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ALTITUDINAL DIFFERENCES IN THERMOREGULATORY BEHAVIOUR IN  
*CALOTES VERSICOLOR* IN THE KNUCKLES REGION, SRI LANKA.

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**ABSTRACT** - Observations have been made on the thermoregulatory behaviour of the agamid lizard *Calotes versicolor* at two different altitudes. Operative temperatures and lizard body temperatures were significantly higher at low altitude (91 metres). The high altitude climate (920+ metres) imposed a behavioural cost for raising body temperature by increased basking. High operative temperatures at low altitude set a premium on shade seeking. Precision of body temperatures, defined as a function of body temperature variance, was not significantly different between populations. Tentative mathematical models for a series of *Calotes* and other squamates, indicated that altitude generally has an influence on body temperatures.

## INTRODUCTION

The physiological processes in reptiles are largely temperature dependent and temperature influences many functions, for example growth, reproduction, muscular energy and oxygen consumption. Heat is therefore a key environmental resource (Magnusson et al., 1979), although there may be limitations on the ability of reptiles to harness thermal energy, particularly in extreme environments. Early studies indicated that reptiles are able to elevate body temperatures even at high altitudes (e.g. Strelnikov, 1944; Pearson, 1954). However more recent studies have shown there are associated costs involved including, among others, costs in time, target body temperatures and behaviour (see Huey, 1982 for review). The theoretical model of reptile thermoregulation predicts that if a thermoregulator is faced by a cooler environment than its preferred temperature, it will compensate by adjusting behaviour, for example by increasing basking intensity (Huey and Slatkin, 1976; Huey, 1982). Although this may not always be the case, (e.g. Meek, 1988; Spencer and Grimmond, 1994) much of the evidence supports the theory. Generally, the costs will be to increase basking intensity and/or lower thermal set points and precision of thermoregulation (Huey, 1982). The

thermoregulatory response to a particular environment is dependent on the environment in question. For example, Shine and Madsen (1996) suggested that in tropical regions reptile behaviour might only be affected in a minor way by thermoregulatory concerns. Luiselli and Akani (2002) argued that although the importance of thermoregulation in the tropics may not be critical, it nevertheless exists and has ecological consequences. Most comparative studies have examined climatic effects on thermoregulatory behaviour in temperate reptiles including species from different altitudes (e.g. Brown and Weatherhead, 2000; Bluin-Demers and Weatherhead, 2001; Gvodzik, 2002; Bauwens, et al., 1990). Rather less information is available about the effects of altitude on reptile thermoregulation in the tropics. This paper details the first study of the climatic effects of altitude on lizard thermoregulatory behaviour in Sri Lanka and seeks to present new information the importance of thermoregulation in tropical reptiles.

To explore thermoregulatory opportunities in reptiles the use of operative temperatures are far more valuable than air or substrate temperatures (Bakken, 1992). Operative temperatures are computed using physical models of the organism that approximate the heating and cooling rates of the real reptiles and have value in describing the distribution of possible body temperatures available. In this study, operative models were employed to determine the consequences for behaviour and body temperatures in the lizard *Calotes versicolor* in two habitats at different altitudes in the Knuckles Massif. The most widespread species of agamid lizard in Sri Lanka, *C. versicolor* operates largely as an arboreal sit-and-wait predator with a limited home territory. It is found over a range of differing biotopes from sea level up to 2000 metres. This makes *C. versicolor* an ideal subject for thermoregulation studies. In addition, we also present tentative mathematical models of general altitudinal influences on body temperatures in both *Calotes* species and other squamates from the region.

## METHODS AND MATERIALS

Observations were made on two populations of *C. versicolor* in the Knuckles region (Bambaradeniya and Ekanayake, 2003). One population was observed at Hettipola, at 91 metres above sea level and a second in the area around Pitawala, at more than 900 metres altitude. The study site at Hettipola was characterised by lowland scrub, including rivers and water tanks, agricultural land and areas of medium sized trees. During the study (July 2005), Hettipola experienced high temperatures with frequent hot winds, which are normal for the time of year (dry season). The lizards were in general observed in trees from which they frequently descended to capture prey. The study area at Pitawala, was composed of dry patana grassland with scattered stands of shrubs and some small trees. The grassland was interspersed with areas of flat, dark-coloured rock which were occasionally used for basking. The territories of individuals appeared to be confined to the areas around single bushes. Frequent cloud cover and cool winds were a feature of the area.

Behaviour observations were continuous on 8 lizards for a mean time (with standard deviation) of  $101 \pm 92.6$  minutes for each individual at Pitawala and on 5 lizards at Hettipola for  $195.6 \pm 71.6$  minutes both between 0900hrs and 1500hrs. Behaviour was categorised as: *Basking*, the lizard was positioned in open sunlight: *Partial Basking*, located in an area with dappled sunlight falling on the body or approximately half in sun and half in shade: *Shade*, in a fully shaded area with no sunlight falling on the body:

*Locomotory Activity*, the lizard was involved in some form of movement. Here both the number of movements and the distances travelled were recorded. To minimise behavioural disturbance no attempt was made to approach or capture any of these animals. In order to gather representative information on body temperatures other lizards were captured by noose and measured immediately after capture by inserting a digital thermometer with a 130mm stainless steel sensor probe into the cloaca. Skin surface temperature was taken using a Electronique Frontal infra red detector (model TS112) directed at the flank. This instrument measures infrared energy being emitted from the lizard and has an error of less than 0.01C. There will, however, be some additional error due to the emissivity of *C.versicolor* skin. In general, reptile skin has an emissivity of around 0.95 (Tracy, 1982).

In this paper we used cloacal temperatures for statistical comparisons since we found only little disagreement between skin surface temperature and cloacal temperature. The regression of the relationship, with skin surface temperature ( $T_{bs}$ ) as the independent variable and cloacal temperature ( $T_b$ ) as the dependent variable was,

$$T_b = 1.03 \pm 0.08 T_{bs} - 1.21, r^2 = 91.2\% \quad (1)$$

The  $r^2$  is the adjusted value, where there will be no increase because of sample size alone. The equation is based on lizards from both study sites (see table 1) and shows both measurements were in good agreement, with the regression coefficient very close to the value of 1 required for parity. The high  $r^2$  value and low standard error therefore indicate that analysis involving skin surface or cloacal temperatures would give similar results.

Operative temperatures at both sites were measured using copper cylinders with dimensions of 12cm in length and 2.5cm in diameter and 0.5 mm thick. These were painted green to reflect the general colour of the lizards – although *C. versicolor* has the ability for partial colour change. To represent the consequences of a lizard remaining in open sunlight continuously, one model was placed permanently in open sunlight. Two models were placed in dappled sunlight – one on the ground and one in a tree at a height of 1.5 metres. This was to represent the potential temperatures for a lizard for remaining continuously either in partial shade on the ground or in partial shade above the ground in a tree. Partial shade is the same way as defined for the lizards. A model was placed in total shade in order to represent the consequences for a lizard remaining in shade throughout the day. The model temperatures were measured approximately every 15 minutes, by directing the infrared detectors to the surface of the models in the same way skin surface temperature was measured in the lizards. The short 15-minute time intervals between measurements minimised the effects of operative temperature fluctuation, particularly at Pitawala where wind speeds were variable (O`Conner, 2000).

Small thin walled copper models are good estimators of the temperatures available to small ectotherms since they respond rapidly to changes in temperature, with the small conduction distances limiting the internal thermal gradients that may obscure patterns of environmental temperature distribution (O`Connor et al., 2000). The operative models are indicators of the potential heat available to the lizards in their environment and represent the point at which a lizard's body temperature would equilibrate if it made no movement or thermoregulatory adjustments – if it behaved as a thermoconformer. By recording the maximum and minimum temperatures we assumed that a lizard could either attain any

body temperature within these extremes by spending all its time in either location or fluctuating body temperature between the highest and lowest available operative temperature by shuttling (Christian et al., 1983). We also assumed that the lizard could equilibrate with dappled sunlight operative temperatures by either being half in sun and half in shade or spending 50% of its time within sun and shade. The type of operative model used is subject to debate (Shine and Kearney, 2001) but recent evidence suggests that operative model type is less important than previously thought (Vitt and Sartorius, 1999; Shine and Kearney, 2001).

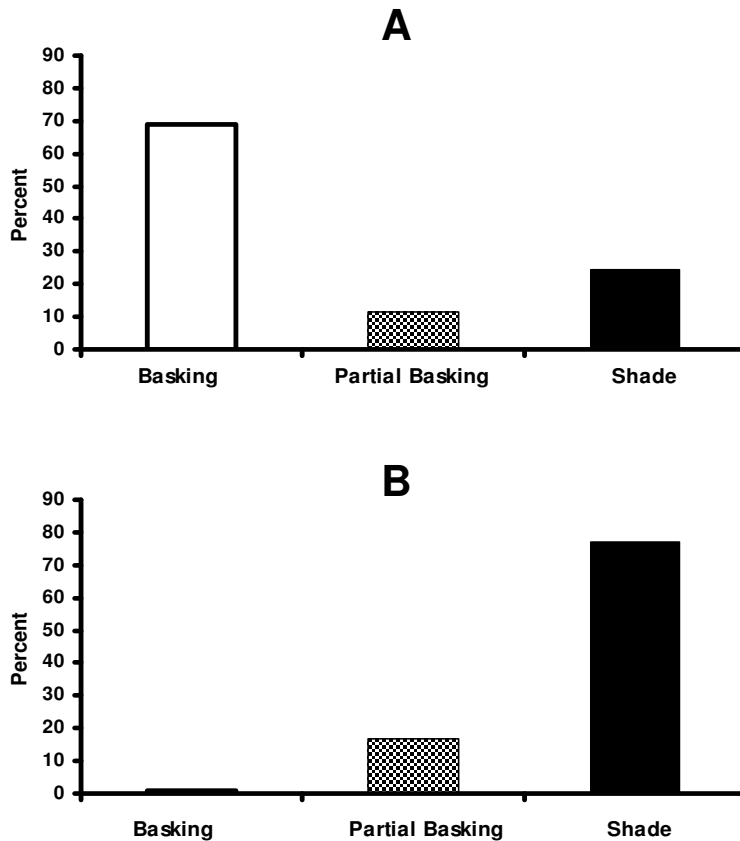
### **Statistical analysis.**

To avoid problems of pseudo-replication, analysis was applied to the medians of percentages of behaviour of individual lizards i.e. giving  $n = 8$  lizards at Pitawala and  $n = 5$  at Hettipola. This method avoids artificially inflating the degrees of freedom, inappropriately rejecting the null hypotheses and committing a type 1 statistical error (Lombardi & Hurlbert, 1996). Behaviour was analysed using non-parametric tests. The body temperatures from lizards captured randomly were treated as single data points and were compared with their corresponding operative measurements. For statistical comparison between study sites, the data for operative temperatures were converted to the mean temperatures per hour and ANOVA applied. Comparisons of regression coefficients were made using  $t$ -tests based on the methods described by Bailey (1981).

## **RESULTS**

*Behaviour.* Figure 1 shows the behaviour patterns at different elevations with the data represented as the medians of the medians of individual lizards. Basking was greater at the higher elevation (Pitawala *grand median* basking = 71%; Hettipola *grand median* = 0.94%) with the differences significant, Mann Whitney  $U$  – test  $w = 76$ ,  $p = 0.004$ . Shade seeking was greater at Hettipola (*grand median* = 77.1%) than at Pitawala (*grand median* = 24.5%) with the difference significant,  $w = 42.0$ ,  $p = 0.048$ . Time spent in partial shade was greater at Hettipola (*median* percents, 11.3 versus 16.7%) but the difference was not significant.

Activity was recorded both as the number of movements and distances travelled for each individual per hour. The number of locomotory movements was greater at Pitawala (*grand median* with interquartile range = 21.4, 17.5 – 36.0,  $n = 7$ ), than at Hettipola (*grand median* = 4.35, 1.8 – 14.9,  $n = 5$ ). The difference was significant  $w = 59.0$ ,  $p = 0.03$ . Although the distances travelled during locomotory movement was greater at Hettipola (*grand median* = 6.4, 0.7 – 18.2,  $n = 5$ ) than Pitawala (*grand median* = 5.4, 2.6 – 8.1,  $n = 7$ ) the difference was not significant,  $w = 44.0$ ,  $p = 0.87$ .



**Figure 1.** Histograms of behaviour at different altitudes. The cells represent the medians of the medians of the percentages of behaviour of individual lizards. Figure 2A shows high altitude (Pitawala) and B low altitude (Hettipola). See text for further information.

*Operative temperatures.* Table 1 gives details of operative temperatures. Pooled operative temperatures for each site were significantly higher at Hettipola ( $F_{(1,223)} = 375.6$ ,  $p < 0.0001$ ). Microhabitat operative temperatures, open, dappled (either on tree trunks or on the ground) and shade, were also higher at Hettipola; ANOVA  $F$ -statistics from 44.12 – 251.04 all at  $p < 0.0001$ .

*Body temperatures.* Table 1 shows mean body temperatures with standard deviations. Mean body temperatures at Hettipola ( $n = 22$ ) were significantly higher than at Pitawala ( $n = 19$ ); two sample  $t$ -test,  $t = 15.28$ ,  $p < 0.0001$ ,  $d.f. = 39$ . Body temperature variance was greater in the Pitawala lizards ( $v = 5.76$  versus  $v = 3.61$ ). However, a Levene's test for variance homogeneity showed that the difference was not significant ( $L = 0.70$ ,  $p = 0.41$ ). These results indicate both groups of lizards had similar thermoregulatory precision.

*Comparison of body and operative temperatures.* At Pitawala mean body temperatures were lower but not significantly lower than mean operative temperatures in open areas ( $F_{(1,34)} = 3.02$ ,  $p = 0.09$ ), dappled operative temperatures on the ground ( $F_{(1,33)} = 0.18$ ,  $p = 0.67$ ) and dappled operative temperatures on tree trunks ( $F_{(1,33)} = 1.31$ ,  $p = 0.26$ ). Body temperatures were significantly higher than shaded operative temperatures ( $F_{(1,33)} = 6.16$ ,  $p = 0.02$ ). At Hettipola, mean body temperatures were significantly lower than open area operative temperatures ( $F_{(1,60)} = 7.20$ ,  $p = 0.009$ ) but significantly higher than operative temperatures in dappled areas on the ground ( $F_{(1,60)} = 36.6$ ), dappled operative temperatures on tree trunks ( $F_{(1,60)} = 49.8$ ) and shade operative temperatures ( $F_{(1,60)} = 77.8$ ) all at  $p < 0.0001$ .

In general, body temperature and operative temperature variances were similar. Levene's tests for homogeneity of variances set at the 95% interval, indicated significant differences only between Hettipola body temperatures and operative temperatures in open areas  $L = 3.6$ ,  $p = 0.05$  where body temperature variance was significantly lower.

**Table 1.** Operative temperatures and body temperatures of *C. versicolor*. Mean values are shown with standard deviations. Definitions are  $T_b$  = cloacal body temperature,  $n$  = sample sizes of body temperatures,  $To_{open}$  = operative temperatures in open areas,  $To_{dappleG}$  = dappled areas on the ground,  $To_{dappleT}$  = dappled areas on tree trunks and  $To_{shade}$  = shaded areas. Temperatures are in degrees centigrade. See text for statistical comparisons.

	$T_b$	$n$	$To_{open}$	$To_{dappleG}$	$To_{dappleT}$	$To_{shade}$
Pitawalla	25.6±2.4	19	27.7±2.4	26.0±2.6	24.9±1.4	23.9±1.3
Hettipola	36.1±1.9	22	38.6±3.8	33.4±1.7	33.1±1.4	31.9±1.7

*General squamate body temperatures in relation to altitude.* Body temperatures from a series of randomly captured reptiles from a range of altitudes within the Knuckles region have been related in a regression analysis. Two regressions have been calculated, one for a series of *Calotes* spp and a second from other lizards and snakes in which the data for *Calotes* have been included. Altitude (in metres) has been treated as the independent variable  $y$  and body temperature as the dependent variable  $x$ . A corrected coefficient of determination ( $r^2$ ) has been applied to estimate the amount of variation in body temperature that can be explained by the variation in altitude. Tests for departures from a hypothetical equation with a 0 regression coefficient, which would indicate no relationship were applied. The results for *Calotes* spp. gave,

$$y = 36.26 - 0.010 \pm 0.001x, r^2 = 0.72 \quad (2)$$

with the departure from 0 significant ( $t = 8.96$ ,  $p < 0.001$ ,  $d.f. = 32$ ). For the series of squamate reptiles the relationship gave,

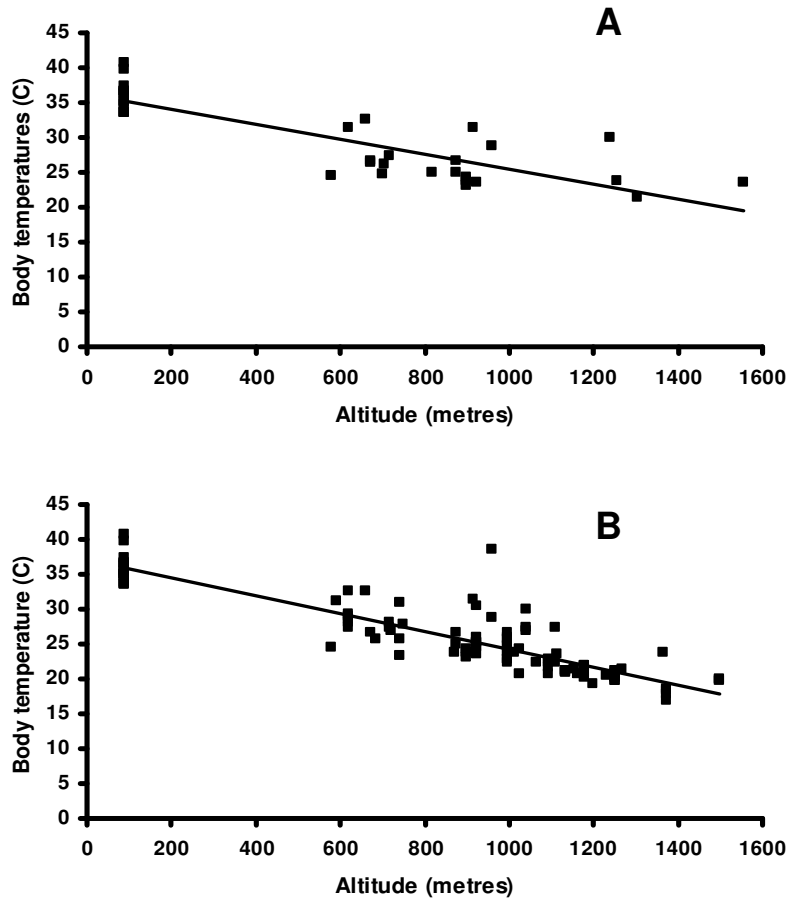
$$y = 37.23 - 0.013 \pm 0.0006x, r^2 = 0.79 \quad (3)$$

with the regression coefficient also significantly different from 0 ( $t = 19.4$ ,  $p < 0.001$ ,  $d.f. = 101$ ). Figure 2A shows the data for *Calotes* spp and Fig. 2B for the different squamate species. The lines taken through the data were calculated using equations (2) and (3). A  $t$ -test for differences between the regression coefficients at  $n - 4$  degrees of freedom showed that the slopes were significantly different,  $t = 2.57$ ,  $p < 0.02$ ,  $d.f. = 154$ ; equation (3) for the randomly captured squamates had a significantly steeper slope and hence a more pronounced relationship. Table 2 gives a list of the species used in the models with basic summary statistics.

**Table 2.** List of squamate species used to compute equations (2) and (3) with summary statistics for the data subsets. Where appropriate, means of altitudes and body temperatures ( $T_b$ ) are given with standard deviations and sample sizes  $n$ . Standard deviation values of 0 for altitude indicate that the animals were located at the same elevation. Data for *C. versicolor* are given in table 1.

Species	Mean Altitude	Std Dev	Mean $T_b$	Std Dev	$n$
<i>Calotes calotes</i>	696.8	77.8	26.7	3.1	6
<i>Calotes liocephalus</i>	1370.6	131.1	22.9	1.1	3
<i>Calotes liolepis</i>	1238.0	0	30.0	0	1
<i>Cophotis ceylonensis</i>	996.0	0	26.7	0	1
<i>Lyriocephalus scutataus</i>	694.3	54.6	27.5	0.5	3
<i>Ceratophora tennentii</i>	1176.0	134.1	21.3	2.6	43
<i>Otocryptis weigmanni</i>	942.5	324.5	25.1	3.6	1
<i>Otocryptis sp</i>	743.0	16.0	28.1	0.15	2
<i>Lankascincus sp</i>	1014.0	0	23.8	0	1
<i>Lankascincus fallax</i>	1065.0	0	22.5	0	1
<i>Mabuya sp</i>	962.0	0	38.5	0	1
<i>Chalcidoseps thwaitesii</i>	924.0	0	25.3	0.4	4
<i>Cnemaspis sp</i>	743.0	0	30.9	0	1
<i>Cyrodactylus fraenatus</i>	1000.5	264.1	25.2	2.2	4
<i>Cyrodactylus soba</i>	686.0	0	25.6	0	1
<i>Geckoella triedrus</i>	1037.3	80.1	23.4	0.7	3
<i>Hemidactylus depressus</i>	668.0	50.0	27.3	1.9	2
<i>Nessia sp</i>	1025.0	0	20.7	0	1
<i>Haplocercus ceylonensis</i>	1110.0	0	27.4	0	1
<i>Uropeltis sp</i>	1095.0	0	21.6	0.75	2
<i>Amphios masculata</i>	996.0	0	24.7	0	1
<i>Colubar mucocus maximas</i>	591.0	0	31.2	0	1
<i>Oligodon sublineatus</i>	1024.0	0	24.3	0	1
<i>Ahaetulla nasutus</i>	743.0	0	25.6	0	1
<i>Trimeresurus sp</i>	618.0	0	28.0	0	1

The graphs clearly show that the highest body temperatures were from reptiles in lowland areas and the lowest from those in the mountains. We recognise that there are inherent difficulties in this approach; for example not all species may be baskers, different species may operate at different body temperatures and some animals may not have been basking at the time of capture and so on. Indeed, the difference between equations (2) and (3) may be partly due to less thermoregulatory effort in several of the non-*Calotes* species; *Calotes sp.* are primary basking reptiles whilst some of the others may not be. However, the general pattern of fit, the high  $r^2$  and low standard errors, indicate a relationship between body temperatures and altitude and warrants further investigation.



**Figure 2.** General plots of body temperature and altitude in squamate reptiles from the Knuckles region. Figure 3A shows the data for *Calotes* species and 3B for other lizards (including *Calotes*) and snakes with the lines representing equations (2) and (3). See text for further details

## DISCUSSION

The results show that *C. versicolor* compensates for reduced thermal resources at higher altitude by increasing basking intensity and number of locomotory movements. However, despite the increased basking effort, the lizards were still unable to maintain similar body temperature to the lizards at Hettipola, which appear to be a consequence of the thermal constraints of the mountain climate. What effect does this have on the lizards general behaviour and ecology? This depends on the evolutionary processes operating on thermal biology. The static theory of thermal evolution predicts that thermal benefits will be fixed and body temperatures must be maintained if the physiological benefits from temperature are to be retained (e.g. Hertz et al., 1983; Crowley, 1985; Van Damme et. al., 1990). An alternative labile theory argues that thermal optima are dynamic and will evolve with changing environments (Huey and Bennett, 1987). If the static theory is in operation, the lowered body temperatures in the Pitiwala lizards must indicate reduced physiological performance, for instance sprint speed (e.g. Torr and Shine, 1993), the ability to chase and secure prey items, prey handling time (Avery and Mynott, 1990) and the ability to escape predators (Avery, et.al., 1982). It has been suggested that locomotory capacity may not be critical for lizards that rarely venture far from cover (Huey and Bennett, 1987), as was the case for *C. versicolor* which usually stayed close to bushes. Escape behaviour might occur earlier at lower body temperatures and when vegetation density is



sparse (Martin and Lopez, 1995). Additionally, ectothermic prey might reasonably be expected to experience the same  $Q_{10}$  effects (Huey, 1982) and hence securing prey or escaping from ectothermic predators may be a limited problem if at all. Ectothermic predators were not recorded at Pitawala although several were observed at Hettipola, including two species of varanids (*Varanus bengalensis* and *V. salvator*) and several colubrid snakes. Of these the widely foraging *V. bengalensis* may be the most important as they were observed searching both terrestrial and arboreal habitats.

Greater basking intensity and locomotory adjustment with altitude has been observed in other reptiles, for example *Lacerta bedriagae* (Bauwens, et al., 1990). High altitude *Lacerta monticola* employ basking orientation to enhance heating rates (Lopez et al., 1995). Other forms may respond to increased altitude by physiological adjustment, as found in the New Zealand skink *Leiopisma maccanni* which apparently did not change behaviour or exploit microhabitats with higher operative temperatures (Spencer and Grimmond, 1994). When thermal resources became limited, female *Testudo hermanni* did not increase basking and operated at lower body temperatures (Meek, 1988). Similarly, body temperature differences with altitude, as found in *C. versicolor*, have also been recorded in other lizards (e.g. Amat et al 2003, Gvozdik, 2002). For example, in *Zootoca* (= *Lacerta*) *vivipara* populations living at altitudes of 2000-2200m, body temperatures were 3-5°C lower than those from 25m above sea level (Van Damme et al, 1990). The montane *Z. vivipara* were found with body temperatures that seriously affected locomotory movement but laboratory studies showed no parallel shift in optimal temperatures for running – i.e. thermal set points were resistant to directional selection. Van Damme et al., (1989) found greater variation in body temperatures with altitude, which differs from the results in this study where there was an agreement in precision of thermoregulation between populations. This indicates careful thermoregulation even outside the set point range, which may be due to tree trunks in open habitats representing very low cost microhabitats that favour precise thermoregulation; the distances between sunlit and shaded areas are small (Huey, 1982) and hence the costs of thermoregulatory precision are low.

The general cost of cool climates on thermoregulation may depend on the lifestyle of the species in question. Compared to *Calotes versicolor*- a sit-and-wait predator living in relatively open habitats, the costs for thermoregulation for a foraging predator living in cooler rather complex habitats may be relatively high (Avery, 1976). Indeed a foraging lifestyle, in addition to greater body mass and hence slower heating rates, may contribute to the absence of *V. bengalensis* at Pitawala. The ability to exploit habitats with low temperatures is a potential fitness advantage and apparently enables *C. versicolor* to exploit areas with cool seasons or high elevations. The costs are increased thermoregulatory effort with a premium on high basking intensity and adjustment to a lower set point temperature. In contrast, the premium on shade seeking and regulation of body temperature below maximum operative temperatures in the Hettipola lizards suggests they were close to physiological optimums. Nevertheless, the time a lizard is able to operate at optimum temperatures may be an important consideration since shorter periods at physiological optimum temperatures may result in less assimilated energy per annum which would have ecological consequences (Angilletta, 2001). A species of skink (*Lygosoma punctata*) and two anurans, *Euphlyctis cyanophlyctis* and *Lymnonectes lymnocharis*, were observed in good numbers at Pitawala and it would be interesting to

know if there are differences in strategies to exploit the available thermal resources. Additionally, although we have shown good evidence for thermoregulation and the constraints of altitude and low temperature on thermoregulatory behaviour, it is not possible with any certainty to address the central question of the ecological costs on preferred body temperatures for physiological processes in *C. versicolor*. This requires laboratory heat gradient studies to examine whether the temperature effects on physiology in *C. versicolor* are static or labile. Future research could focus on these questions.

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