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Comparative Metabolic Rate-temperature Curves of Five Species of Snakes of the Families Viperidae, Colubridae and Leptotyphlopidae

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Abstract. Five species of snakes (*Vipera russelii, Malpolon monspessulanus insignitus, Coluber florulentus, Spalerosophis diadema*, and *Leptoty-phlops microrhynchus*) of the families Viperidae, Colubridae, and Leptot-yphlopidae were collected from Pakistan, Egypt, and Saudi Arabia for the comparative study of their metabolic rate-temperature (M-T) curves. The resting oxygen consumption ($\dot{V}O_2$) rate of each species was measured in a double-chamber, volumetric closed system at ambient temperatures from 10 to 35°C. The M-T curves and the linear regression lines were found to be directly and significantly proportional in all species. A significant inverse proportionality of the metabolic rate weight-specific relationship was noticed in all species, but was most pronounced in the subadult and adult *L. microrhynchus*. The Q_{10} values indicated both thermal dependent shifts and preferred body temperature ranges. The variations and similarities observed in these parameters can be attributed to geographical and environmental factors.

Introduction

Extremes of temperature and water are always critical and demanding to animals, especially in arid regions [1-4]. The selection and regulation of a preferred body temperature (PBT) range by reptiles has been reported to be species-specific, and is an important factor in ecological isolation [5]. Such thermoregulation is of paramount importance for withstanding changes in environmental temperature [1]. Several studies have been undertaken on the behavioral and physiological responses of reptiles in response to temperature [6-12; 3].

At various temperature levels oxygen consumption can provide an indirect measure of oxidative metabolism in ectothermic animals such as reptiles [13]. The rate of oxygen consumption normally shows a steady increase with rise in the ambient temperature, in a manner according to Van't Hoff's generalization [14]. However, more recent studies [15; 16] have shown that such a relationship is not always linear.

The present study aims to carry out allometric investigations on the metabolism of five snake species, of three different families, from various geographical locations to detect any significant correlations in the patterns of their metabolic rate-temperature (M-T) curves and their Q_{10} values.

Materials and Methods

Experimental animals

Ten animals of each species were used in the experiment. *Vipera russelii* ($\overline{X}$ W = 54.6 g; SEM=3.8) is a representative of the family Viperidae and was collected in the cultivated lowlands of eastern Pakistan. The species is solenoglyphous (i.e., has long hinged erectile front fangs), has very potent venom, and leads a mainly nocturnal life. The family Colubridae is represented by the weakly-venomous, opisthoglyphous (back-fanged) diurnal snake *Malpolon monspessulanus insignitus* ($\overline{X}$ W = 91.2 g; SEM = 4.5), specimens of which were collected at Alexandria, Egypt on the Mediterranean coast. The other two species of the family Colubridae were *Coluber florulentus* ($\overline{X}$ W = 64g; SEM = 10.8), and *Spalerosophis diadema,* ($\overline{X}$ W = 51 g; SEM = 1.73), were collected from the Central deserts Region of Saudi Arabia. Both are diurnal colubridae, non-venomous and aglyphous (without fangs). The family Leptotyphlopidae was represented by a subadult ($\overline{X}$ W = 0.3 g; SEM = 0.036) and an adult ($\overline{X}$ W = 2.3 g; SEM = 0.286) groups of *Leptotyphlops microrhynchus.* These thread-snakes or worm-snakes are burrowers and lead a subterranean nocturnal life. They were collected from the cultivated areas of Wadi Haniefa near the city of Riyadh, in the Central Region of Saudi Arabia.

All the experimental animals were maintained in the serpentarium of the animal facility of the Zoology Department, College of Science, King Saud University in Riyadh. They were kept in large transparent perspex tanks (100 x 50 x 45 cm) with sliding tops of wire netting. Each tank was provided with a substratum of sand, to simulate the snakes' natural habitat. A 100-watt lamp was placed overhead inside each tank to give a light period of 9 h per day automatically. This provided a thermal gradient from 20 to 40°C. The large snakes were fed on laboratory-bred mice once every fortnight. However, the worm-snakes were fed mealworms and other small insects. Water was provided *ad libitum* in dishes. In order to achieve a post-absorptive state, the animals were not fed for 5 days prior to experimentation.

Resting metabolic rate (RMR)

The resting metabolic rate of the snakes was measured in terms of resting ($\dot{V}O_2$) rate (ml g^{-1} h^{-1}) using the double chamber, volumetric closed system [13; 17] at temperatures ranging from 10- 35°C,and at intervals of 5°C.

Statistical analyses and figure drawings were made with the aid of the Biosoft model [18] and the two-tail *t-test* was employed for comparison of the $\overline{X}$ ($\dot{V}O_2$) of the different groups. All tests were considered to be significant at $P \leq 0.05$.

Results

Metabolic rate-temperature (M-T) curves

Resting $\dot{V}O_2$ (RMR) of the five snake species at the various experimental temperature levels were presented in Figs. 1 - 4. The linear regression analysis of the M-T curves clearly demonstrated that the ($\dot{V}O_2$) rate of each species increased directly with temperature (Table 1.). The values for *L. microrhynchus* subadults which had smaller body masses ($\overline{X}$ W = 0.3g), were significantly ($P<0.01$) higher than those of the adults ($\overline{X}$ W = 2.3g). The observed and predicted (O/P) ($\dot{V}O_2$) of all species is around unity, but was very much reduced in the case of adult *L. microrhynchus* (Table 2). The M-T curve shapes were variable. Those of *S. diadema,* and of both the subadult and adult of *L. microrhynchus* were triphasic (Figs. 3 and 4). Those of *V. russelii* and *M. m. insignitus* depicted a steady increase without any middle phase or plateau (Figs. 1 and 2). On the other hand, the M-T curve of *C. florulentus* showed a decreasing phase between 10°C and 20°C, followed by a steady increase, similar to that of *V. russelii* and of *M. m. insignitus* (Figs. 1-3).

Table 1. Linear regression analysis of the $\dot{V}O_2$ of five snake species

Species	$\overline{X}$ W ± SEM* (g)	XY** correlation (r)	r2	P (t)
V. russelii	54.6 ±3.8	0.93	0.86	$P < 0.002$
M .m. insignitus	91.1 ±4.5	0.98	0.96	$P < 0.002$
C . florulentus	64 ±10.8	0.87	0.76	$P < 0.002$
S. diadema	51 ± 1.73	0.97	0.95	$P < 0.002$
L. microrhynchus (Subadults)	0.3 ± 0.04	0.96	0.93	$P < 0.002$
L. microrhynchus (Adults)	2.3 ± 0.29	0.89	0.80	$P < 0.002$

SEM* = Standard Error of Mean.
XY** = Intercepts.

Table 2. The observed and predicted* means resting oxygen consumption values (ml/g/h) of the five snake species

Species	20°C			30°C			35°C		
	observed	predicted	ratio (O/P)	observed	predicted	ratio (O/P)	observed	predicted	ratio (O/P)
V. russelii	0.051	0.048	1.10	0.147	0.110	1.37	0.189	0.170	1.11
M. m. insignitus	0.056	0.043	1.32	0.103	0.095	1.10	0.134	0.151	0.89
C. florulentus	0.031	0.046	0.70	0.118	0.103	1.20	0.148	0.164	0.90
S. diadema	0.075	0.049	1.53	0.098	0.109	0.90	0.140	0.173	0.81
L. microrhynchus (Subadults)	0.519	0.159	3.30	0.596	0.374	1.60	0.663	0.594	1.12
L. microrhynchus (Adults)	0.061	0.099	0.62	0.078	0.229	0.34	0.094	0.364	0.26

* Calculated for the three temperatures using the regression equations of Bennett and Dawson (1976) and Bennett (1982).

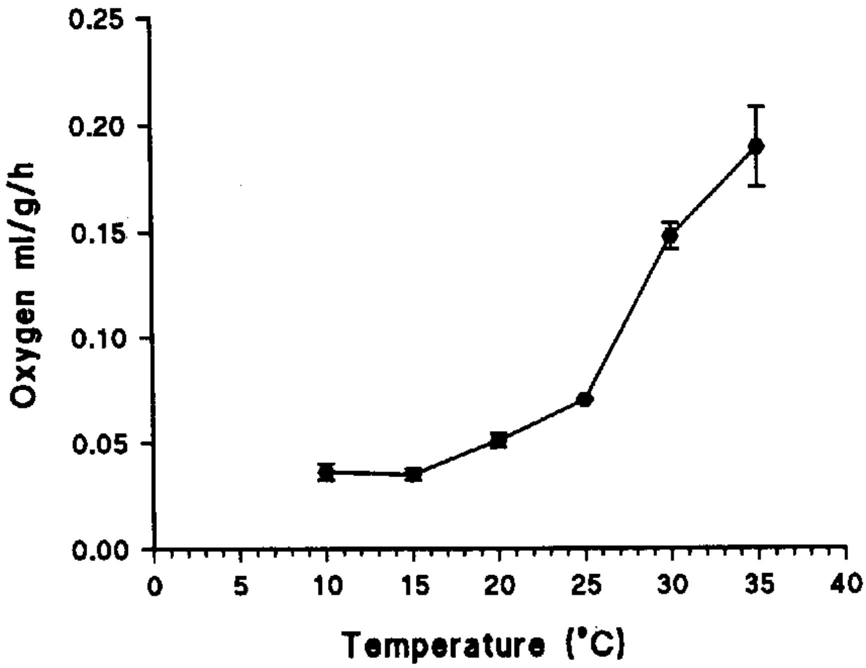

Fig. 1. Relationship between the oxygen consumption rates and the experimental temperatures of *vipera russelii.* [Each point represents the mean of different individual snakes. Vertical lines represent standard errors (S.E.)].

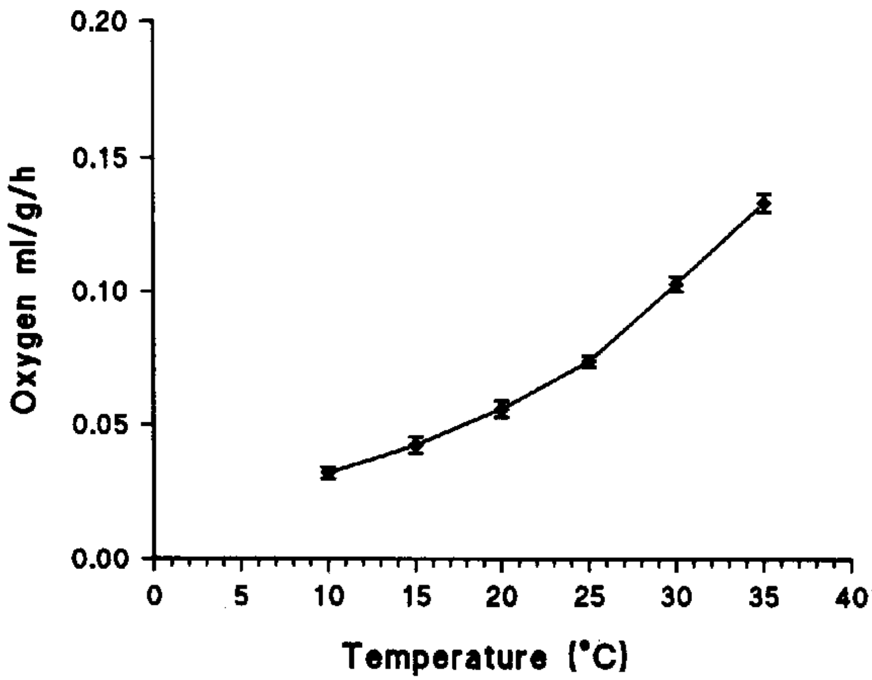

Fig. 2. Relationship between the oxygen consumption rates and the experimental temperatures of *Malpolon monspess- ulanus insignitus.*
[Each point represents the mean of different individual snakes. Vertical lines represent standard errors (S.E.)].

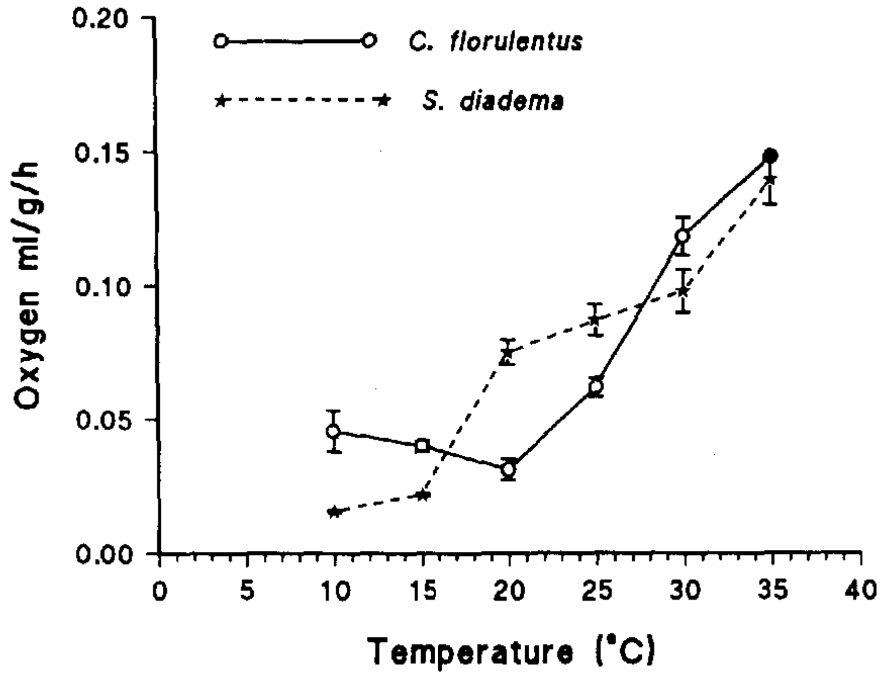

Fig. 3. Relationship between the oxygen consumption rates and the experimental temperatures of *Coluber florulentus* (o — o) and of *Spalerosophis diadema* (★-----★).
[Each point represents the mean of different individual snakes. Vertical lines represent standard errors (S.E.)].

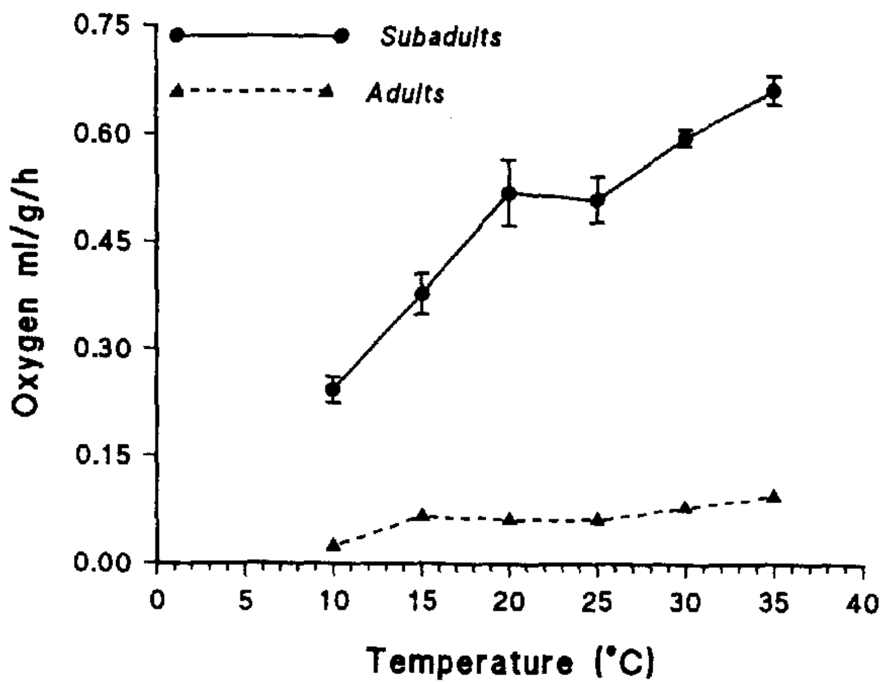

Fig. 4. Relationship between the oxygen consumption rates and the experimental temperatures *Leptotyphlops microrhy-nchus* (● — ●, subadults) and (Δ-------Δ adults).
[Each point represents the mean of different individual snakes. Vertical lines represent standard errors (S.E.)].

Q_{10} Values

Table 3 showed the Q_{10} values of the *L. microrhynchus* adults and subadults with an increase in the subadults (2.4, 1.9 at 10-15 and 15-20°C) followed by a level plateau (1.0 at 20-25°C) then by an increase of 1.4 at 25-30°C. The adult Q_{10} values showed an increase of 7.4 at 10-15°C followed by a decrease of 0.9 at 15-20°C and of 1.0 at 20-25°C, then an increase of 1.6 at 25-30°C. The Q_{10} values of *S. diadema* showed a rise of 11.6 at 15-20°C followed by a decline of 1.3 both at 20-25°C and at 25-30°C. Then followed an increase to 2.0 at 30-35°C (Table 2).

Table 3. The thermal dependence (Q_{10} values) of resting oxygen consumption of the five snake species

Species	Q_{10} values of resting oxygen consumption..					
	10-15 C	15-20 C	20-25 C	25-30 C	30-35 C	10-35 C
V. russelii	1.0	2.1	1.0	4.4	1.7	1.9
M.m. insignitus	1.7	1.8	1.8	1.9	1.7	1.8
C. florulentus	0.8	0.6	4.0	3.6	1.6	1.6
S. diadema	2.0	11.6	1.3	1.3	2.0	2.4
L. microrhynchus (Subadults)	2.4	1.9	1.0	1.4	1.2	1.2
L. microrhynchus (Adults)	7.3	0.9	1.0	1.6	1.5	1.7

The Q_{10} values of *V. russelii* and *M. m. insignitus* showed a very narrow plateau and a slight variation in thermal dependence. Those of *M. m. insignitus* depicted a rising value of 1.8 at 15-20°C which became stationary at 1.8 at 20-25°C, then there was a slight increase to 1.9 at 25-30°C. Those of *V. russelii* reached 2.1 at 15-20°C, then dropped lightly to 1.9 at 20-25°C, before rising sharply to 4.4 at 25-30°C. In contrast the Q_{10} values of *C. florulentus* decreased to 0.8 and 0.6, respectively at 10-15 and 15-20°C, before rising sharply to 4.0 at 20-25°C. The overall Q_{10} value for all species was around 2.0, except for subadult *L. microrhynchus* in which it was only 1.2. (Table 2).

Discussion

The RMR of the five snake species studied appeared to vary according to the particular species. However, both of the M-T curves and the Q_{10} parameters indicated some degree of similarity in all species. Both Q_{10} values and the shape of the M-T curves of subadult and adult *L. microrhynchus* showed increasing biphasic thermal dependence with a low thermal dependence phase (Q_{10} level around 1.0) between the two phases. This burrowing, nocturnal species inhabits comparatively cool microhabitats in the cultivated areas of Al-Diriyah near Riyadh from which it has been collected for this study. Although these cooler microhabitats can reach high temperature levels in summer, in harmony with the desert climate of the Central Region of Saudi summer, in harmony with the desert climate of the Central Region of Saudi Arabia, this species is capable of withstanding wide ranges of temperature within its habitat. This is also true to some extent for the diurnal snake *S. diadema*, which inhabits the same habitat in the Central Region of Saudi Arabia. That could, however, refer to the range of its voluntary body temperature (VBT), which has been considered [19] to be a mechanism of metabolic homeostasis. On the other hand the M-T curves of the nocturnal viper *V. russelii* and the diurnal colubrid *M. m. insignitus* have shown some degree of similarity in the steady increase, as well as in the narrow range of their low thermal dependence. This may be correlated with the damp habitats of both species. The former was collected from damp cultivated areas of Eastern Pakistan and the latter from the damp Mediterranean coast near Alexandria in Northern Egypt. Similar observations on the effect of climate and environment on the metabolic rate of various reptiles were indicated by other research workers [8; 20-24].

An interesting feature was observed in the M-T curve of *C. florulentus,* in which the Q_{10} values were low (decreasing) at the temperature range of 10-20°C. This has previously only been observed in cool, temperate snakes such as *Thamnophis sirtalis* [25] and has been interpreted as a mechanism of instantaneous temperature dependence shift. Such a feature has not previously been observed in any tropical or subtropical snake species. This low phase was immediately followed by a sharp rise at 20-25°C. At higher temperatures (30-35°C), a low Q_{10} was observed which could be attributed to physiological thermoregulation at high temperature.

Several research workers are of the opinion that Q_{10} values are indicative of the three phase-shaped M-T curves of the majority of species [19; 24; 26-31]. With the exception of *L. microrhynchus,* the present results demonstrate that the O/P ($\dot{V}O_2$) values of all the species of snakes tested are around unity. This is a clear indication of their close similarity to prediction [19; 32]. The variable ratios attained by the subadult and adult *L. microrhynchus* could be attributed to the fact that the regression equations derived [19] depict the interspecific relationships of large reptiles, whereas *L. microrhynchus* has a very small body mass. Similar results have been obtained by the present writer and his colleagues [11; 17; 33-35]. Moreover, burrowing and nocturnal species have generally low RMR [36].

The highest RMR recorded was that of the *L. microrhynchus* (subudults). These have the lightest body mass of the snakes tested in the present study. This could be attributed to the mass-specific metabolism which is inversely proportional to body mass. This feature is, however, also apparent, but with some minor anomalies, in the position of the M-T curves worked out in the present study for all the snakes tested. The most anomalous of those was that of the adult *L. microrhynchus* and it could well explain that anomaly. At the same time, Q_{10} values of the relatively heavier snakes were higher than those of the lighter ones. This observation is in good agreement with previous studies [37; 19] and could be attributed to many thermal factors, including climate and environment. More inter and intra-specific studies, especially related to geographical barriers, are needed for a better understanding of the thermal ecophysiology of desert reptiles.

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دراسة مقارنة للمنحنيات الحرارية لمعدل الأيض لخمسة أنواع من الثعابين تنتمي إلى عائلة الأفاعي، الثعابين الحقيقية والثعابين الديدانية

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الرياض ١١٤٥١ ، المملكة العربية السعودية

(استلم للنشر في ١٤١٩/٢/١٤هـ؛ وقبل للنشر في ١٤١٩/٧/١٩هـ)

ملخص البحث. تم جمع خمسة أنواع من الثعابين (*فيبرا راسلياي، مالبولون مونسبسيولانس إنسقنيتس، كولبر فلوريولنتس، سباليروزوفس دايادبما وليبتوتيفلوبس مايكرورينكس*)، والتي تنتمي إلى العوائل *فيبردي، كولبريدي، وليتوتيفلوبيدي*، من دولة الباكستان، مصر، والمملكة العربية السعودية، للقيام بدراسة مقارنة للمنحنيات الحرارية لمعدل الإيض. تم قياس معدل استهلاك الأوكسجين الساكن لكل نوع في درجة حرارة الوسط في المدى الحراري ١٠-٣٥°م في الجهاز الحجمي المغلق مزدوج الغرف. أظهرت المنحنيات الحرارية لمعدل الأيض وتحليل خطوط الانحدار المستقيمة، أن هناك ثمة دلالة معنوية ذات تناسب طردي لكل الأنواع. ولوحظت دلالة معنوية ذات تناسب عكسي للعلاقة بين معدل الأيض والوزن النوعي لكل العينات وكانت الملاحظة أكثر وضوحا للطور اليافع والبالغ لثعبان *ليبتوتيفلوبس مايكرورينكس*. بالرغم من أن قيم الارتباط الحراري (Q_{10}) أشارت إلى وضوح إزاحات الارتباط الحراري ومدى درجات حرارة الجسم المفضلة إلا أن أوجه التباين والتشابه التي وجدت في هذه القياسات يمكن إرجاعها لتأثير العوامل الجغرافية والبيئية.