

## PASSIVE BODY MOVEMENT AND GAS EXCHANGE IN THE FRILLED LIZARD (*CHLAMYDOSAURUS KINGII*) AND GOANNA (*VARANUS GOULDII*)

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### Summary

The sacculus lung in lizards is large and highly compliant compared with mammalian lungs, and these properties led us to question to what extent body movements could affect pulmonary gas exchange and the partial pressure of arterial blood gases. Specimens of two species of lizards, the frilled lizard (*Chlamydosaurus kingii*, approximately 600 g body mass) and the goanna (*Varanus gouldii*, approximately 1400 mass), were anaesthetised, maintained at approximately 36 °C and mechanically hyperventilated to lower the arterial partial pressure of carbon dioxide ( $P_{aCO_2}$ ) to below apnoeic threshold. Respiratory system compliance ( $C_{rs}$ ) averaged 0.112 ml kg<sup>-1</sup> Pa<sup>-1</sup> (goanna) and 0.173 ml kg<sup>-1</sup> Pa<sup>-1</sup> (frilled lizard), which is approximately 7–11 times the predicted value for a mammal of similar body mass. Mechanical ventilation was interrupted, and the changes in  $P_{aCO_2}$  and

$P_{aO_2}$  were monitored over the following 10 min as the animal was either left immobile or subjected to imposed lateral body movements. During the post-hyperventilation apnoea,  $P_{aCO_2}$  increased whereas  $P_{aO_2}$  did not always fall, sometimes even increasing, suggesting a reduction in the importance of pulmonary shunts. No significant differences were detected in the time course of changes in arterial blood gas levels or heart rate between runs with or without body movement. We conclude that in these species of lizards, despite the high  $C_{rs}$ , lateral chest wall movements neither hinder nor favour pulmonary gas exchange.

Key words: locomotion, pulmonary function, reptile, reptilian respiration, respiratory compliance, cardiac shunt, right-to-left shunt, *Chlamydosaurus kingii*, *Varanus gouldii*.

### Introduction

In most reptiles, the respiratory system consists of two large sacculus lungs with numerous variations in the degree of compartmentalisation (Tenney and Tenney, 1970; Perry, 1992). The large dimensions find a functional correlate in the mechanical properties of the respiratory system and, in particular, in its passive compliance. In fact, in both snakes and lizards, the compliance of the respiratory system can be several orders of magnitude higher than that of mammals of similar body mass. However, large variations occur that are probably related to the degree of complexity of lung structure (Gratz, 1978; Perry and Duncker, 1978, 1980; Milsom, 1989; Perry, 1992).

A large and highly compliant respiratory system easily accommodates the changes in body shape required for locomotion and various forms of behavioural display, and also contributes to the regulation of buoyancy in aquatic reptiles. At the same time, the compromise of lung structure and function between gas exchange and non-ventilatory tasks raises the issue of what impact changes in body shape may have on pulmonary gas exchange. In the garter snake (*Thamnophis sirtalis*), when body posture was passively changed from the straight to the coiled position, the compliance of the respiratory system was halved (Bartlett *et*

*al.* 1986). It is not clear whether changes in body configuration, which modify the mechanical properties of the respiratory system, have any impact on gas exchange. Since the distortion of lung parenchyma and vessels could interfere with the regional distribution of ventilation-perfusion, any pressure applied to the sacculus lungs could favour gas mixing and reduce stratification (Powell and Gray, 1989), thus improving the effectiveness of gas exchange.

In the present study, we attempted to estimate the effect of body motion on arterial blood gases in two species of lizards: the frilled lizard (*Chlamydosaurus kingii*, an agamid with unicameral lungs) and Gould's goanna (*Varanus gouldii*, a varanid with multicameral lungs). The rate of rise in arterial  $P_{CO_2}$ , which reflects the rate of CO<sub>2</sub> elimination, and the drop in arterial  $P_{O_2}$ , reflecting the rate of O<sub>2</sub> uptake at the level of the pulmonary capillaries, were measured in anaesthetised intubated lizards during post-hyperventilation apnoea in the presence or absence of artificially imposed rhythmic lateral body movements.

### Materials and methods

Experiments were conducted on five specimens of

*Chlamydosaurus kingii* (mass  $600 \pm 48$  g, mean  $\pm$  S.E.M.) and four specimens of *Varanus gouldii* ( $1378 \pm 91$  g) after approval by the Animal Ethics Committee of La Trobe University. The lizards were captured in the surroundings of Darwin, Northern Territory, Australia (under appropriate wildlife permits), and delivered by air-freight to the laboratory at La Trobe University.

The lizard was intubated and anaesthetised with fluothane (induction 5%, maintenance 2%) in  $O_2$ . The laryngeal cannula was connected to a mechanical ventilator *via* a T-piece. One arm of the T-piece was connected to a water manometer for measurements of airway pressure ( $P$ ). Stability of  $P$  when the expiratory line was occluded with the respiratory system inflated above the passive volume indicated an absence of leaks around the larynx. On some occasions, dental casting polymer (Impregum, ESPE) was used to guarantee a proper seal. Cloacal temperature ( $T_{cl}$ ) was monitored using a thermocouple and maintained at  $36^\circ C$  by radiant heat. A polyvinyl catheter prewashed with heparin solution was inserted into the carotid artery *via* a small incision in the neck and connected to a three-way stopcock for the purpose of collecting arterial blood samples. Heart rate ( $f_H$ , beats  $min^{-1}$ ) was calculated from the cardiogenic oscillations in the blood meniscus within the catheter, over 15 s intervals.

To measure blood gas levels, a volume of blood approximately equal to four times the catheter volume was withdrawn into a separate syringe. A  $200 \mu l$  sample of blood was then collected and immediately analysed for arterial partial pressure of  $O_2$  ( $P_{aO_2}$ ) and  $CO_2$  ( $P_{aCO_2}$ ) in a blood gas analyser (BMS-3, Radiometer) set at  $36^\circ C$ . Calibrations were performed before and during the experiment. The blood was then returned to the animal to ensure minimal blood volume loss during the experiment.

Experiments were performed with the animal in the prone position on a smooth surface, with the forelimbs directed forwards and the hindlimbs backwards. The pelvic region was slightly lifted and positioned over a glass support, which could be made to slide easily on either side of the longitudinal axis of the lizard. Its motion, therefore, determined a lateral movement of the whole chest wall that pivoted approximately around the pectoral girdle. The movement consisted of an excursion of the longitudinal axis of  $35^\circ$  in either direction and was obtained by manually moving the glass support at the rate of one full excursion every 2 s under the guide of a metronome. In this way, movement occurred with no force applied directly on the chest wall, therefore avoiding any regional compression.

At the onset of the experiment, the animal was hyperventilated (peak airway pressure 98 Pa, at  $20$  breaths  $min^{-1}$ ) to abolish spontaneous breathing. During the post-hyperventilation apnoea, the lizard's lungs were inflated to approximately 500–600 Pa to standardise lung volume history and to expand the lungs fully. Upon passive deflation to the resting volume,  $P$  was measured by injecting known volumes (10 or 20 ml) with a calibrated syringe and waiting for  $P$  to decay as a result of stress relaxation, which in lizards can be substantial (Milsom, 1989).

Artificial ventilation was resumed again and maintained until  $P_{aCO_2}$  was approximately 2 kPa. The ventilator was then disconnected and the T-piece of the laryngeal cannula rapidly

connected to a steady flow of humidified air enriched with  $O_2$  (98%) with an expiratory load which provided an end-expiratory positive pressure ( $P_{EEP}$ ) of 98 Pa. A constant airflow of  $200$  ml  $min^{-1}$  was maintained using a calibrated flowmeter. The airways therefore remained open and the lungs were maintained distended slightly above the passive resting volume of the respiratory system. By maintaining a constant flow of gas at the laryngeal cannula, the alveolar side retained a constant  $O_2$  and  $CO_2$  mixture and a constant lung volume. Measurements of  $P_{aO_2}$ ,  $P_{aCO_2}$ ,  $T_{cl}$  and  $f_H$  were taken during the ensuing apnoea at 2.5, 5, 7.5 and 10 min. A series of experiments were performed (1) with no movement, (2) with body movement, and (3) with no movement. The results of experiments 1 and 3 were then averaged and compared with those of experiment 2.

In three frilled lizards, two additional experiments were performed, one with and one without body movement, with the respiratory system inflated at a  $P_{EEP}$  of 98 Pa but with the airways kept closed throughout. In this case, lung volume decreases at first during the apnoea because, during the equilibration of the alveolar gas with the venous blood, the drop in  $P_{aO_2}$  far exceeds the increase in  $P_{aCO_2}$  and, later, because the rate of  $O_2$  consumption exceeds the rate of  $CO_2$  production.

At the end of the experiments, the arterial catheter was removed, the wound closed with separate stitches and anaesthesia discontinued. The lizards were allowed 3 days to recover before being shipped back to the Northern Territory and freed into their home environment.

Data are presented as mean values  $\pm 1$  S.E.M. Blood gas values between runs with and without body movement were statistically analysed by repeated-measures analysis of variance

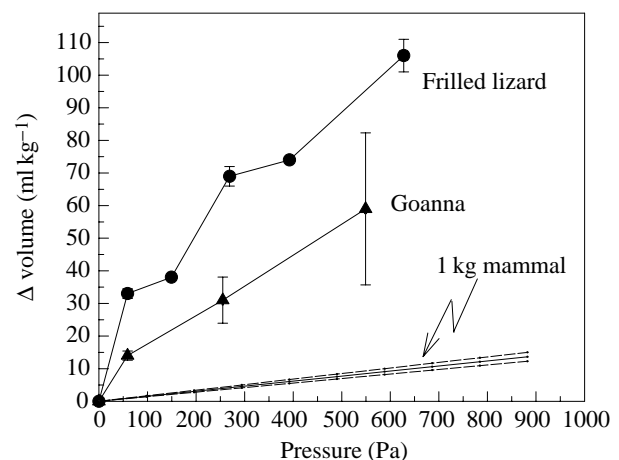


Fig. 1. Passive static pressure–volume ( $P$ – $V$ ) curve of the respiratory system in frilled lizards (*Chlamydosaurus kingii*) and goannas (*Varanus gouldii*), obtained by lung inflation from the resting volume ( $\Delta$  volume). Values are means  $\pm 1$  S.E.M.,  $N=5$  for the frilled lizard,  $N=4$  for the goanna. For comparison, the  $P$ – $V$  curve of a 1 kg mammal, as predicted from allometric relationships ( $C_{rs}=0.0154M$ , where  $M$  is the mass in kg) is also indicated (continuous line) with its 95% confidence intervals (broken lines). In these lizards, the compliance of the respiratory system was 7–11 times larger than in a mammal of the same body mass.

(ANOVA) followed by *post-hoc* contrasts using the Bonferroni limitation for the absolute values at 0 min (baseline), 2.5, 5, 7.5 and 10 min of apnoea and for the corresponding changes from baseline. This latter approach was to take into account occasional small difference in  $P_{aCO_2}$  at the start of the runs. A difference was considered statistically significant at  $P < 0.05$ .

**Results**

*Compliance of the respiratory system ( $C_{rs}$ )*

Fig. 1 presents mean values for the passive pressure–volume relationships obtained by inflation from the resting volume of the respiratory system. As expected, the curves tended to be slightly convex with respect to the pressure axis; hence, the value of  $C_{rs}$  varied according to the pressure range considered for the calculation. Above 500 Pa,  $C_{rs}$  averaged  $0.112 \text{ ml kg}^{-1} \text{ Pa}^{-1}$  in the goannas and  $0.173 \text{ ml kg}^{-1} \text{ Pa}^{-1}$  frilled lizards. The value of  $C_{rs}$  of a 1 kg adult mammal, averaged from a number of inter-species allometric curves (Mortola, 1987), is  $0.015 \text{ ml Pa}^{-1}$ . Hence,  $C_{rs}$  of these lizards was approximately 7 and 11 times, respectively, the value of a similarly sized mammal.

*Post-hyperventilation apnoea*

Cloacal temperature was maintained constant at

approximately  $36^\circ\text{C}$  in both species irrespective of the type of experiment. During the 10 min of post-hyperventilation apnoea,  $P_{aCO_2}$  invariably increased. In frilled lizards, it rose from  $1.87 \pm 0.13$  to  $3.60 \pm 0.13 \text{ kPa}$  during the no-movement experiments and from  $1.87 \pm 0.13$  to  $3.47 \pm 0.13 \text{ kPa}$  in experiments with body movement. The corresponding values in goanna were an increase from  $2.27 \pm 0.40$  to  $3.47 \pm 0.53 \text{ kPa}$  in the absence of body movement and from  $1.99 \pm 0.53$  to  $3.20 \pm 0.40 \text{ kPa}$  when body movements were imposed. There was no difference ( $P < 0.05$ ) in the  $P_{aCO_2}$  change between experiments with and without body movement in either species (Fig. 2B). A similar conclusion could be reached by comparing the change in  $P_{aCO_2}$  from baseline ( $\Delta P_{aCO_2}$ ) (frilled lizard,  $1.73 \pm 0.27 \text{ kPa}$  without body movement and  $1.47 \pm 0.13 \text{ kPa}$  with body movement; goanna,  $1.33 \pm 0.13 \text{ kPa}$  without body movement and  $1.20 \pm 0.40 \text{ kPa}$  with body movement).

$P_{aO_2}$  (Fig. 2A) showed a much greater variability between animals than did  $P_{aCO_2}$  (Fig. 2B), partly because the latter, but not the former, was the controlled variable that initiated the post-hyperventilation runs. In the goanna,  $P_{aO_2}$  decreased both with and without body movement, although the drop was significantly smaller in the former case ( $-3.07 \pm 1.33 \text{ kPa}$  versus  $-8.26 \pm 0.8 \text{ kPa}$  without body movement,  $P < 0.05$ ). This was accompanied by a trend for heart rate to decrease less towards the end of the apnoea

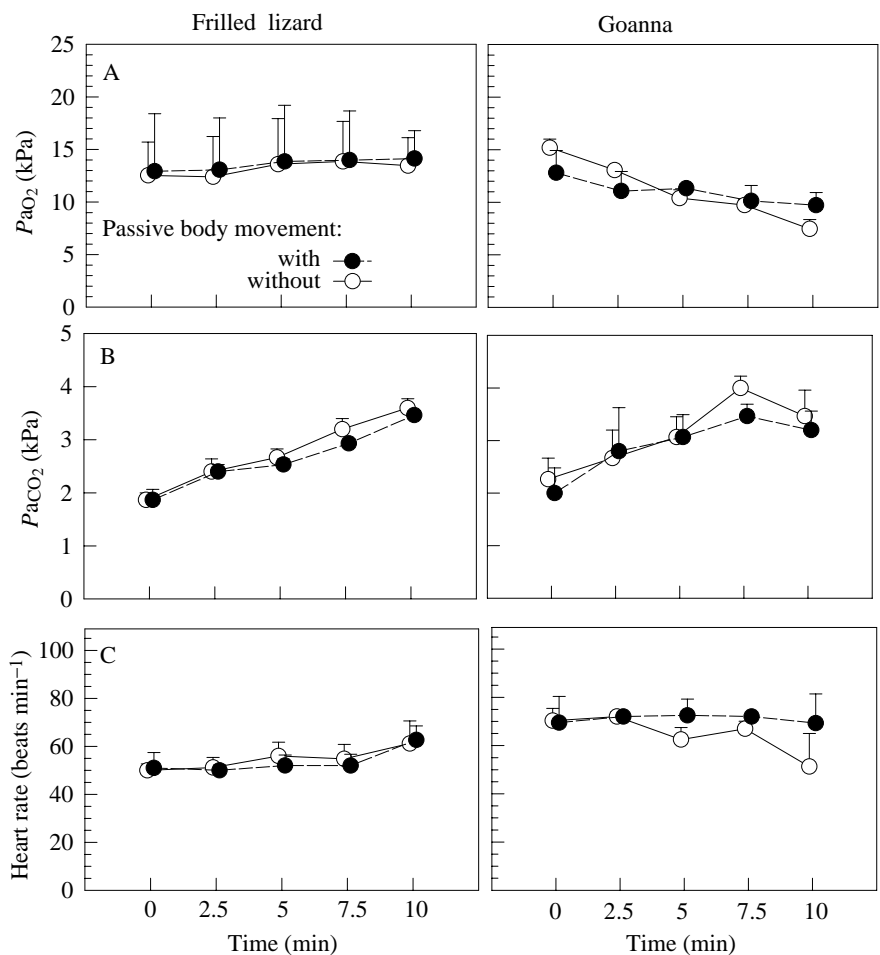
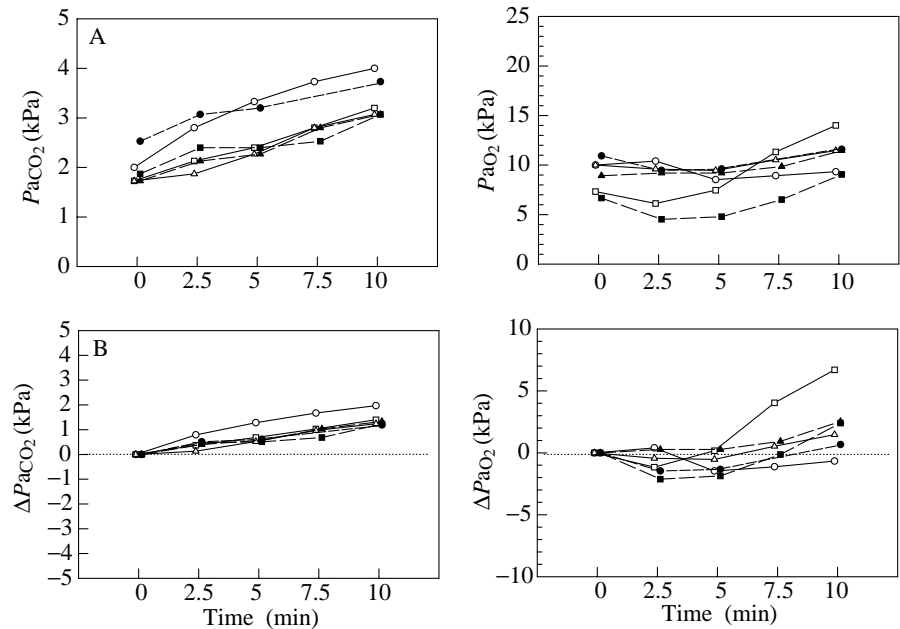


Fig. 2. Time course of changes in the levels of arterial oxygen ( $P_{aO_2}$ ) (A) and carbon dioxide ( $P_{aCO_2}$ ) (B) and heart rate (C) during 10 min of post-hyperventilation apnoea with (filled symbols) or without (open symbols) passive lateral body movements. In neither the frilled lizard (*Chlamydosaurus kingii*) nor the goanna (*Varanus gouldii*) did any of the curves differ significantly between the two conditions. Values are means  $\pm 1$  S.E.M.,  $N=5$  for the frilled lizard,  $N=4$  for the goanna.

Fig. 3. Data from three frilled lizards (*Chlamydosaurus kingii*) during post-hyperventilation apnoea, airways closed, in the absence (open symbols, continuous lines) and in the presence (filled symbols, dashed lines) of passive lateral body movements. (A) Absolute values of arterial partial pressure of CO<sub>2</sub> ( $P_{aCO_2}$ ) and O<sub>2</sub> ( $P_{aO_2}$ ) during the 10 min apnoea. (B) Values represented as changes ( $\Delta P_{aCO_2}$  and  $\Delta P_{aO_2}$ ) from baseline (dotted lines). Each lizard is represented by a different symbol. No significant difference occurred between experiments with and without body movement. Note that  $P_{aO_2}$  often rose towards the end of the apnoea, sometimes even above the pre-apnoea value.



compared with the runs without body movement ( $-23 \text{ beats min}^{-1}$ ) (Fig. 2C). In frilled lizards,  $P_{aO_2}$  did not fall and heart rate did not change significantly in either type of run.

#### Post-hyperventilation apnoea with closed airways

These experiments were performed in only three frilled lizards (cloacal temperature  $36^\circ\text{C}$ ) and the individual data are presented in Fig. 3. The general pattern of changes in blood gas levels during these experiments was very similar to that observed with the airways open, with the rise in  $P_{aCO_2}$  not being significantly different between experiments with and without body movement. On average,  $P_{aO_2}$  was maintained throughout the whole apnoea, although it often tended to decrease at first and to increase later and, in several cases, it even exceeded the pre-apnoea (baseline) value by the end of the experiment. Heart rate was maintained or slightly increased by the end of the apnoea, irrespective of the type of run (results not shown).

#### Discussion

Although no data were specifically available for the frilled lizard and goanna, the finding of a high mass-specific  $C_{rs}$  was not surprising since this supported the hypothesis of a large and compliant respiratory system in reptiles compared with that of mammals of similar body mass (Milsom, 1989). A highly compliant respiratory system provides minimal constraint to even major changes in body posture and shape. In addition, the minimal pressures required for its inflation imply a very low cost of breathing. However, such a system is more prone to distortion and its gas exchange function is more likely to be subjected to interference by non-ventilatory tasks. Any force applied to the lungs could enhance the effectiveness of gas exchange by improving gas mixing and could also compromise the distribution of ventilation and perfusion. In the reptilian sacculus lung, it appears reasonable that the former may prevail when applied to the sacculus regions not directly involved in gas

exchange and that the latter could prevail when distorting forces are applied to the appropriate gas exchange areas. It is difficult to evaluate the magnitude of these factors during the pattern of movement that we imposed on the lizard, and it would be even more complex to extrapolate this to the chest wall distortion occurring during normal locomotion in lizards. In fact, although the activity and function of the muscles involved in lizard locomotion have been studied (Carrier, 1990; Ritter, 1996), the nature and magnitude of compressive and expansive forces on the lungs during locomotion have never been estimated. We attempted to avoid any direct external compression, relying entirely on the mechanical inertia of the internal viscera for gas mixing. We found no appreciable effects on blood gas levels, possibly indicating that, under the present experimental conditions, mechanisms favouring and hindering gas exchange cancelled each other on average. However, the possibility that the results might have been different had the motion protocol been different, either in pattern or in rate, cannot be excluded.

Our experimental approach was based on measurements of  $P_{aCO_2}$  instead of  $P_{aO_2}$  because, within the physiological range,  $P_{aCO_2}$  is almost directly proportional to the volume of CO<sub>2</sub> in the blood. The curvilinearity of the content/partial pressure relationship for O<sub>2</sub> precludes any proportionality between  $P_{aO_2}$  and changes in O<sub>2</sub> content, especially if, as in the present case, the animal is breathing an O<sub>2</sub>-enriched gas. Indeed, during hyperoxic breathing,  $P_{aO_2}$  can show enormous variations for minimal changes in arterial O<sub>2</sub> content. In this respect, the significantly greater fall in  $P_{aO_2}$  of the goannas during experiments without body movements compared with those with body movements is of little importance, since it can be explained entirely by the difference in  $P_{aO_2}$  at the onset of the apnoea between the two experiments. In addition, the existence in reptiles of pulmonary and cardiac right-to-left shunts, the former often of variable degree (Seymour, 1989), increases the difficulties of interpreting  $P_{aO_2}$  as a parameter reflecting

pulmonary gas exchange (Wang and Hicks, 1996) whereas  $P_{aCO_2}$  is hardly affected by shunted blood. The assumption of a complete stability in the metabolic processes in our experiments seems a reasonable one, considering that the preparation used was anaesthetised and at constant body temperature. Furthermore, the precaution of averaging the data from experiments 1 and 3 (without body motion) for the comparison with experiment 2 (with body motion) should have excluded any possibility of subtle time-dependent changes in metabolic rate.

The existence of major cardiac and pulmonary right-to-left shunts in the reptilian circulation explains why baseline  $P_{aO_2}$  rarely exceeded 13.33 kPa, even when the lizards were hyperventilated with an  $O_2$ -enriched gas mixture. Large right-to-left shunts have been reported during both air- and  $O_2$ -breathing in other species of lizards (Hlastala *et al.* 1985; Ishimatsu *et al.* 1988). What seemed puzzling was the finding that  $P_{aO_2}$  remained approximately constant throughout the apnoea and in some cases even increased, with a possible increase in heart rate. This should imply a reduction in the amount of shunted blood that more than compensated for the expected worsening of the hypoxaemia due to oxygen consumption. An analogous condition is that of some aquatic reptiles in which, during dive-induced apnoea,  $P_{aO_2}$  can actually rise because of an increase in pulmonary blood flow and a reduction in the amount of blood shunted (Seymour and Webster, 1975; Burggren and Shelton, 1979; Seymour *et al.* 1981). The sensors mediating these readjustments in pulmonary flow could involve blood chemoreceptors as well as chemo- and mechanoreceptors in the airways (Fedde *et al.* 1977). In the closed system of the diving condition lung, volume is reduced because the alveolar/mixed venous pressure equilibration involves a larger transfer of  $O_2$  from the airways to the vascular bed than of  $CO_2$  in the opposite direction. This would also be the case in the present experiments where, during apnoea, the airways were kept closed. However, an involvement of lung mechanoreceptors in shunt regulation seems unlikely. In fact, the same phenomenon of  $P_{aO_2}$  stability during apnoea was observed in the majority of our experiments in which the airways were open; in this case, especially after ventilation with  $O_2$ -enriched gas, lung volume does not change. The maintenance of  $P_{aO_2}$  means that it cannot itself have been an important stimulus and therefore one can hypothesise that the rise in  $P_{aCO_2}$  may have been the important factor in the shunt regulation of the lizard.

In conclusion, frilled lizards and goannas have high  $C_{TS}$  values. From an analysis of the changes in  $P_{aO_2}$  and  $P_{aCO_2}$  during post-hyperventilation apnoea, there seem to be important right-to-left shunts, which decrease in importance with the increase in  $P_{aCO_2}$ . Passive body movements do not modify this pattern and neither hinder nor facilitate gas exchange.

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