

THE INTERRELATIONSHIP BETWEEN PULMONARY MECHANICS AND THE SPONTANEOUS BREATHING PATTERN IN THE TOKAY LIZARD, *GEKKO GEKKO*

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SUMMARY

The normal breathing pattern of the Tokay gecko (*Gekko gekko*) consists of single breaths or bursts of a few breaths separated by periods of breath holding. Increases in pulmonary ventilation that accompany rises in body temperature are caused by increases in respiratory frequency due to shortening of the periods of breath holding. Tidal volume and breath duration remain relatively constant. Measurements of the mechanical work associated with spontaneous breathing yielded values that were similar to those calculated for breaths of the same size and duration based on work curves generated during pump ventilation of anaesthetized animals. In this species, the pattern of periodic breathing and the ventilatory responses to changes in respiratory drive correspond with predictions of optimal breathing patterns based on calculations of the mechanical cost of ventilation. Bilateral vagotomy drastically alters the breathing pattern producing an elevation in tidal volume, a slowing of breathing frequency, and a prolongation of the breath duration. These alterations greatly increase the mechanical cost of ventilation. These data suggest that periodic breathing in this species may represent an adaptive strategy which is under vagal afferent control and which serves to minimize the cost of breathing.

INTRODUCTION

In a previous paper (Milsom & Vitalis, 1984), it was shown that the total work required to pump ventilate the Tokay gecko resulted primarily (>70%) from the work required to overcome elastic forces resisting lung inflation. For each level of alveolar minute ventilation, there was an optimum combination of ventilation frequency and tidal volume at which minute work was minimum. These data would suggest that for reptiles, as for mammals (Otis, Fenn & Rahn, 1950), there is a breathing pattern that optimizes the mechanical cost of ventilation. The purpose of the present study was to examine how the spontaneous breathing patterns of the Tokay gecko, under control conditions and following warming, compared with the predicted optimum breathing patterns based on the mechanical studies which were performed on anaesthetized animals using continuous pump ventilation. In addition,

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the effects of bilateral vagotomy on ventilation and the cost of breathing were also determined.

METHODS

Experiments were performed on specimens of the Tokay gecko (*Gekko gecko*) (36–151 g) obtained commercially and maintained in glass aquaria at 22–23 °C. This species is primarily nocturnal and tropical in distribution being found commonly throughout the Philippine Archipelago. Although 22–23 °C is probably below the preferred temperature of this species, all individuals fed heartily on live locusts and grew rapidly during the 2–3 months before experiments were conducted. Food was withheld from each individual for approximately 1 week before it was used in any experiment.

Pulmonary ventilation was measured using a head-body plethysmograph as described by Gratz (1978). The volume of the body chamber was 600 ml and the opening between the head and body chambers was surrounded by a plastic collar held in place by wing nuts. A metal ring was sutured to the neck of each lizard after complete infiltration of the neck with local anaesthetic and the head of each lizard was then passed through a small hole in a sheet of rubber dental dam. The metal ring was used to tether the animal to the opening between head and body chambers and the dental dam was secured by the plastic collar surrounding the opening, providing an air-tight seal between the two chambers. The hole in the dental dam was designed to be loose enough to allow swallowing movements, yet snug enough to be air-tight with the aid of stopcock grease or petroleum jelly. All animals were allowed to adjust to the chamber for 24 h before any measurements were made. The body chamber was open to air through a single opening fitted with a Fleisch no. 00 pneumotachograph. Air flow across the pneumotachograph was sensed with a Validyn DP 103-18 differential pressure transducer and this air flow signal was fed through a Gould integrating amplifier to give tidal volume (V_T). Measurements of respiratory airflow and tidal volume associated with spontaneous ventilation were made on six animals at both 24 and 34 °C, and recorded on a Gould chart recorder.

In three of the animals, a saline-filled catheter was also introduced through the skin into the body cavity at the level of the lungs and stitched in place. Since the lungs of this species lie in a pleuroperitoneal cavity, intrapulmonary and intra-abdominal cavity pressures must be in equilibrium. The movements of the ribs which power ventilation create changes in intra-abdominal cavity pressure which, when transferred to the lungs, generate air flow. Thus in spontaneously breathing animals, intra-abdominal and intrapulmonary pressure are equivalent. In these animals, the measurements of intra-abdominal pressure, made with a Statham P23V pressure transducer and Gould transducer amplifier, as well as ventilatory air flow and tidal volume, were continuously recorded on the chart recorder during spontaneous ventilation and the pressure and volume signals were also plotted on an Esterline Angus XY plotter.

In a further three animals, recordings were made of respiratory air flow and tidal volume both before and after bilateral vagotomy. Vagotomies were performed under

Halothane anaesthesia and animals were allowed to recover for at least 24 h before post-vagotomy measurements were made.

Following all experimental runs, the animals were killed by anaesthetic overdose and measurements of resting lung volume (V_{LR}) and ventilatory dead space (V_D) were made. Resting lung volume was determined by removing air from the lungs with a syringe, *via* an intratracheal cannula, after opening the cannula to atmosphere with the animals placed in a normal supine position. The lungs and trachea, complete with glottis were then removed from each animal and the trachea tied closed at the lung hilus. The dead space volume was then determined by carefully measuring the volume of water required to fill the trachea from lung hilus to glottis.

All measurements in this paper are given as means \pm s.e. Direct comparisons of variables in all Tables were tested with the Student *t*-test.

RESULTS

The ventilatory pattern associated with normal resting conditions in the Tokay gecko is depicted in Fig. 1. The effects of warming to 34°C and of spontaneous activity are shown for comparison. Mean values of respiratory variables measured during resting breathing at 24 and 34°C are given in Table 1 along with values obtained from anatomical measurements. At 34°C, tidal volume (V_T) is relatively unchanged but breathing frequency (f) is elevated solely by reducing the periods of breath holding (T_{NVP}). The duration of each individual breath (T_{tot}) remains unchanged. The number of breaths taken during each breathing episode (breaths/ventilatory period, VP) remains the same but the period between episodes is reduced until breathing becomes almost continuous. Since T_{tot} does not change, the instantaneous breathing frequency ($f' = 60/T_{tot}$) does not change appreciably. Both

Table 1. Values of respiratory variables and parameters during resting ventilation in the Tokay gecko at various temperatures

		24°C	34°C
Tidal volume (V_T)	(ml 100 g ⁻¹)	1.2 \pm 0.1	1.0 \pm 0.2
Ventilation frequency (f)	(min ⁻¹)	9 \pm 2	34 \pm 9*
Minute ventilation (\dot{V}_E)	(ml min ⁻¹ 100 g ⁻¹)	10 \pm 3	28 \pm 7*
Breaths/ventilatory period		1.7 \pm 0.3	2.1 \pm 1.4
Bursts/min		6.0 \pm 1.6	20.8 \pm 5.6*
Alveolar minute ventilation (\dot{V}_A)	(ml min ⁻¹ 100 g ⁻¹)	6.3	17.0*
Breath duration (T_{tot})	(s)	1.6 \pm 0.2	1.5 \pm 0.2
Non-ventilatory period (T_{NVP})	(s)	14 \pm 6	2 \pm 0.1*
Instantaneous breathing frequency (f')	(min ⁻¹)	37 \pm 7	40 \pm 10
Ventilatory dead space (V_D)	(ml 100 g ⁻¹)		0.50 \pm 0.03
Resting lung volume	(ml 100 g ⁻¹)		6.3 \pm 1.0
$\frac{V_T - V_D}{V_{LR} + V_T} \times 100$	(%)		7-9
Weight	(g)		100 \pm 21

* Indicates values recorded at 34°C were significantly different ($P \leq 0.05$) from values recorded at 24°C.

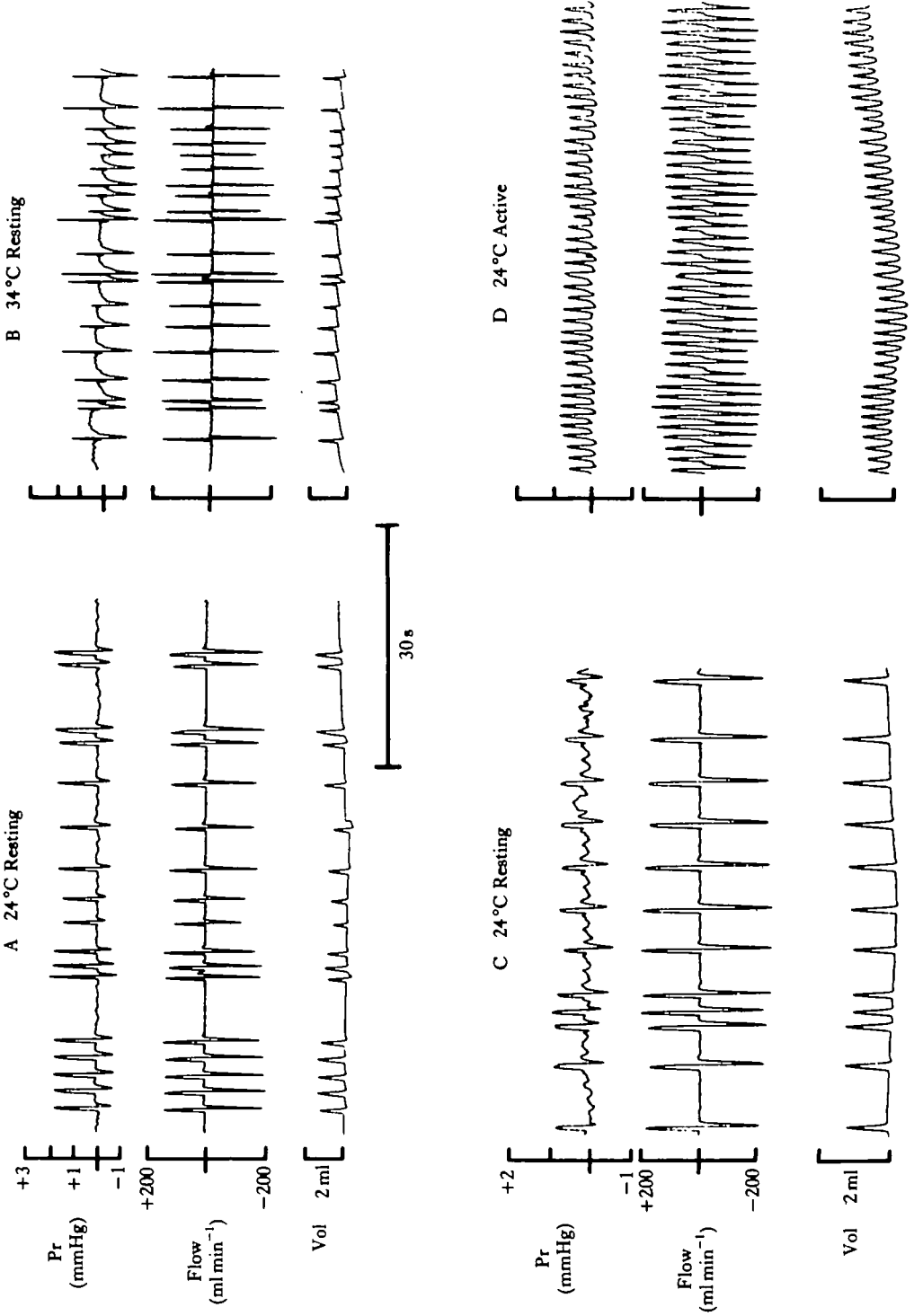


Fig. 1

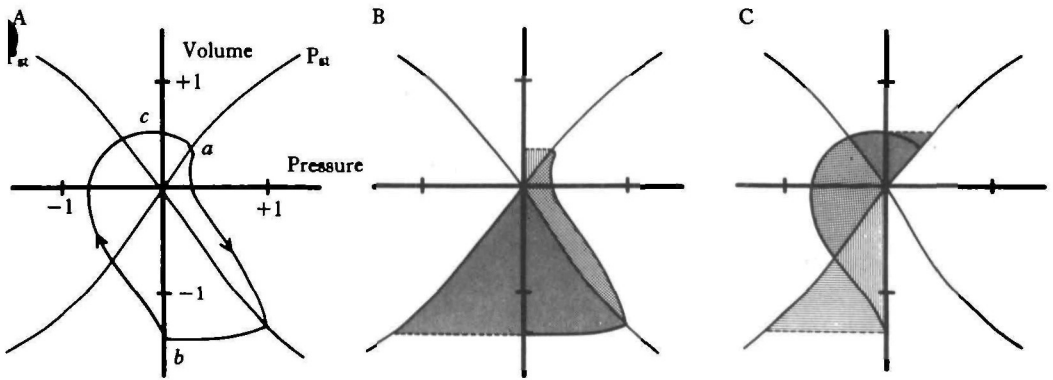


Fig. 2. (A) Schematic diagram of the pressure-volume loop generated by a single ventilation cycle in the Tokay gecko. Pressure is intra-abdominal pressure in mmHg (0 pressure = atmospheric pressure) and volume is the change in lung volume in ml (0 volume = V_{LR}). P_{st} and $-P_{st}$ represent the static pressure-volume curve of the intact respiratory system and its mirror image respectively. Arrows denote the direction of change and various points associated with each ventilation cycle (*a*, *b*, *c*) are described in the text. (B) Graphical representation of the mechanical work of expiration. Vertically hatched area; stored energy of previous inflation available for expiration. Diagonally hatched area: work done by expiratory muscles to overcome flow resistance. Stippled area: work done by expiratory muscles to overcome elastic resistance. (C) Graphical representation of the mechanical work of inspiration. Horizontally hatched area: work done against persistent activity of expiratory muscles. Vertically hatched area; stored energy of deflation available to power inspiration. Diagonally hatched area: work done by inspiratory muscles to overcome elastic resistance. Stippled area: work done by inspiratory muscles to overcome flow resistance.

minute ventilation (\dot{V}_E) and alveolar minute ventilation [$\dot{V}_A = f(V_T - V_D)$] increase 2.7 to 2.8 times. Since breath holding occurs at end-inspiration, the volume of the lung at this time will be $V_{LR} + V_T$ and the percentage of this volume which is exchanged with each breath [$(V_T - V_D / V_{LR} + V_T)100$] remains small but relatively constant.

The mechanical work performed during spontaneous breathing can be determined from a graphical analysis of the pressure-volume diagrams associated with each breath (Fig. 2A). In lizards, ventilation terminates at end-inspiration (*c* in Fig. 2A) when the glottis closes and a variable period of breath holding commences. The respiratory muscles relax and elastic recoil acting on the expanded lung generates a slight positive pressure. Thus, during the interbreath interval (T_{NVP}), lung volume is above resting lung volume and the intrapulmonary pressure is positive (*a* in Fig. 2A). The next breath begins with an active expiration which generates a large positive pressure and reduces lung volume well below V_{LR} . Inspiration follows immediately. There is a transient phase as intrapulmonary pressure rapidly returns to atmospheric (*b* in Fig. 2A) before the negative pressures associated with lung inflation are generated by the inspiratory muscles. As inspiratory flow slows and inspiration terminates with the closing of the glottis, pressure again returns to atmospheric transiently (*c* in Fig. 2A) and positive pressure is again established in the lungs throughout the next breath-hold (*a* in Fig. 2A). This pressure-volume curve has been superimposed on the static pressure-volume relaxation curve for the intact system (P_{st}) and its mirror image ($-P_{st}$). The P_{st} curve represents the pressure generated by static lung inflation or

Fig. 1. Breathing patterns of spontaneously breathing geckos. Traces represent intra-abdominal pressure (P_r), ventilatory air flow and tidal volume from top to bottom, respectively. A and B are taken from one individual, C and D from a second individual. The time marker applies to all traces.

deflation, and the $-P_{\text{at}}$ curve represents the pressures which must be generated by the lizard to produce the same volume changes against an open glottis.

Once the glottis opens, expiration is rapid. Work must be done to overcome the elastic forces resisting deflation below V_{LR} , as well as to overcome flow-resistive forces. This work is offset to a small degree by elastic energy stored from the previous lung inflation. The magnitude of the components of expiratory and inspiratory work are shown in Fig. 2B and 2C, respectively. During the early phase of inspiration some work is done to overcome persistent activity of expiratory muscles, while throughout inflation work must be done to overcome flow-resistive forces and to overcome elastic forces resisting inflation. This mechanical work is partially offset by elastic energy stored during lung deflation. This graphical analysis is based on a similar analysis outlined by Agostoni, Campbell & Freedman (1970), modified for the pressure-volume profile associated with spontaneous breathing in this species. The magnitude of each of these components of work was determined by measuring the respective areas represented graphically by planimeter.

The measurements of the mechanical work of spontaneous breathing are given in Table 2. Using measured values of T_{tot} (hence f') and V_{T} for each breath analysed, the work of each breath can also be calculated from the work curves determined for continuous pump ventilation in anaesthetized animals by Milsom & Vitalis (1984). These values are listed for comparison.

Table 2. *Mechanical work of spontaneous breathing in the Tokay gecko*

Lizard	T_{tot} (s)	f' (min^{-1})	V_{T} (ml)	Work breath $^{-1}$	
				Measured ($\text{ml cmH}_2\text{O}^{-1} 100 \text{g}^{-1}$)	Calculated ($\text{ml cmH}_2\text{O}^{-1} 100 \text{g}^{-1}$)
1	1.8 ± 0.1	33 ± 2	1.61 ± 0.06	1.61 ± 0.15	$2.66 \pm 0.16^*$
2	1.0 ± 0.1	60 ± 6	0.75 ± 0.04	0.78 ± 0.06	0.88 ± 0.06
3	1.2 ± 0.1	50 ± 4	0.99 ± 0.06	1.41 ± 0.14	1.50 ± 0.16

Values are means \pm s.e. of six breaths/animal.

* Indicates calculated values were significantly different ($P \leq 0.05$) from measured values.

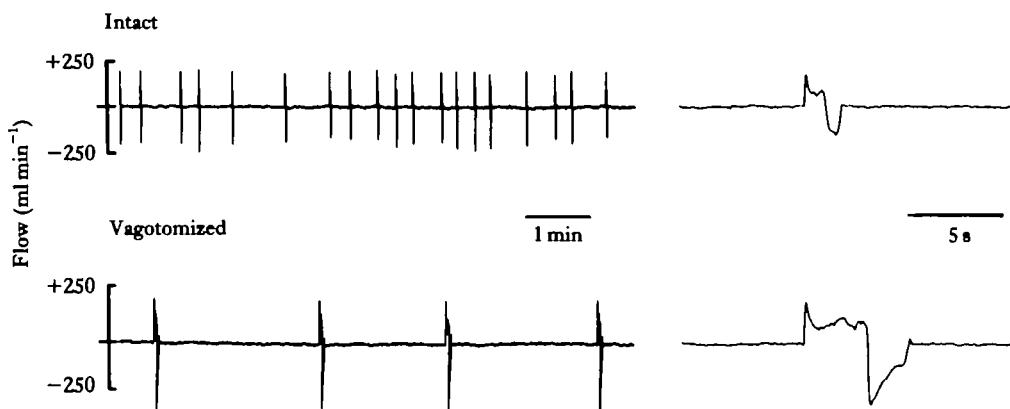


Fig. 3. Breathing traces of a Tokay gecko before and after bilateral vagotomy. The traces depict ventilatory air flow. The right hand traces show individual breaths with an expanded time scale.

Table 3. Values of respiratory variables before and following vagotomy in the Tokay gecko

		Intact	Vagotomized
V_T	(ml 100 g ⁻¹)	1.8 ± 0.2	6.5 ± 0.5*
f	(min ⁻¹)	2.2 ± 0.6	0.4 ± 0.5*
\dot{V}_E	(ml min ⁻¹ 100 g ⁻¹)	3.6 ± 0.6	2.6 ± 0.5
T_{tot}	(s)	2.1 ± 0.2	5.5 ± 0.3*
T_{NVP}	(s)	22 ± 13	181 ± 50*
f'	(min ⁻¹)	29 ± 1	11 ± 1*
$V_{I_{max}} s^{-1}$	(ml min ⁻¹)	213 ± 29	381 ± 33*
$V_{E_{max}} s^{-1}$	(ml min ⁻¹)	211 ± 15	259 ± 21
$W_{breath^{-1}}$	(ml cmH ₂ O ⁻¹)	2.3	38.3*
\dot{W}	(ml cmH ₂ O ⁻¹ min ⁻¹)	59.8	459.6*

* Indicates values recorded following vagotomy were significantly different ($P \leq 0.05$) from values recorded in intact animals.

Abbreviations as in Table 1.

Fig. 3 illustrates the effects of bilateral vagotomy on the breathing pattern of these lizards while the mean values of respiratory variables measured in the three animals before and following vagotomy are listed in Table 3. Vagotomy tremendously elevates V_T and prolongs both T_{tot} and T_{NVP} , greatly reducing f . The net result is a small reduction in \dot{V}_E . Despite the prolongation of T_{tot} , the elevated V_T is generated by enhanced peak inspiratory ($V_{I_{max}} s^{-1}$) and expiratory ($V_{E_{max}} s^{-1}$) flow rates. On the basis of the work/breath curves of Milsom & Vitalis (1984), this change in breathing pattern results in an almost 20-fold increase in the work required to take each breath, which is calculated to be a 7.5-fold increase in minute work (\dot{W}).

DISCUSSION

The breathing pattern of the Tokay gecko consists of single breaths or bursts of a few breaths separated by a highly variable period of breath holding. Although there are no values reported in the literature for this species, the values reported here are within the range of values of f and weight-specific values of V_T reported for other lizard species (Bennett, 1973; Wood, Glass & Johansen, 1977; Wood, Johansen, Glass & Maloiy, 1978; Nielsen, 1961; Cragg, 1978). The measured increases in \dot{V}_E and calculated increases in \dot{V}_A show a Q_{10} of 2.7 to 2.8, similar to the expected Q_{10} of CO₂ production. This is atypical of reptiles in general but similar to values reported for varanid lizards (Wood *et al.* 1977). Although blood gases were not measured in this study, these results would suggest that arterial P_{CO₂} and pH should change very little with increasing temperature and that this species may regulate a constant arterial pH rather than a constant degree of relative alkalinity of blood relative to the neutral pH of water (Howell & Rahn, 1976). There is no doubt that the use of a head-body plethysmograph for the measurement of V_T leads to higher values of many respiratory variables than would be measured in undisturbed individuals not thus confined (Cragg, 1978). To minimize such effects, the animals used in this study were given

ample time to adjust to the plethysmograph box and care was taken to ensure that all animals were resting quietly at the time measurements were made. As a consequence, both the resting breathing pattern and the trends shown in the respiratory responses to warming in this study are believed to be accurate reflections of the breathing patterns which would occur in fully undisturbed individuals. These measurements indicate that the primary response to warming is a reduction in the pause between breaths and maintenance of a relatively constant tidal volume and breath duration.

Measurements of the mechanical cost of spontaneous breathing were extremely similar to values calculated for breaths of the same V_T and T_{tot} from the work curves generated during pump ventilation of anaesthetized animals (Milsom & Vitalis, 1984). This indicates that the pulmonary mechanics were not significantly different in the two studies and that predictions based on measurements of mechanical work in anaesthetized animals should apply to awake, spontaneously-breathing individuals. Because the dead space volume of the respiratory system is fixed, anatomically, there are limits to how small V_T may be reduced before alveolar ventilation volume ($V_A = V_T - V_D$) becomes disproportionately small and alveolar ventilation is jeopardized. It was shown in the previous paper that for any given level of \dot{V}_A , there was an optimum combination of f and V_T at which the mechanical work of breathing was a minimum. At lower ventilation frequencies, the concomitant increase in V_T led to a dramatic increase in mechanical work, while at frequencies above these optima the relative cost of dead space ventilation increased rapidly, more than offsetting any energy savings due to further reductions in V_T . On the basis of similar relationships described in mammals, Otis (1954) has derived theoretical equations which predict that for a purely elastic system, the optimum combination of V_T and f occurs when $V_A = V_D$, that is, when $V_T = 2V_D$. Given that the major component (>70%) of the mechanical cost of breathing in this species is required to overcome elastic forces, it is interesting to note that V_T was tightly maintained at 1.0–1.2 ml 100 g⁻¹ in the gecko while V_D was measured at 0.50 ml 100 g⁻¹. It thus appears that the regulation of V_T in this species is consistent with theoretical predictions.

Although breathing is arrhythmic and respiratory frequency relatively low in this species, breathing is a rather explosive event and the low frequencies stem from the prolonged periods of breath holding. In terms of the mechanical cost of ventilating the lungs, only the intervals of active expiration and inspiration are important. Little or no work is done to maintain inspiration volume after the glottis closes and the respiratory muscles relax. As a consequence, it is the instantaneous breathing frequency (f'), which is calculated from the periods of active ventilation ($f' = 60 / (T_I + T_E)$), which is important in considerations of the work of breathing. There are, however, two ways to assess the significance of the measured values of f' (or T_{tot}) in terms of mechanical work; on the basis of individual breaths considered as isolated events and on the basis of each breath as part of a continuous breathing pattern.

If each breath is considered as an isolated event, the optimum instantaneous breathing frequency in this species can be predicted from work breath⁻¹ curves (Fig. 4) derived from data presented in the previous paper (Milsom & Vitalis, 1984). It can be seen in Fig. 4 that to maintain a minute ventilation of at least 10 ml min⁻¹ 100 g⁻¹ or an alveolar minute ventilation of 6 ml min⁻¹ 100 g⁻¹ (the resting \dot{V}_E and \dot{V}_A respectively at 24°C) and a V_T of 1 ml, there is an optimum frequency of 32 breaths min⁻¹

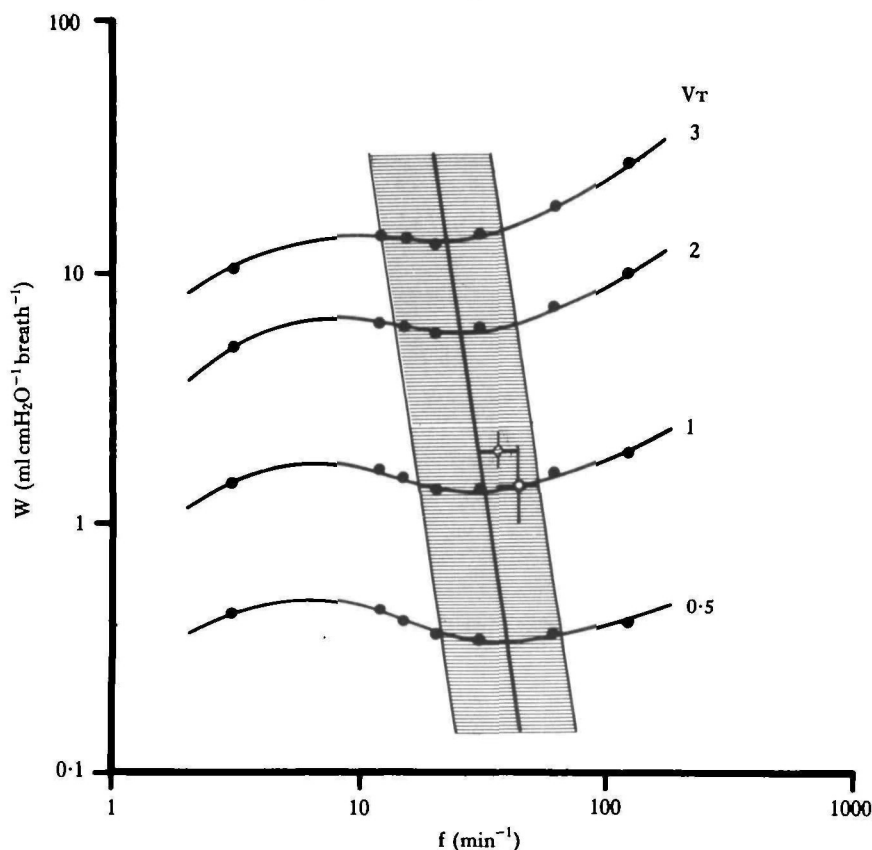


Fig. 4. The relationship between total work breath⁻¹ (W) and ventilation frequency (f) for different levels of tidal volume (V_T) in ml. Data points represent mean values from five animals, taken from Milsom & Vitalis (1984). The central vertical line joins points of minimum W breath⁻¹ on each V_T isopleth above 10 breaths min⁻¹. The hatched area represents the range within which W is less than 10% above minimum. The diamond represents the mean \pm s.e. of values of f and V_T measured in spontaneously breathing animals at 24°C, the open circle, values recorded at 34°C.

at which the cost per breath is minimum. This indicates that it is less expensive to take 10 breaths of 1 ml volume at an instantaneous rate of 32 min⁻¹ than to breathe continuously at 10 breaths min⁻¹, although both patterns would move the same amount of air. At 34°C when \dot{V}_E is elevated to 28 ml min⁻¹ 100 g⁻¹, the optimum pattern would be predicted to be one in which the lizard took 28 breaths of 1 ml volume at a rate of 32 breaths min⁻¹. At this stage breathing would be almost continuous. The values recorded in this study and the changes which occurred with warming coincide very closely with these predictions.

Since T_{tot} and V_T appear to be tightly regulated in the Tokay gecko, if breathing were to become continuous by simply eliminating all periods of breath holding, the resulting breathing pattern would yield a V_T of 1.0 ml 100 g⁻¹, an f of 37–40 breaths min⁻¹, and a \dot{V}_A of 18.5–20 ml min⁻¹ 100 g⁻¹. Using the minute work curves derived in the previous study for a \dot{V}_A of 20 ml min⁻¹ 100 g⁻¹ and assuming a continuous breathing pattern, an optimum combination of 1.03 ml 100 g⁻¹ V_T and an f of 38 breaths min⁻¹ is obtained. The data fit these predictions even more closely.

The outcome of this analysis appears to argue strongly for some form of physiological control of the breathing pattern in terms of the mechanical cost of breathing. Note, however, that the data argue just as strongly for the independent control of f' and of V_T to generate optimum single breaths as they do for the inter-related control of both variables to produce an optimum combination that, in a continuous breathing pattern, would minimize the mechanical costs at each level of \dot{V}_A .

It should be noted that in the calculations of \dot{V}_A described above, V_D is equal only to the anatomical dead space of the respiratory passages. The amount of physiological dead space present due to the saccular nature of the lung has not been taken into account and thus the values of \dot{V}_A will be overestimates of the true \dot{V}_A . Furthermore, this physiological dead space will vary with breath-holding time. Increased respiratory frequency will decrease breath-hold time and, due to the decreased time available for mixing of luminal (dead space) and faveolar gas, physiological dead space should increase. This has been shown to be the case in varanid lizards where temperature-induced increases in minute ventilation significantly increase total dead space ventilation (Wood *et al.* 1977). Thus the increase in \dot{V}_A with increasing temperature calculated here will also be an overestimate. At present there is insufficient information available with which to quantify physiological dead space and any frequency-dependent shifts in total dead space in this species. Since all calculations in the previous study also assumed V_D was only equal to the anatomical dead space of the respiratory passages, the prediction of an optimum combination of f and V_T will be accurate and unaffected by such considerations.

In mammals, it has been difficult to postulate, let alone demonstrate, physiological mechanisms involved in establishing optimal breathing patterns in terms of mechanical work loads. Such control would involve a complicated integration of information (Agostoni *et al.* 1970). It has been shown that spontaneous breathing frequency in mammals also corresponds closely with the frequency at which the minimum average force is required to power ventilation (Mead, 1960), and since average muscle force involves a simple method of detection and can be more easily related to O_2 consumption, it has been suggested that mammals regulate breathing frequency in accordance with minimum average muscle force (Mead, 1960; Agostoni *et al.* 1970). It should be noted that, as in mammals, bilateral vagotomy in the gecko leads to large changes in the breathing pattern which tremendously increase both the mechanical work of taking single breaths (19-fold increase) and the minute work which would be associated with continuous breathing (7.5-fold increase). As these animals lack a diaphragm and breathing is powered solely by the muscles of the body wall, vagotomy should not affect detection of the average muscle force required for ventilation. Denervation of arterial chemoreceptors innervated by the vagosympathetic trunk remains a possible contributing factor to the changes seen in the breathing pattern following vagotomy, although it seems doubtful that sensory input from arterial chemoreceptors could regulate airflow rates and the timing of inspiration and expiration during an ongoing breath. The evidence thus suggests that it is sensory information arising from pulmonary mechanoreceptors which is involved in regulating V_T and f' in these lizards and that this information may be integrated in such a way as to detect and minimize the mechanical work of breathing.

Throughout the lower vertebrates arrhythmic breathing is the norm (see Shelton

& Boutilier, 1982; Shelton, Jones & Milsom, 1984 for reviews). The primary, regulated variable in these breathing patterns is the duration of the maintained inspiration (T_{NVP}) between breaths or groups of breaths. Both tidal volume and mean breath duration remain relatively constant when ventilation volume is increased in response to such stimuli as warming or inhalation of hypercarbic or hypoxic gas mixtures (Glass & Johansen, 1976; Milsom & Jones, 1980; Benchetrit & Dejours, 1980; Boutilier, 1981). Perry & Duncker (1980) demonstrated that a good correlation exists between these resting breathing patterns and lung compliance in reptiles. Species with relatively stiff lungs tend to use a higher frequency and lower tidal volume breathing pattern than species with relatively high lung compliances, which exhibit a lower breathing frequency and higher tidal volume. Dynamic pulmonary mechanics will reflect the static mechanics of the respiratory system, and our data suggest that it is the dynamic mechanics which may determine breathing patterns. The data presented here suggest that for animals with low metabolic rates, where continuous breathing is not required to meet metabolic demands, the most efficient breathing pattern is an arrhythmic breathing pattern. Although it is not totally clear what combination of sensory inputs initiate and terminate breathing (Lenfant & Johansen, 1968; Lenfant, Johansen, Petersen & Schmidt-Nielsen, 1970; Toews, Shelton & Randall, 1971; Burggren & Shelton, 1979; Ackerman & White, 1979; Boutilier, 1981), once breathing is initiated, the breath length and tidal volume appear to be regulated to optimal values which reduce the mechanical work of taking each breath. In response to an increase in respiratory drive, it is energetically least expensive to increase \dot{V}_E by taking more breaths at this optimum combination of V_T and f' , thus altering only T_{NVP} , than by either increasing V_T or by shortening the breath duration. This appears to be the adaptive strategy adopted by these animals.

There is one series of observations which is inconsistent with such an hypothesis of ventilatory control. Exercise in many reptiles brings about an increase in minute ventilation primarily through increases in tidal volume (Wood & Lenfant, 1976; Cragg, 1978). Perry & Duncker (1980) have argued that although such changes are mechanically more expensive than changes in respiratory frequency, strenuous exercise in reptiles is generally transient and associated with fleeing from danger or prey capture where conserving work is not of primary concern. Although such an argument does not address the question of why differential responses exist to different forms of metabolic stress, it does point out that the consequences are not great for most species. Other considerations, such as the linkage of locomotor and respiratory movements may be of more importance in determining breathing patterns at such times. It is interesting to note, however, that species which are known to undergo prolonged bouts of activity do deviate from the trend mentioned above. Varanid lizards, which are renowned for their high metabolic rate and active predatory behaviour, increase both V_T and breathing frequency during activity (Wood *et al.* 1977) while marine turtles, which are capable of prolonged periods of aerobic activity, increase \dot{V}_E primarily by increases in breathing frequency during spontaneous activity (Prange & Jackson, 1976; Jackson & Prange, 1979).

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