rates of eastern fence lizards, *Sceloporus undulatus*. *Herpetologica*, 1995, **51**, 487–496.
64. Galan, P., Sexual maturity in a population of the lacertid lizard *Podarcis bocagei*. *Herpetol. J.*, 1996, **6**, 87–93.
65. Rohr, D. H., Demographic and life-history variation in two proximate populations of a viviparous skink separated by steep altitudinal gradient. *J. Anim. Ecol.*, 1997, **66**, 567–578.
66. Forsman, A. and Shine, R., Parallel geographic variation in body shape and reproductive life history within the Australian scincid lizard, *Lampropholis delicata*. *Funct. Ecol.*, 1995, **9**, 818–828.
67. Mathies, T. and Andrews, R. M., Thermal and reproductive biology of high and low elevation populations of the lizards *Sceloporus scalaris*: implications for the evolution of viviparity. *Oecologia*, 1995, **104**, 101–111.
68. Stearns, S. C. and Crandall, R. E., Quantitative predictions of delayed maturity. *Evolution*, 1981, **35**, 455–463.
69. Tinkle, D. W. and Dunham, A. E., Comparative life histories of two syntopic Sceloporine lizards. *Copeia*, 1986, **1986**, 1–8.
70. Tinkle, D. W., Wilbur, H. M. and Tilley, S. C., Evolutionary strategies in lizard reproduction. *Evolution*, 1970, **24**, 55–74.
71. Ballinger, R. E., Intraspecific variation in demography and life history of the lizard, *Sceloporus jarrovi*, along an altitudinal gradient in South-eastern Arizona. *Ecology*, 1979, **60**, 901–909.
72. Smith, C. C. and Fretwell, S. D., The optimal balance between size and number of offspring. *Am. Nat.*, 1974, **108**, 499–506.
73. Brockelman, W. Y., Competition, the fitness of offspring, and optimal clutch size. *Am. Nat.*, 1975, **109**, 677–699.
74. McGinley, M. A., Temme, D. H. and Geber, M. A., Parental investment in offspring in variable environments: theoretical and empirical considerations. *Am. Nat.*, 1987, **130**, 370–398.
75. Roff, D. A., *The Evolution of Life Histories*, Chapman and Hall, New York, 1992.
76. Stearns, S. C., *The Evolution of Life Histories*, Oxford University Press, New York, 1992.
77. Ferguson, G. W., Bohlen, C. H. and Wooley, H. P., *Sceloporus undulatus*: comparative life history and regulation of a Kansas population. *Ecology*, 1980, **61**, 313–322.
78. Berven, K. A. and Gill, D. E., Interpreting geographic variation in life history traits. *Am. Zool.*, 1983, **23**, 85–97.
79. Stearns, S. C., The evolutionary significance of phenotype plasticity. *BioSciences*, 1989, **39**, 436–445.
80. Niewiarowski, P. H. and Roosenberg, W., Reciprocal transplant reveals sources of variation in growth rates of the lizard *Sceloporus undulatus*. *Ecology*, 1993, **74**, 1992–2002.
81. Pigliucci, M., Phenotypic plasticity. In *Evolutionary Ecology: Concepts and Case Studies* (eds Fox, C. W., Roff, D. A. and Fairbairn, D. J.), Oxford University Press, Oxford, 2001, pp. 58–69.
82. Macey, J. R., Schulte II, J. A., Larson, A., Ananjeva, N. B., Wang, Y., Pethiyagoda, R., Rastegar-Poyani, N. and Papenfuss, T., Evaluating trans-tethys migration: an example using acrodont lizard phylogenetics. *Syst. Biol.*, 2000, **49**, 233–256.

ACKNOWLEDGEMENTS. I thank my colleague Daniel Warner and ‘anonymous’ reviewers for providing constructive suggestions to improve the MS, and Prof. B. A. Shanbhag and Prof. S. K. Saidapur for encouragement to undertake research on tropical reptiles. I acknowledge financial support received from Department of Science and Technology (DST, India), Council of Scientific and Industrial Research (CSIR, India), Karnataka University, Dharwad during various stages of my research on tropical reptiles, and Australian Research Council (ARC, Australia) during preparation of this manuscript.

Received 26 September 2005; revised accepted 2 August 2006