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Diurnal Ventilatory Patterns in the Garter Snake, *Thamnophis elegans*

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Summary. Garter snakes, *Thamnophis elegans*, were entrained to a 14L (06.30–20.30 h)/10D (20.30–06.30 h) cycle for five weeks at 25 °C. Following entrainment, simultaneous measurements of ventilation and oxygen uptake were made. Pulmonary oxygen uptake ($\dot{V}_{O_2}$) exhibited a diurnal rhythm with minimum values of $\dot{V}_{O_2}$ occurring during 10D. The diurnal rhythm persisted during continuous darkness (24D) and was considered to be endogenous. Minute ventilation ($\dot{V}_E$) decreased during 10D. The decrease in $\dot{V}_E$ persisted during 24D. Diurnal alterations in $\dot{V}_E$ were attributed to a change in breathing frequency (*f*). The decrease in *f* during 10D was postulated to be characteristic of a 'sleeping' state. The decrease in $\dot{V}_E$ of the 'sleeping' state was of a greater magnitude than that for $\dot{V}_{O_2}$. Consequently, a pronounced diurnal rhythm in air convection requirement ($\dot{V}_E/\dot{V}_{O_2}$) resulted. The data suggest that the regulatory mechanisms of the 'sleeping' state differ from that of the 'waking' state.

Introduction

Diurnal changes in ventilation have received little attention in reptilian respiratory studies. In the few cases where ventilation and gas exchange has been monitored over time periods greater than 24 h, significant diurnal variations have been observed. Glass et al. (1979a) recorded ventilation in the box turtle, *Terrapene ornata*, for up to 96 h and reported a pronounced diurnal rhythm. In the lizard, *Varanus exanthematicus*, a marked nocturnal decrease in ventilation has been observed (Wood et al. 1977). The pronounced changes in ventilatory patterns and volume reported in these studies were observed at constant temperature. Changes in the ventilation of resting animals may result in significant shifts in air convection requirement ($\dot{V}_E/\dot{V}_{O_2}$). The air convection requirement has been shown to be an important respiratory parameter in reptilian acid-base regulation (Jackson 1971).

The purpose of the present study was to determine if diurnal fluctuations in ventilation occur in the garter snake and if such variations resulted in diurnal shifts in air convection requirement. A preliminary report of this study has appeared elsewhere (Hicks 1980).

Materials and Methods

Collection and Maintenance. Garter snakes, *Thamnophis elegans*, were collected in northern New Mexico during July and August. All animals, upon arrival at the laboratory (4–6 h after collection) were weighed and measured. The snakes were housed in 19, 38, or 57 liter aquaria. Each aquarium contained from 2–4 snakes. All of the aquaria contained paper towel lining, cardboard shelters, and a constant supply of water. Rocks or broken pieces of brick were also added to aid the snakes during periodic shedding. The snakes were fed 2–3 goldfish every 10–14 days. All animals appeared to be in good health throughout the study and each snake maintained a body weight of ±6.0% of the original capture weight. The aquaria were housed in an environmental chamber under a 14 h light (06.30–20.30 h) and 10 h dark regime (14L/10D). The ambient temperature was 25±1 °C.

Experimental Protocol. Eight *T. elegans* (31.7 to 62.8 g, $\bar{x}$= 44.1 g) were entrained to the 14L/10D regime for five weeks before the studies commenced during the ensuing summer months. The snakes were placed in a plethysmograph which was shielded from all visual disturbances by surrounding the plethysmograph with an L-shaped wooden wall. The plethysmograph was shielded from vibration by being placed on a thick foam rubber base. All experiments were conducted in an environmental chamber under the 14L/10D regime or a continuous darkness (24D) regime. The light source was a fluorescent lamp at 3 m distance and gave no incident heat. Ambient

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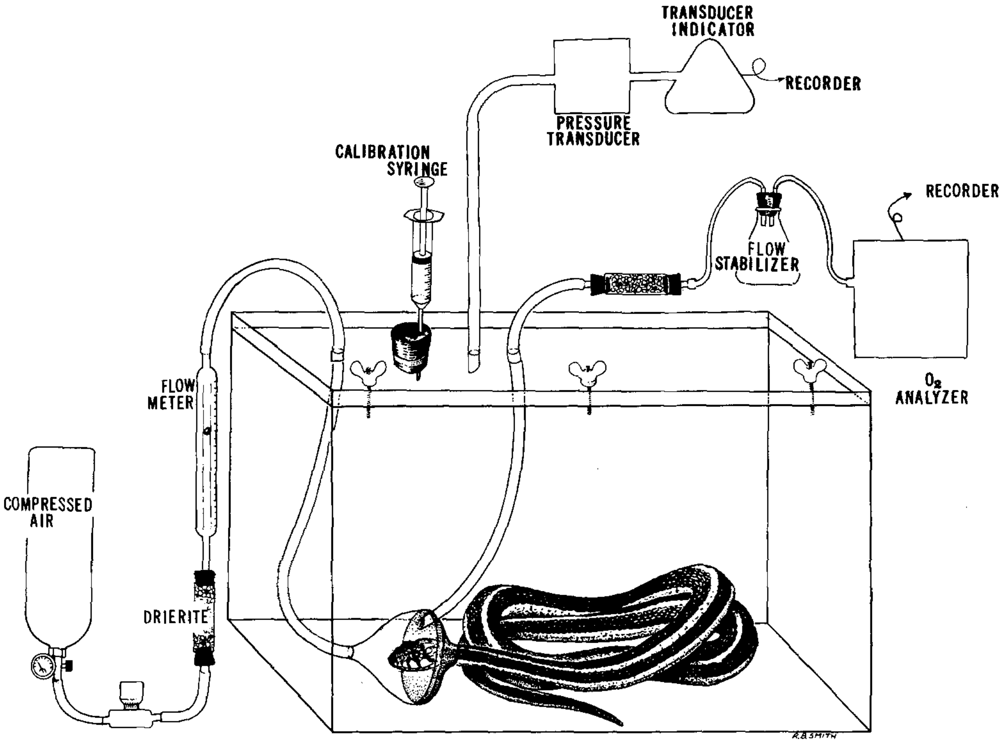

Fig. 1. Schematic diagram of arrangement of equipment used to measure gas exchange and ventilation in the garter snake

temperature during the experiment was 25±1 °C. The preferred body temperature is reported to be 26.5 °C for the *Thamnophis* species (Brattstrom 1965). The animals were fasted 7 days prior to the experiments. The fasting minimized the effect that digestion may have on ventilation and gas exchange (Glass et al. 1979b). The animals were in the plethysmograph at the experimental temperature 4–24 h before measurements began. Simultaneous measurement of ventilation and oxygen uptake were continuously recorded for 48–96 h.

Plethysmograph. The experimental setup is illustrated in Fig. 1. Ventilation ($\dot{V}_E$) was monitored by a plethysmographic technique. The plethysmograph, consisted of either a 2 l flask or a 4 l plexiglass chamber, depending on the size of the snake. A lightweight (7–14 g) plexiglass cylinder (volume 35–60 ml), henceforth referred to as the head compartment, was sealed to the animal's head. Before attachment of the head compartment, the snakes were cooled to 5 °C by packing them in crushed ice. This procedure reduced struggling. A rubber collar was constructed by cutting strips from latex rubber gloves, approximately 5 mm by 25 mm. The collar was attached to the snake's neck, 1 cm posterior to the head, by wrapping the rubber strip around the neck and attaching to the skin with cyanoacrylate cement.

A diaphragm was constructed by removing a finger from a latex surgical glove with the finger tip cut off. The rubber diaphragm was placed over the opening of the head compartment. Finally, the snake's head was placed through the hole of the diaphragm and was fixed to the rubber collar with cyanoacrylate cement. Extreme care was taken to assure that the opening in the rubber diaphragm was loose enough to permit venous flow to the periphery and prevent edema of the head region. However, it was essential that the connection between the diaphragm and neck be secure to prevent air leakage. Leaks were detected by visibly inspecting the seal and reinforcing it with 748 RTV adhesive/sealant (Dow Corning Corp., Midland, Michigan 48640, USA). This adhesive was an especially good sealing material as it adhered both to the skin of the animal (without visible toxic affects) and to the rubber diaphragm. After drying, this sealant remained flexible, allowing the seal to stretch when the animal occasionally struggled. Vinyl tubing was inserted into the head compartment such that air would flow through that compartment. The snake was placed in the plethysmograph which was sealed.

The experimental setup consisted of a head-body plethysmograph. Changes in body volume caused by inspiration and expiration resulted in chamber pressure changes which were monitored by a Valydine differential pressure transducer (MP45-1), with a Valydine transducer indicator (CD12) and were recorded with an E&M physiograph (E&M Instrument Co, Inc., Houston, Texas, USA). Calibration of the system was achieved during breath-holds by injecting or withdrawing known volumes of air. Leaks occasionally developed in the seal of the head compartment, being detected as a decrease in the amplitude of the calibration signals. If leaks occurred, the snake was removed from the plethysmograph and more sealant was applied.

Gas Exchange. An open system respirometer permitted measuring pulmonary oxygen uptake ($\dot{V}_{O_2}$) and $\dot{V}_E$ simultaneously. A continuous flow of air was passed through the head compartment. Flow rate was controlled by a micrometer valve and was adjusted such that the change between incurrent and excurrent gas concentrations during steady rate was never more than 0.50%. A 125 ml flask added to the excurrent line increased dead space. The added dead space decreased the amplitude of fluctuations in the oxygen signal due to periodic breathing. The flask increased response time of the gas signal, but did not effect $\dot{V}_E/\dot{V}_{O_2}$, as only steady state values were used. Excurrent air flowed into an oxygen analyzer (Applied Electrochem-

Table 1. Summary of respiratory variables for *Thamnophis elegans* during L/D and 24D at 25 °C. Values from 14L and D-I were measured between 06.30–20.30 h and values from 10D and D-II were measured between 20.30–06.30 h. Differences between corresponding values (14L:D-I or 10D:D-II) were not significant except where indicated by $^+$ ($P<0.05$). Differences in respiratory values within a group (14L/10D or D-I/D-II) are indicated by: * $P<0.0025$; ** $P<0.005$; *** $P<0.01$; **** $P<0.05$. Values are expressed as means ± SE

Condition	N	f (breaths·min^{-1})	$\dot{V}$T (ml BTPS·kg^{-1})	$\dot{V}$E (ml BTPS ·kg^{-1}·min^{-1})	$\dot{V}_{O_2}$ (ml STPD ·kg^{-1}·min^{-1})	$\dot{V}$E/$\dot{V}_{O_2}$ (ml BTPS/ml STPD)
a) L/D						
14L	8	2.2±0.2**	16.4±0.9	33.5±3.5*	0.98±0.09***	34.9±3.0*
10D	8	1.5±0.2	15.5±1.2$^+$	20.5±2.7	0.90±0.08	24.0±2.8
b) 24D						
D-I	6	2.0±0.3**	17.3±1.0****	32.6±3.8**	0.97±0.09****	33.6±2.0****
D-II	6	1.4±0.2	19.7±1.6$^+$	26.5±3.2	0.84±0.06	29.3±2.5

istry Model S3A). The oxygen concentration of the excurrent air was continously recorded (Coleman Recorder, Hitachi 165). The $\dot{V}_{O_2}$ was calculated from the flow rate and changes in fractional concentrations of O_2 using a correction for $R<1.0$ (Hill 1972).

Analysis and Presentation of Data. Continuous 24 h recordings of ventilation were analyzed in 30-min blocks. Respiratory frequency (f) was the mean number of breaths per minute over the 30-min periods. The mean volume of the breaths which occurred during the 30-min block was taken as the tidal volume ($\dot{V}$T), expressed as ml BTPS·kg^{-1}. Minute ventilation ($\dot{V}$E) was the product of f and $\dot{V}$T and was expressed as ml BTPS·kg^{-1} ·min^{-1}.

Continuous 24 h recordings of oxygen uptake were also analyzed in 30-min blocks. The area under the oxygen recording (made with a polar planimeter) represented the percent oxygen in the excurrent line. Pulmonary oxygen uptake ($\dot{V}_{O_2}$) was expressed as ml STPD·kg^{-1}·min^{-1}.

Day and night mean values used in the statistical analyses represented the mean of 15 values randomly chosen for each animal during each of the 14L and 10D periods. Only ventilatory and gas exchange measurements representing steady state were used for calculation of means. The data were analyzed using a paired sample t-test. Differences at the 5% level of confidence were considered significant.

Results

Gas Exchange

Table 1 summarizes the values for gas exchange and ventilation in *Thamnophis elegans* during 14L/10D and 24D. During 14L/10D, $\dot{V}_{O_2}$ exhibited a diurnal rhythm (Fig. 2A). During the dark hours (24.00–06.30 h), $\dot{V}_{O_2}$ was never constant, but fluctuated around a mean. Minimum $\dot{V}_{O_2}$ usually occurred between the hours of 01.30–03.30 h. When the lights were switched on at 06.30 h, there was nearly always an immediate increase in $\dot{V}_{O_2}$ which lasted for the next 1–2 h. This increase in $\dot{V}_{O_2}$ was usually associated with a heightened level of activity in the animals. Occasionally, struggling was observed although behavioral observations were kept at a minimum to prevent needless disturbance of the experimental animals. During the rest of the light period $\dot{V}_{O_2}$ fluctuated around a new mean level. A second peak in $\dot{V}_{O_2}$ was observed towards the end of the light period (18.00–20.00 h). Increased activity was also observed at this time. Fol-

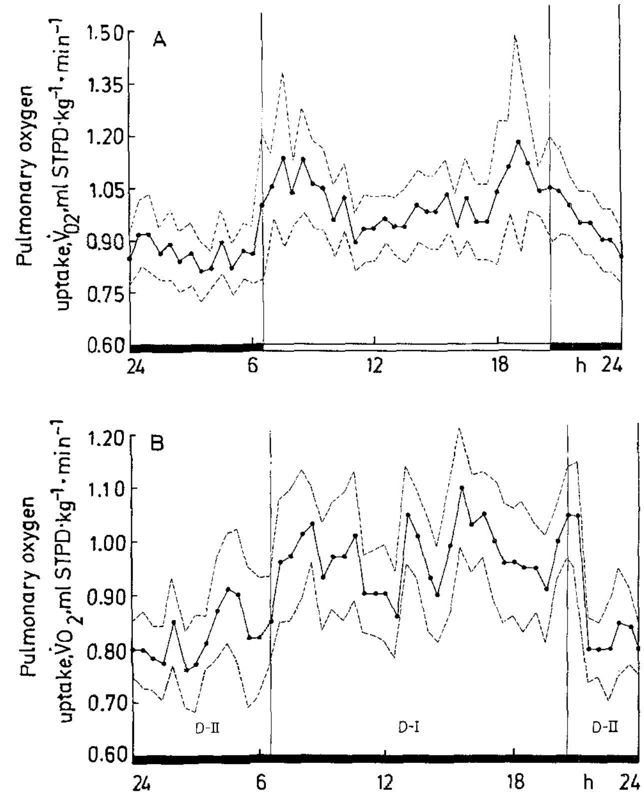

Fig. 2. Pulmonary oxygen uptake ($\dot{V}_{O_2}$) during 14L/10D (**A**) and 24D (**B**), at 25 °C. *Solid circles* represent the mean for each 30-min period. *Broken line* above and below mean values represent the standard error. **B** Note that the ordinate scale is expanded

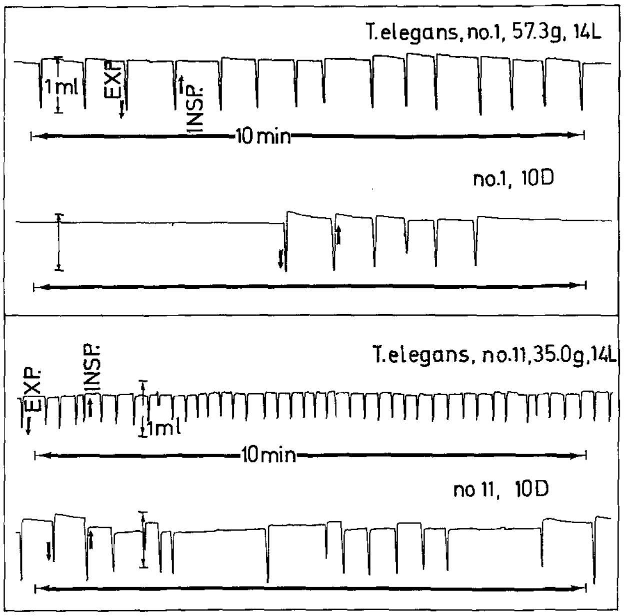

Fig. 3. Continuous recordings of ventilatory patterns of two garter snakes during 14L/10D, at 25 °C. For each snake, the upper recording is during 14L and the lower recording is during 10D

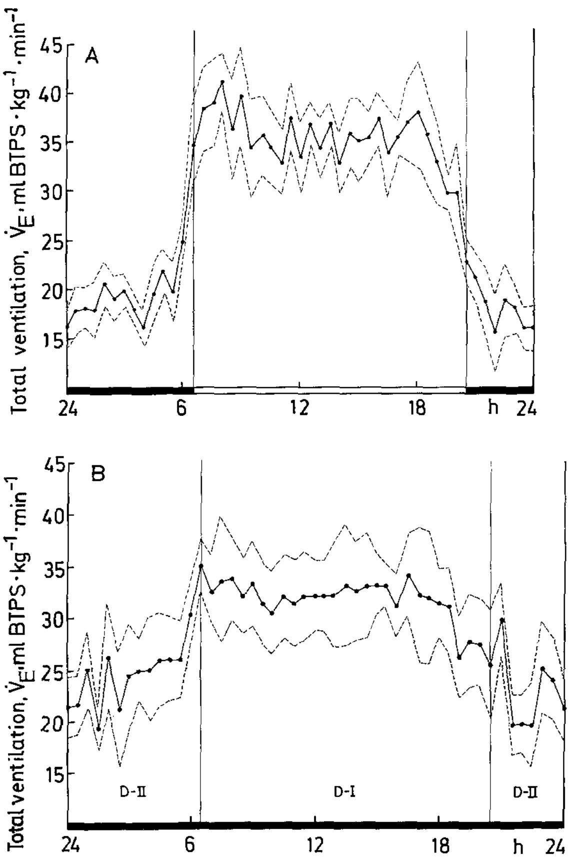

Fig. 4. Minute ventilation ($\dot{V}$E) during 14L/10D (**A**) and 24D (**B**) at 25 °C. *Solid circles* represent the mean for each 30-min period. *Broken line* above and below mean values represent the standard error

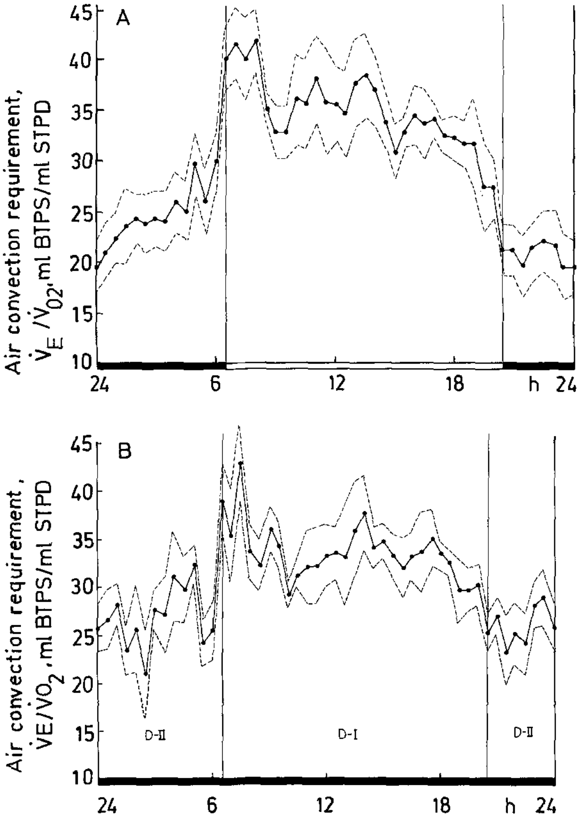

Fig. 5. Air convection requirement ($\dot{V}$E/$\dot{V}_{O_2}$) during 14L/10D (**A**) and 24D (**B**) at 25 °C. *Solid circles* represent the mean for each 30-min period. *Broken line* above and below mean values represent the standard error

lowing the onset of darkness (20.30 h) $\dot{V}_{O_2}$ declined over the next 4 h.

The continous darkness regime (24D) was divided into two major subdivisions. The hours between 06.30–20.30 h are referred to as D–I and the hours of 20.30–06.30 h are referred to as D–II. During 24D, $\dot{V}_{O_2}$ continued to exhibit a diurnal rhythm but with an increased variability (Fig. 2B). The $\dot{V}_{O_2}$ during D–I was extremely variable but fluctuated about a mean level. Minimum values of $\dot{V}_{O_2}$ were recorded during D–II. Behavioral observations were not made during 24D.

Ventilatory Patterns and Air Convection Requirement

The ventilatory patterns of all animals were found to be biphasic – expiration followed by inspiration. In some animals, an occasional triphasic pattern was apparent – expiration, followed by an inspiration, a breath-hold and then a second inspiration. It was difficult to determine with a plethysmograph if these small (0.1–0.4 ml) second inspirations actually represented air flow into the animal.

Ventilatory movements during 14L were regular with tidal volume (V_T) exhibiting little breath-to-breath variability (Fig. 3). During 10D, ventilatory movements became irregular, with variable V_T and extended apneic periods (Fig. 3). Minute ventilation ($\dot{V}_E$) decreased during 10D (Fig. 4A). The diurnal alterations in $\dot{V}_E$ were a result of changes in breathing frequency (see Table 1). Ventilatory movements recorded during 24D were not different from those observed during 14L/10D. Consequently, the decrease in $\dot{V}_E$ persisted during 24D (Fig. 4B).

The decrease in $\dot{V}_E$ was of greater magnitude than that for $\dot{V}_{O_2}$ resulting in a pronounced diurnal rhythm in air convection requirement ($\dot{V}_E/\dot{V}_{O_2}$) (Fig. 5A). Minimum $\dot{V}_E/\dot{V}_{O_2}$ was always recorded during 10D. During 24D, changes in $\dot{V}_E/\dot{V}_{O_2}$, over D–I and D–II, were not as pronounced as during the corresponding periods of 14L/10D (Fig. 5B). However, an analysis of $\dot{V}_E/\dot{V}_{O_2}$ in individual snakes indicated that the decrease in $\dot{V}_E/\dot{V}_{O_2}$ persisted during 24D.

Discussion

Gas Exchange

The resting or 'waking' pulmonary oxygen uptakes ($\dot{V}_{O_2}$) reported in this study were 30% lower than the metabolic rates calculated for similar size snakes for $T_b = 25$ °C (Bennett and Dawson 1976). The 'waking' $\dot{V}_{O_2}$ of 0.98 ml STPD·kg^{-1}·min^{-1} was 60% lower than the $\dot{V}_{O_2}$ reported for *T. elegans* at a similar temperature (28 °C) (Siedel and Lindborg 1973). Both 'sleeping' and 'waking' $\dot{V}_{O_2}$ were considerably lower ($<30\%$) than the $\dot{V}_{O_2}$ calculated for a similar species, *T. proximus* (Jacobson and Whitford 1970). The lower values reported in the present study probably reflect the experimental procedure which resulted in minimal disturbance of the animal.

The cyclic change in oxygen uptake during the 14L/10D cycle indicates that a diurnal rhythm exists. The 10% decrease in oxygen uptake recorded during the night is less than the range of decrease (30–80%) reported for other reptiles (Kramer 1934; Roberts 1968; Mautz and Case 1974; Cragg 1978a; Wood et al. 1978). In the diamondback water snake, *Natrix rhombifera*, nocturnal metabolic rates were 15% less than those recorded during the day (Gratz and Hutchison 1977). The persistance of a diurnal oscillation in oxygen uptake during constant dark suggests an endogenous rhythm. Endogenous fluctuations in oxygen uptake have not been investigated for other snakes. Diurnal fluctuations in oxygen uptake reported in this study cannot predict activity patterns of *T. elegans* in the field because acclimation temperatures in the lab may influence recorded patterns (Gratz and Hutchison 1977).

Ventilatory Patterns

Ventilatory patterns in snakes have been reported to be either biphasic or triphasic (Rosenberg 1973; Glass and Johansen 1976; Donnelly and Woolcock 1977; Gratz 1978). Both patterns are typical of a variety of reptiles (Wood and Lenfant 1976). However, recent studies (Gans and Clark 1978) have questioned the triphasic mode often reported, and have suggested that the small degree of expiration recorded after inspiration represents the following: (1) an unnatural phenomenon resulting from the animal being physically restrained or hyperexcited, (2) an artifact of closed manometric techniques used to monitor breathing, (3) compression of lung gases or (4) a combination of several of the preceding. *Thamnophis elegans* exhibited both periods of triphasic and biphasic breathing. Periods of triphasic breathing occurred spontaneously in the animals, but represented less than 10% of the ventilatory movements. It is of interest that the triphasic pattern – expiration, inspiration, breath-hold, small second inspiration – is quite different from the expiration, inspiration, expiration pattern reported for other reptiles (Wood and Lenfant 1976). However, for the reasons stated above, it is difficult to conclude that this second inspiration involves air flow into the animals. Biphasic ventilation appears to be the primary mode of breathing in *T. elegans*. Biphasic ventilatory patterns have been recorded for *Thamnophis sirtalis* (Clark et al. 1978).

The limited number of respiratory studies on various snake species does not allow for detailed comparisons. Aquatic snakes, belonging to the family Hydrophidae and Acrochordidae, tend to have larger tidal volumes (ranging from 25–48 ml·kg^{-1}) and lower breathing frequencies (0.15–0.35 breaths·min^{-1}) (Heatwole and Seymour 1975, 1976; Glass and Johansen 1976). The lower breathing frequencies result from the long periods of voluntary submergence; however the acrochordids and sea snakes, when removed from water, retain the diving rhythm and continue to exhibit long periods of voluntary apnea (Heatwole 1978). Terrestrial snakes exhibit more rapid frequencies (0.4–7.0 min^{-1}) and somewhat smaller tidal volumes (10–35 ml·kg^{-1}) (Dmi'el 1972; Donnelly and Woolcock 1977; Gratz 1978; Stinner 1982).

The pronounced increase in the length of apneic periods during the night, resulting in a decrease in minute ventilation, clearly represents a diurnal rhythm. The persistence of this oscillation in the absence of light cues, suggests an endogenous rhythm in ventilation. It is possible that the nocturnal hypoventilation may have been induced by the experimental technique. Hypoventilation following the application of masks has been observed in snakes (Stinner, personal communication). This mask-induced hypoventilation is usually observed after initially attaching the mask to the animal or after a disturbance. However, a mask-induced alteration in ventilation would be expected to occur randomly from animal to animal and not to occur repeatedly in the cyclical nature reported in this study.

Periodic decreases in both breathing frequency and minute ventilation at constant temperature have been reported for a variety of reptiles. During 'sleep' in the carpet phython, *Morelia spilotes variegata,* breathing frequency decreased by 67% and apneic periods lasting up to 4 min were reported. Minute ventilation in these animals decreased by 60%, while tidal volume remained unchanged (Donelly and Woolcock 1977). Cragg (1978b) reported that in the lizard, *Lacerta viridis,* minute ventilation recorded during 'sleep' was 40% of the value recorded during a wakeful state. The decrease in minute ventilation resulted from both decreases in tidal volume and breathing frequency. In *Varanus exanthematicus,* a pronounced decrease in tidal volume and breathing frequency was recorded as the lizards entered a 'sleeping' state (Wood et al. 1977). Studies which have described the 'sleeping' state in reptiles have consistently noted a pronounced decrease in ventilation during sleep (Flanigan 1973; Flanigan et al. 1974).

The periodic appearance of distinct alterations in ventilatory patterns suggests changes in the mechanisms which control ventilation as the animal enters a 'sleeping' state. Decreases in ventilation during sleep have been observed in fishes (Tauber et al. 1969), amphibians (Hobson 1967), and mammals, including man (Sullivan 1980) and may represent a universal respiratory response associated with the sleeping state among the vertebrates.

Air Convection Requirements

There have been few studies which have measured air convection requirements in snakes. The 'waking' values reported in this study are in the same range (17–42 ml BTPS/ml STPD) as values reported for other terrestrial species at a comparable temperature (Donnelly and Woolcock 1977; Gratz 1978; Stinner 1982).

The pronounced decrease in minute ventilation recorded at night was not matched by a proportional decrease in oxygen uptake, resulting in a diurnal fluctuation in air convection requirement. The differences in mean $\dot{V}_E/\dot{V}_{O_2}$ appeared to be somewhat suppressed during constant darkness (24D). However, the persistence of such an oscillation in the absence of light cues does reflect an endogenous component.

The diurnal variation in $\dot{V}_E/\dot{V}_{O_2}$ at constant temperature has not been reported for other reptiles and is surprising. Current concepts in reptilian acid-base regulation predicts that $\dot{V}_E/\dot{V}_{O_2}$ is temperature dependent and thus at constant body temperature $\dot{V}_E/\dot{V}_{O_2}$ should remain constant (Howell and Rahn 1976; Reeves and Rahn 1979). The inverse relationship of plasma pH to body temperature observed in ectothermic vertebrates is not the result of a passive physico-chemical process, but is actively regulated so as to maintain a constant α_{im} and OH^-/H^+ (Reeves and Rahn 1979). Examination of the Henderson-Hasselbalch equation:

$$\mathrm{pH} = \mathrm{pK} + \log \frac{[\mathrm{HCO_3^-}]}{\alpha \cdot P_{CO_2}} \tag{1}$$

reveals that changes in pH can result from alterations in plasma $[HCO_3^-]$ and alveolar (arterial) P_{CO_2}. Although regulation of plasma $[HCO_3^-]$ by exchange of ions across intestinal and/or tubular epithelium could occur, most evidence favors a constant $[HCO_3^-]$ with temperature in reptiles (Howell and Rahn 1976). Therefore, as body temperature changes, air breathing ectothermic vertebrates regulate pH by adjustments in P_{CO_2}. Changes in alveolar (arterial) P_{CO_2} result from alterations in the air convection requirement:

$$\dot{V}_A/\dot{V}_{CO_2} = RT/P_{A_{CO_2}}. \tag{2}$$

The expired minute ventilation, $\dot{V}_E$, is an approximation of alveolar ventilation, $\dot{V}_A$ (Glass et al. 1979a). Oxygen uptake, $\dot{V}_{O_2}$, reflects carbon dioxide production, $\dot{V}_{CO_2}$, for a constant gas exchange ratio: $\dot{V}_{CO_2} = R \cdot \dot{V}_{O_2}$.

Stinner (1982) reported the $\dot{V}_E/\dot{V}_{O_2}$ for many reptiles over a temperature range of 10–30 °C. Calculations indicate that $\dot{V}_E/\dot{V}_{O_2}$ decreases as temperature increases with a mean $\Delta(\dot{V}_E/\dot{V}_{O_2})/\Delta °C$ of -1.7 (ml BTPS/ml STPD)/°C (range: -1.4 to -2.7 (ml BTPS/ml STPD)/°C. This magnitude of change in $\dot{V}_E/\dot{V}_{O_2}$ results in a sufficient change in P_{CO_2} so as to maintain a constant OH^-/H^+ and α_{im}.

This pattern of temperature dependent acid-base regulation by adjustments in $\dot{V}\mathrm{E}/\dot{V}_{\mathrm{O}_2}$ appears to operate in turtles (Jackson 1971; Kinney et al. 1977), lizards (Giordano and Jackson 1973; Worsham and Maclean 1979), snakes (Stinner 1982) and crocodilians (Davies 1978). However, temperature-dependent respiratory regulation of acid-base status may not operate in species with a high aerobic requirement (Wood et al. 1981) or during periods of chronic exposure to low temperature (i.e. hibernation) (Glass et al. 1979a).

The pronounced decrease in $\dot{V}\mathrm{E}/\dot{V}_{\mathrm{O}_2}$ exhibited in the 'sleeping' garter snake is of a magnitude which would correspond to a 7 °C increase in body temperature. Such a change could result in an increase of arterial P_{CO_2} by as much as 7 Torr. The shift of P_{CO_2} would result in a 'sleeping' acidosis which would conflict with a constant α_{im} and $\mathrm{OH}^-/\mathrm{H}^+$. An increase in arterial P_{CO_2} has been reported in sleeping mammals (Sullivan 1980). Unfortunately, the small size of the animals used in this study prevented the repeated blood sampling needed to follow changes in blood gas tensions and the acid-base status of 'waking' and 'sleeping' snakes. However, the decrease in breathing frequency and ventilation reported in other reptilian studies during 'sleep' would justify further studies in acid-base status and control of ventilation of 'waking' and 'sleeping' reptiles.

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