

Lung ventilation during walking and running in four species of lizards

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Abstract. The relationship between locomotion and aspiration breathing was investigated in the lizards *Iguana iguana*, *Ctenosaura similis*, *Varanus exanthematicus* and *Varanus salvator*, and the quail *Coturnix coturnix*. Respiratory air-flow during walking and running on a 7.3 m track or on a treadmill was measured with a bidirectional flow meter attached to one nostril. In all four species of lizards, lung ventilation drops markedly during locomotion. Tidal volume decreases as speed increases, often by more than an order of magnitude at intermediate and high speeds, and the rate of decline is most pronounced at the lowest speeds. Minute ventilation peaks at or before the reported maximum aerobic speed and decreases at higher speeds. In contrast, quail increase their minute ventilation during running.

Several observations support the hypothesis that the aspiration of lizards is mechanically constrained by locomotion which employs lateral vertebral bending and sprawling posture. 1. Minute ventilation decreases as running speed increases. 2. Disruption of ventilation is temporally coincident with the locomotor movements. 3. During running the largest breaths correspond to the strides of longest duration or to brief pauses in the locomotor movements.

Key words: Lung ventilation – Locomotion – Lizards – Mechanical constraint

Introduction

Few studies have addressed the issue of lung ventilation during locomotion in tetrapods. Vigorous

locomotion is the activity most likely to place the largest demands on the ventilatory system. Moreover, the postcranial organization of amniotes seems to entail a mechanical linkage between the locomotor and respiratory systems. A strong mechanical coupling is suggested by the tight phase locking of the locomotor and respiratory cycles of running mammals (Hornicke et al. 1983; Bramble and Carrier 1983; Bramble 1986), flying birds (Berger et al. 1970) and bats (Suther et al. 1972; Thomas 1981; Carpenter 1986). Green sea turtles are the only ectothermic tetrapods for which we have equivalent information (Jackson and Prange 1979). During terrestrial locomotion, these turtles alternate periods of vigorous activity without breathing with periods of rest during which they breathe. Jackson and Prange suggest that these animals may not be able to locomote and breathe at the same time, because some of the same muscles are involved in both processes. This raises questions about ventilation in other tetrapods.

Lizards are costal breathers (Wood and Lenfant 1976). They lack additional ventilatory muscles (see Nishi 1938), such as the diaphragmaticus of mammals or the functionally analogous muscles of crocodilians (Gans and Clark 1976). The volume of the thorax appears to be changed solely by active movements of the ribs. However, the ribs and trunk musculature of lizards also play an important role in locomotion. The major part of the axial musculature and some of the appendicular muscles attach directly to the ribs. Transverse processes of the vertebrae are short (see Hoffstetter and Gasc 1969; Romer 1956), so that not only the hypaxial but also the bulk of the epaxial muscles insert directly on the ribs (Gasc 1981). Thus, two seemingly distinct and important functions

are effected by some of the same elements of the axial musculo-skeletal system.

Lizards clearly ventilate their lungs effectively while they are walking slowly on treadmills (Mitchell et al. 1981a, b; Gleeson and Bennett 1982). However, no data exist for more rapid movement. This study was undertaken to provide data on the ventilation of lizards during walking and running over the full range of locomotor speeds.

Materials and methods

Investigation centered on lizards of four species: *Varanus exanthematicus* (4 specimens, mass = 359–818 g), *Varanus salvator* (1 specimen, mass = 1124 g), *Iguana iguana* (5 specimens, mass = 67–530 g) and *Ctenosaura similis* (3 specimens, mass = 54–307 g). Of these, *Varanus exanthematicus* is noted among lizards for its relatively high aerobic capacity and high locomotor stamina (Wood et al. 1978). The other three species are fast runners, but have a relatively low aerobic capacity (Gleeson 1981; Moberly 1968; Garland 1984).

Part of this analysis is concerned with short duration burst activity. Ventilation during burst activity has previously not been studied in any tetrapod. For this reason, Japanese quail (*Coturnix coturnix*: 4 specimens, mass = 119–190 g) were also included in the analysis. Birds have a high aerobic capacity and great locomotor stamina, and are known to breathe during rapid, sustained running (Brackenbury et al. 1982). The quail, therefore, provide a control on the experimental protocol because they do breathe while running.

Flow probe

The circuitry and method of calibration of the flow probe used for ventilatory measurements was developed by C. D. Mills and K. Schmidt-Nielsen (unpublished manuscript), and has been described by Thomas (1981). The probe operates on the principle of the hot-wire anemometer, using the rate of heat loss from heated thermistors to indicate the rate of air flow. The voltage output of the probe is linearly related to the tidal volume and was recorded on a Gould chart recorder. Because hot-wire anemometers are sensitive to air temperature, tidal volume was determined for inspiration only.

Stride interval and running speed

The animals were initially run on a plywood track. The 7.3 m long and 0.45 m wide running surface was overlain with aluminium window screening, which provided excellent traction. Stride interval was recorded with a low current (15 mA) circuit. One lead was attached by tape or a safety pin to one of the rear legs and the other lead to the screen, so that contact of the foot with the screen sent a signal to the chart recorder. Running speed was recorded via five photo cells spaced at one meter intervals along the track. As an animal ran down the track it interrupted beams of light that illuminated the cells, thus sending signals to the chart recorder.

During treadmill locomotion, stride frequency was recorded with a mercury length gage (Prochazka 1984) that was attached to the skin, parallel and lateral to the vertebral column. As a lizard bent its body from side to side the resistance of the gage changed. Belt speed of the treadmill was recorded through a circuit that closed briefly with each revolution of a treadmill drum.

Experimental protocol

The room in which the lizards were housed and run was maintained at 29 °C. Cages were supplied with heat lamps so that the rectal temperature of the lizards was generally between 30° and 38 °C. Rectal temperature was maintained within two degrees of 35 °C during recording sessions.

Both the lizards and quail could usually be induced to run, from one end of the track to the other, simply by approaching the animal or by light contact or pinching of their tail region. Upon reaching the darkened end of the runway the animals generally remained stationary if left undisturbed. This made it possible to record ventilation during the recovery period after each run. Lizards could usually be run 8 to 15 track lengths before they fatigued noticeably, at which time the animal was retired for the day. Animals could be induced to walk by positioning them in the center of the track and then backing slowly out of sight. After a few minutes the subject usually got up and strolled to one of the darkened ends of the track.

Whenever they ran on the polywood track the lizards were free to choose their own speed. For every animal studied, however, there was a range of speeds between a walk and a run that was not used. The maximum sustainable speed of these species falls in or at the lower end of this range of unused speeds. In order to gain an understanding of what occurs when the animals move at speeds not employed on the solid track, ventilation during treadmill activity was recorded in *Varanus exanthematicus* (3 specimens, mass = 531–818 g) and *Iguana iguana* (3 specimens, mass = 264–530 g).

Calibration of the flow-meter was checked at the end of each recording session.

Testing of protocol

To eliminate the possibility that air flow occurred through the mouth rather than through the nares, controls were run in which the mouth of the lizard was taped shut and the lips sealed with a bead of Vaseline. Trials in which the probe was attached to the snout, away from the pathway of the respiratory air flow, indicated that the apparent wind produced as the animals ran down the track had a negligible effect on the flow meter.

Plugging of the nostril without the probe with a cotton ball (so that all air had to flow through the probe), resulted in the measured air-flow through the probe being two times that recorded when the nostril was not blocked. Consequently, increased resistance to air flow through the probe did not have a significant effect.

Data analysis

This analysis compares ventilation during activity to ventilation during recovery from vigorous running. Such ventilation, immediately following the cessation of locomotor activity, represents a response to the metabolic demands induced by the activity. Recovery metabolism should more closely approximate activity metabolism than does resting metabolism. Ventilation during recovery is, therefore, the most appropriate comparison for a test of the hypothesis that locomotor movements limit ventilation. In order to facilitate comparison with previous studies, most of the figures and tables also include data for pre-run (i. e., resting) ventilation.

Lizards seem to avoid steady state running. In the present study, they often ran intermittently and abruptly changed pace. For locomotion on the solid track, ventilation was analyzed for periods during which the animals were moving at a steady pace. In the case of treadmill activity, however, erratic movement was more ubiquitous and so was not excluded from the analysis.

Average tidal volume, breath frequency and minute volume were calculated from the interval of time required for the animals to cover the one meter distances over which speed was measured on the solid track. The values of maximum tidal volume are the maximum values that occurred in these one meter intervals. Recovery ventilation represents breathing that occurred immediately (i. e., within the first few seconds) after the animal stopped running.

Treadmill use provided locomotor bouts of longer duration for each speed. This facilitated statistical analysis. Mean tidal volume was calculated from four 20-s-intervals recorded midway through the exercise session. Recordings at nonsustainable speeds were of such short duration that ten second intervals had to be used in calculating tidal volume. Sample size for the calculation of mean tidal volume was always greater than sixty breaths. Mean minute ventilation was calculated from the values of minute volume obtained from the four intervals.

Results

Ventilation during locomotion on track

All the lizards tested showed greatly diminished lung ventilation whenever they moved faster than a slow walk (Fig. 1). Disruption of aspiration was coincident with the beginning of locomotion, and resumption of "normal" breathing followed shortly after the cessation of running. This occurred during both bipedal and quadrupedal locomotion. Individuals of *Ctenosaura similis* always ran bipedally, as did the smaller individuals of *Iguana iguana*. In contrast, the larger green iguanas and both species of *Varanus* ran quadrupedally. Breathing did not differ discernibly during locomotion of these two modes.

Average tidal volume decreased as locomotor speed increased (Fig. 2). The drop in amplitude of individual breaths was most pronounced in *Iguana iguana* and *Varanus salvator*. In all four species, however, tidal volumes recorded during running at intermediate to high speeds were an order of magnitude less than those recorded during recovery.

During running, the largest breaths coincided with the strides of longest duration or to brief pauses in the locomotor movements (Fig. 3). At lower stride frequencies the variation in breath amplitude increased. Whereas, low stride frequencies were characterized by both large and small breaths, high stride frequencies were characterized by only small breaths.

Frequency of breathing increased with stride frequency (Fig. 4). In three of the species, this increased by an order of magnitude. Tidal volume decreased abruptly as breath frequency increased during running. A doubling of the breathing fre-

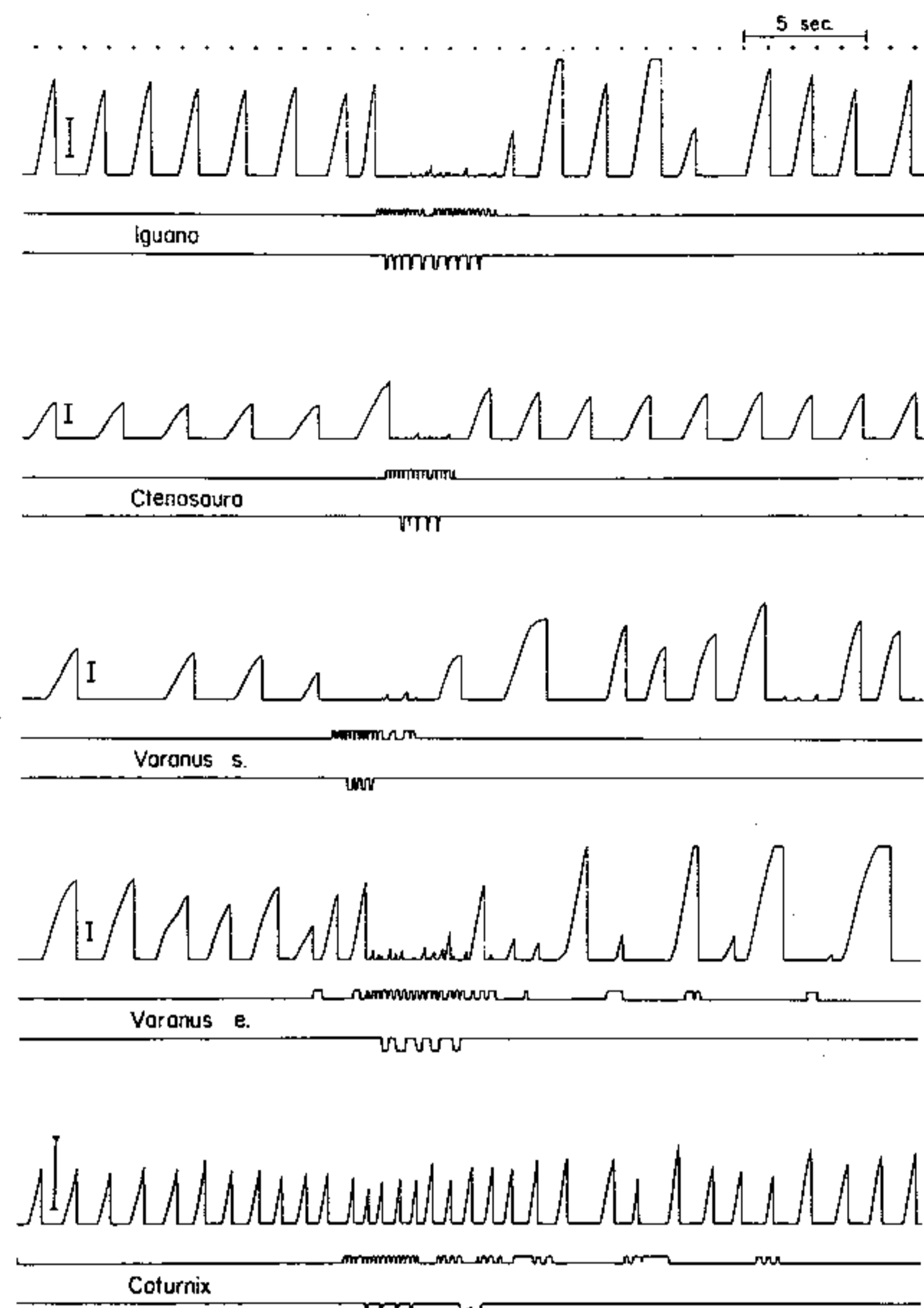


Fig. 1. Sample recordings of the lung ventilation of four lizards and a Japanese quail (*Coturnix*). Each record includes three measurements. The upper trace is a record of the amplitude of inspiratory air flow at one nostril. The vertical scale after the first breath equals one cubic centimeter. The center trace is a recording of the contact pattern of one rear foot and is an indication of stride interval. An upward deflection occurs whenever the foot is not in contact with the track surface. The lower trace records the tripping, by the animal, of a series of photo-cells spaced at 1-m-intervals. The time between deflections indicates running speed. Body masses: *Iguana iguana*, 353 g; *Ctenosaura similis*, 307 g; *Varanus salvator*, 1124 g; *Varanus exanthematicus*, 818 g; Quail, 54 g

quency was often accompanied by a tenfold reduction in tidal volume.

Minute ventilation decreased as running speed increased (Fig. 5). During recovery, minute volume was generally twice the magnitude of that at the higher running speeds. Due to the large increase in frequency of ventilation, the decline in minute ventilation with increases in speed was not nearly as pronounced as was the drop in tidal volume.

It is possible that lizards might ventilate their lungs to a greater extent during locomotor bouts of longer duration. To test this, three *Iguana iguana* and three *Ctenosaura similis* were chased con-

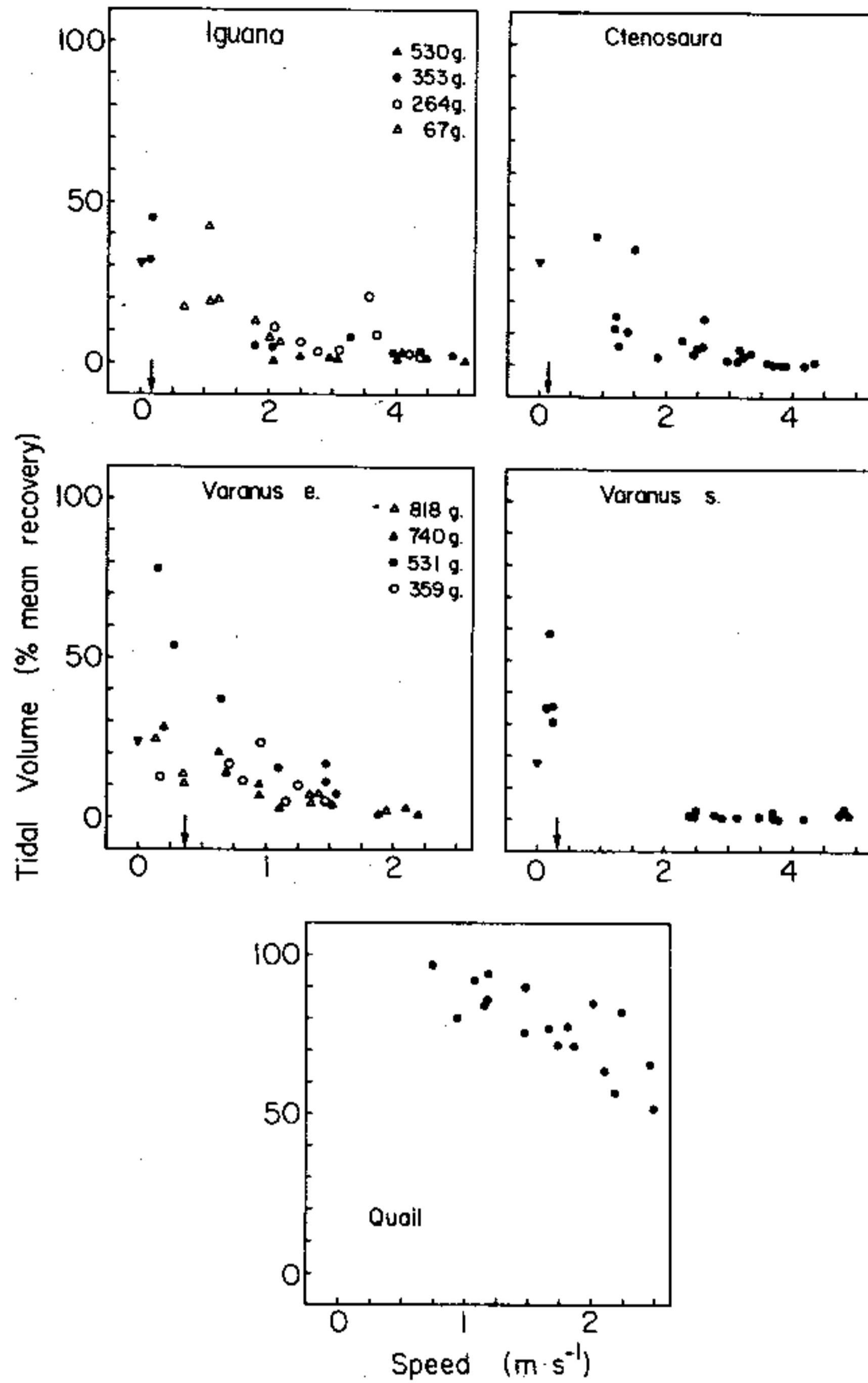


Fig. 2. Average tidal volume versus locomotor speed from four individuals of *Iguana iguana* and *Varanus exanthematicus*, and from single individuals of the other species. Average tidal volume is plotted as a percentage of each animal's mean recovery tidal volume. In each case, the *upside-down triangle at zero velocity* represents the mean tidal volume of twenty breaths recorded during pre-run ventilation (values from the 353 g *Iguana iguana* and the 818 g *Varanus exanthematicus* are plotted, *Arrows* on the ordinate indicate the maximum aerobic speed (i.e., maximum sustainable speed) of each species (Gleeson et al. 1980; Garland 1984; Gleeson 1981). Data for maximum sustainable speed and pre-run ventilation are not available for quail. Mean maximum tidal volume for *Iguana iguana* 530 g = 9.29 ± 1.93 cm³, 353 g = 6.99 ± 1.14 cm³, 264 g = 5.23 ± 1.68 cm³, 67 g = 1.19 ± 0.27 cm³; *Ctenosaur similis* 307 g = 7.8 ± 1.7 cm³; *Varanus exanthematicus* 818 g = 21.0 ± 7.5 cm³, 740 g = 17.8 ± 2.7 cm³, 531 g = 14.7 ± 4.6 cm³, 359 g = 13.6 ± 4.0 cm³; *Varanus salvator* 1124 g = 16.5 ± 4.5 cm³; Quail 54 g = 1.65 ± 0.26 cm³

tinuously up and down the track until their running performance was greatly curtailed by fatigue. Each such running bout lasted from 40 to 100 seconds, at which point locomotor movements had become greatly exaggerated and running speed

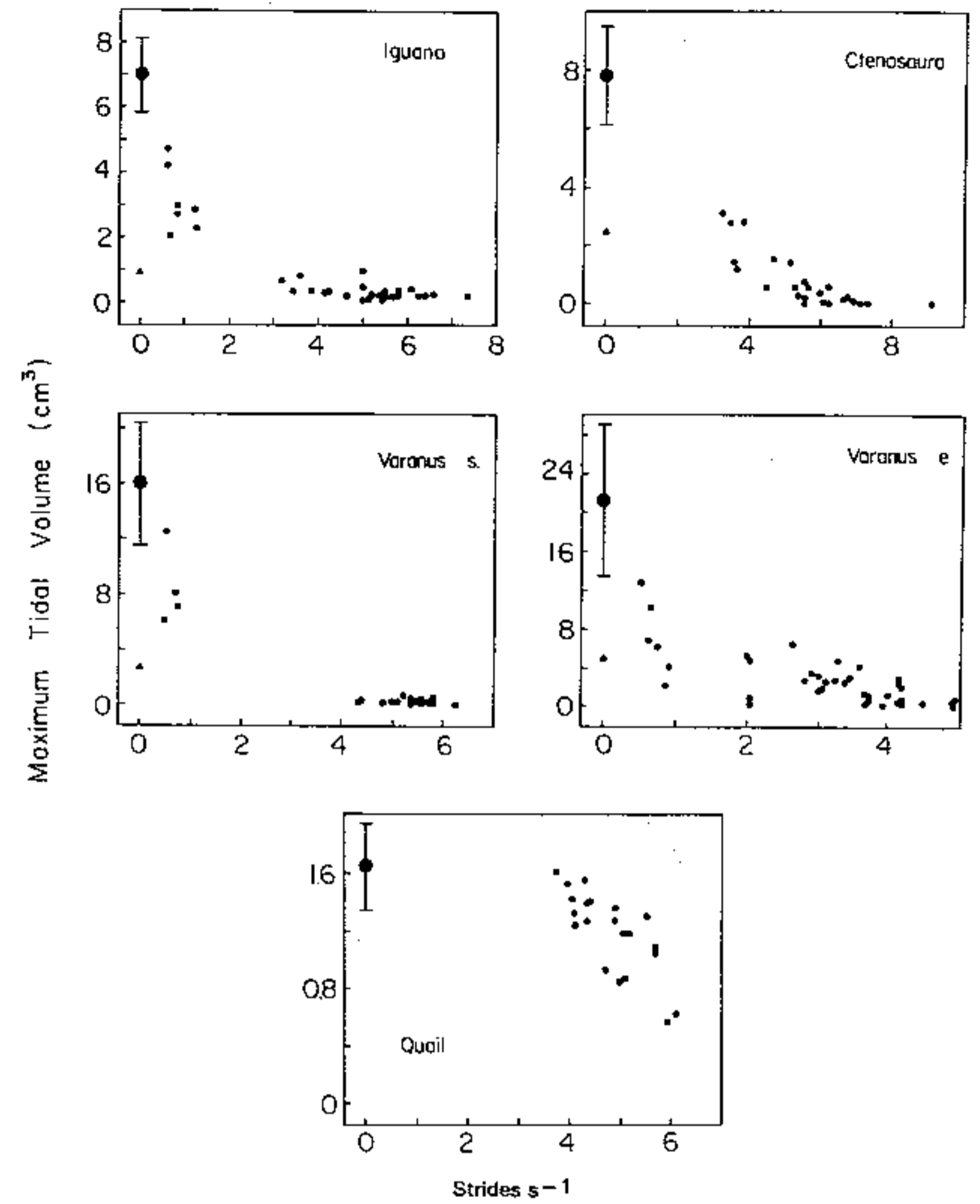


Fig. 3. Maximum tidal volume versus stride frequency of four lizards and a quail. The *large dot and bars* at zero strides/s represents the mean and standard deviation of recovery ventilation. Each of the *small dots* represents the largest breath recorded during running of the 1-m-intervals over which stride frequency was measured. The *triangle* at zero strides/s is the mean tidal volume of twenty breaths recorded during pre-run ventilation

had dropped to that of a walk. Breathing remained diminished throughout these runs (Fig. 6). Table 1 summarizes one such run to fatigue. The same pattern was seen in shorter runs lasting only a few seconds.

Table 1. Summary of the lung ventilation of a green iguana (*Iguana iguana*, 206 g) during a continuous running sequence that led to exhaustion in 77 s. Data are presented for ventilation occurring during recovery and during running at stride frequencies of less than 2.5 strides/s and greater than 2.5 strides

Strides/s	N	Time (s)	V _t (cm ³)	Breaths/s	V (cm ³ /min)
0	15	39	6.24 ± 0.49	0.37	140
(Recovery)					
<2.5	35	21	1.57 ± 1.27	1.39	131
>2.5	103	39	0.44 ± 0.33	2.58	68

N number of breaths measured
V_t tidal volume
V minute volume

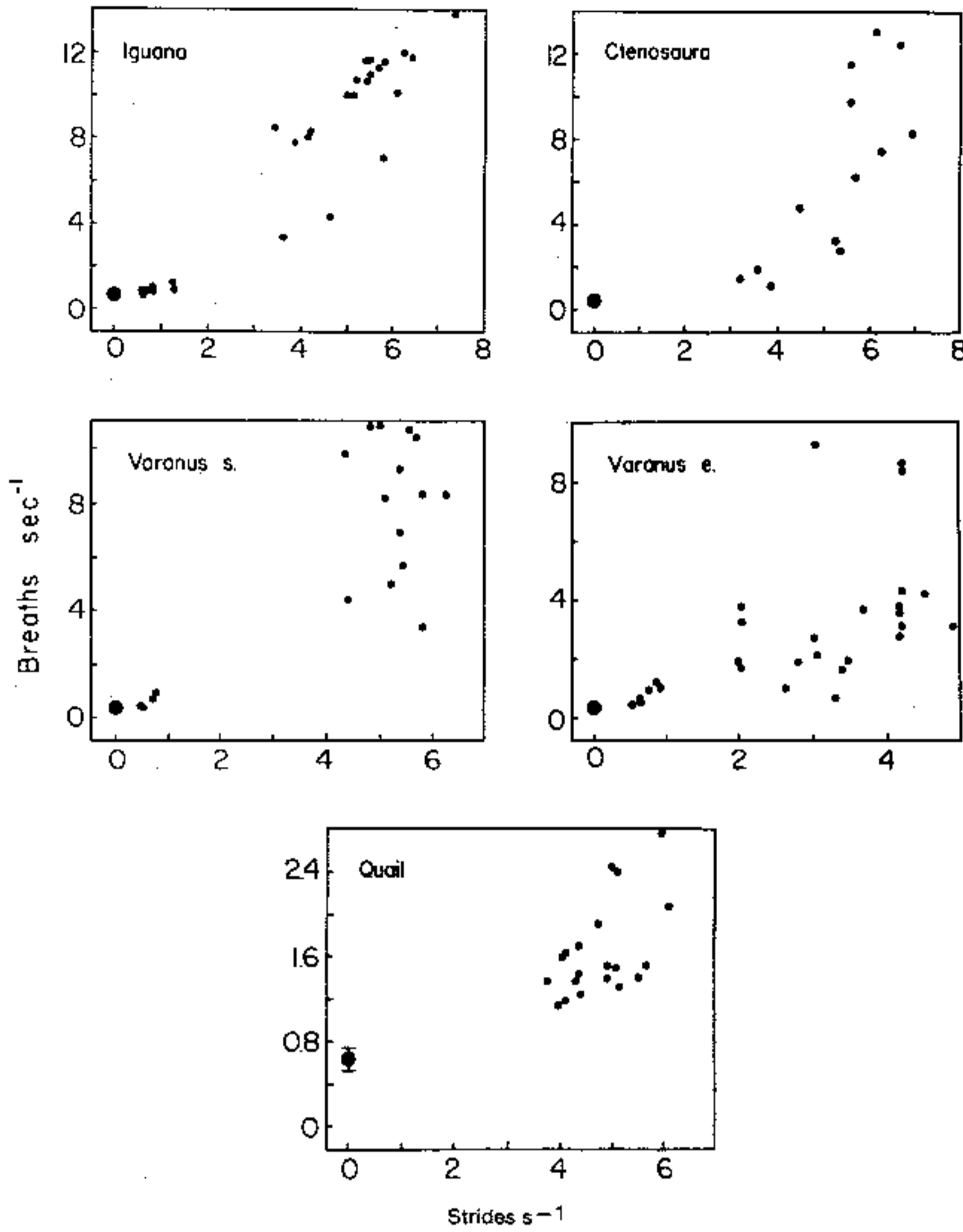


Fig. 4. Breath frequency versus stride frequency of four lizards and a quail. The *large dot* and *bars* at zero strides/s represents the mean and standard deviation of recovery ventilation. Each of the *small dots* represent the average breath frequency recorded during running of the 1-m-intervals over which stride frequency was measured

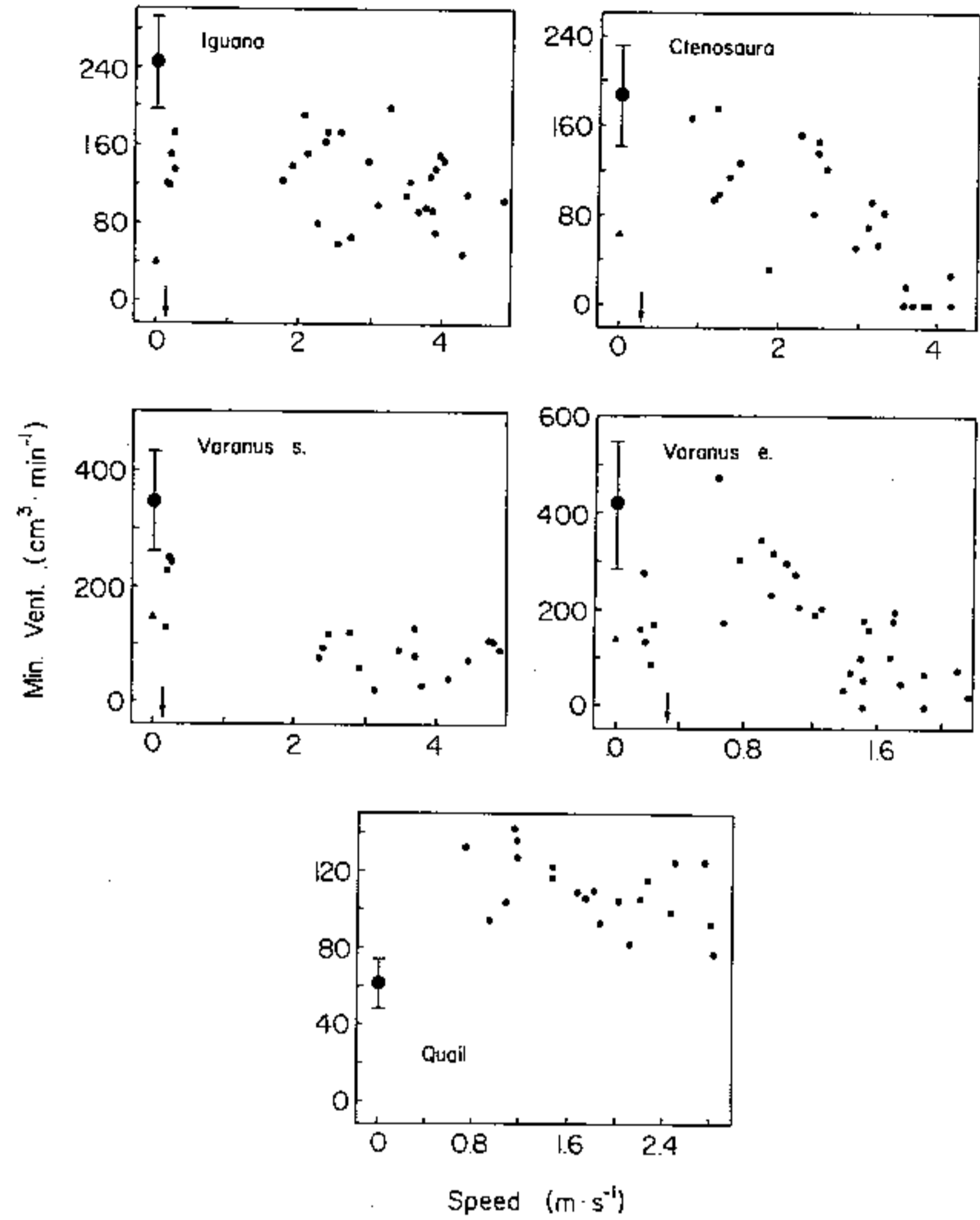


Fig. 5. Minute ventilation versus locomotor speed of four lizards and a quail. The *large dot* and *bars* at zero velocity represents the mean and standard deviation of recovery ventilation. Each of the *small dots* represents the minute ventilation recorded during running the 1-m-intervals over which speed was measured. *Arrows* indicate the maximum aerobic speed (Gleeson et al. 1980; Garland 1984; Gleeson 1981), similar data are not available for quail

Ventilation during treadmill exercise

Lizards were exercised on a treadmill at belt speeds ranging from 0.14 to 0.80 m/s for *Varanus exanthematicus* and from 0.10 to 0.71 m/s for *Iguana iguana*. The maximum belt speeds repres-

ent only 35% and 15% respectively of the maximum running speeds for these species recorded on the solid track. However, in *Varanus exanthematicus* the maximum belt speed was more than twice the reported maximum aerobic speed (Ben-

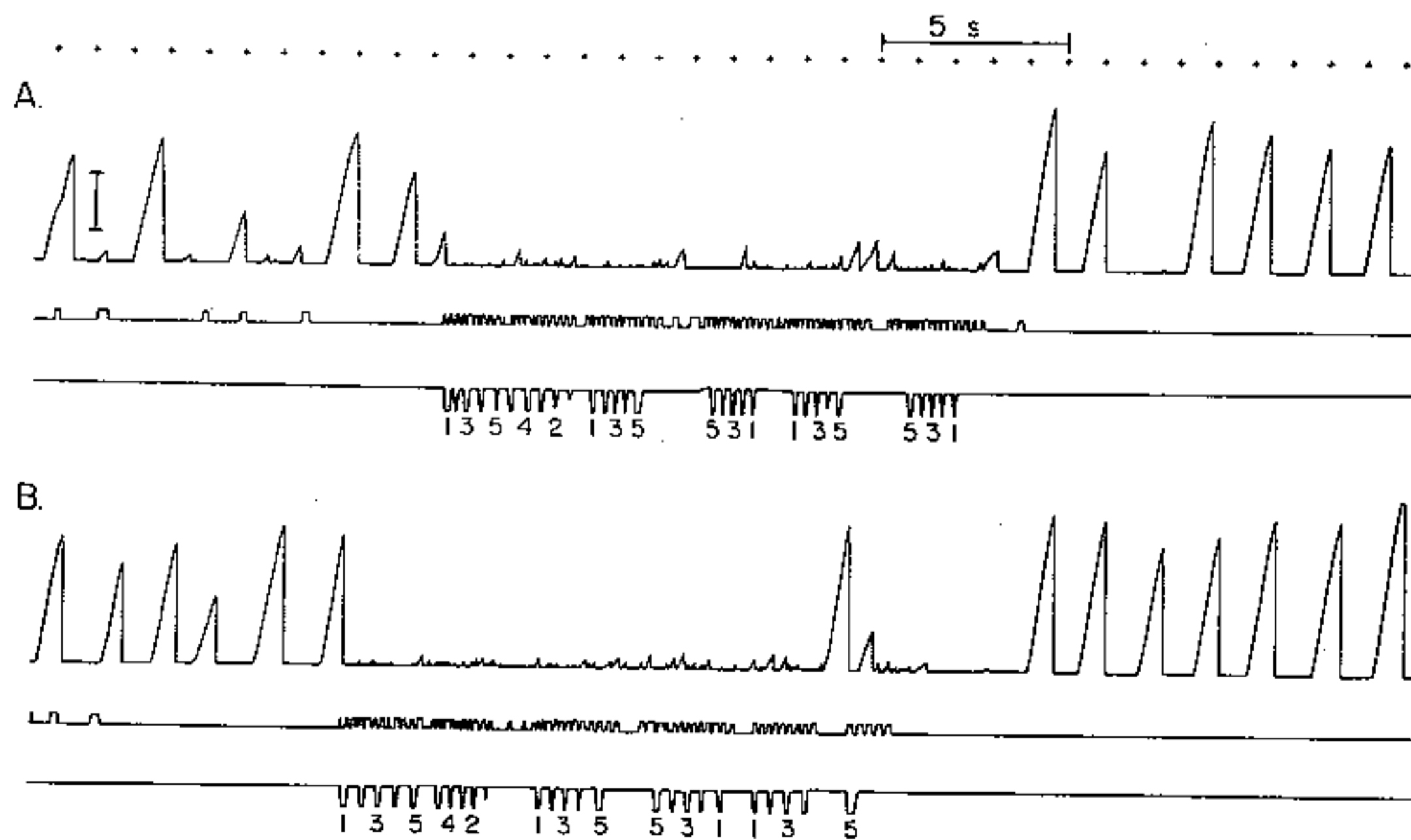


Fig. 6. Ventilation of a green iguana during a run of long duration. The animal was chased continuously up and down the 7.3-m-track; running six lengths in sequence A, and after resting for 76 s running five more lengths in sequence B. The 1-m-intervals of the lower trace are numbered. For further explanation see Fig. 1

nett 1982); in *Iguana* it was over five times the maximum aerobic speed.

Both species moved erratically and intermittently on the treadmill (Fig. 7). Examination of the recordings showed that stride frequency varied considerably, even during periods when the animals appeared to be moving uniformly. *Varanus* walked more steadily than *Iguana*, but both changed their pace frequently. Pauses in the locomotor movements became more frequent as the animals became fatigued. The erratic nature of the locomotion did not improve noticeably with training.

Tidal volume of *Iguana* declined at increased belt speeds (Fig. 8). Increased speed produced an increase in tidal volume in the varanids at the lower end of their speed range. However, this was true only at the lowest speeds, and tidal volume began to decline with increasing belt speed well below the maximum sustainable speed. For both species, the rate of decline was greatest at low speeds, and the mean tidal volume at the maximum aerobic speed was less than half the mean recovery tidal ventilation. At velocities of only 0.6 m/s, tidal ventilation had dropped to less than 20% of the mean value during recovery. Tidal ventilation became less variable at higher speeds. Minute ventilation reached peak values at roughly the maximum aerobic speed (Fig. 8). At greater speeds, minute ventilation was reduced.

Comparison of ventilation occurring during locomotion on the treadmill with that occurring on the track is difficult because the animals used different speeds on the two substrates. However, values of ventilation recorded during treadmill activity did correspond to those obtained during track locomotion. Table 2 lists mean values of breathing, for three individuals of both species, during walking and slow running on a treadmill. Belt and track speeds did overlap for *Varanus exanthematicus* at the upper range of belt speeds; making a direct comparison possible. Mean tidal and minute ventilation of three individuals of *Varanus*, that were moving on the treadmill at a belt speed of 0.8 m/s, were $1.7 \pm 0.5 \text{ cm}^3$ and $186 \pm 67 \text{ cm}^3 \cdot \text{min}^{-1}$ respectively. Corresponding values recorded during locomotion at this speed on the track range from 1.4 to 2.5 cm^3 for tidal volume (Fig. 2) and from 220 to 350 $\text{cm}^3 \cdot \text{min}^{-1}$ for minute volume (Fig. 5).

As with running on the solid track, the largest breaths corresponded to brief pauses in the locomotor activity (Fig. 7). Even during travel at sustainable speeds (i. e., walking) a significant fraction of minute ventilation occurred during these pauses.

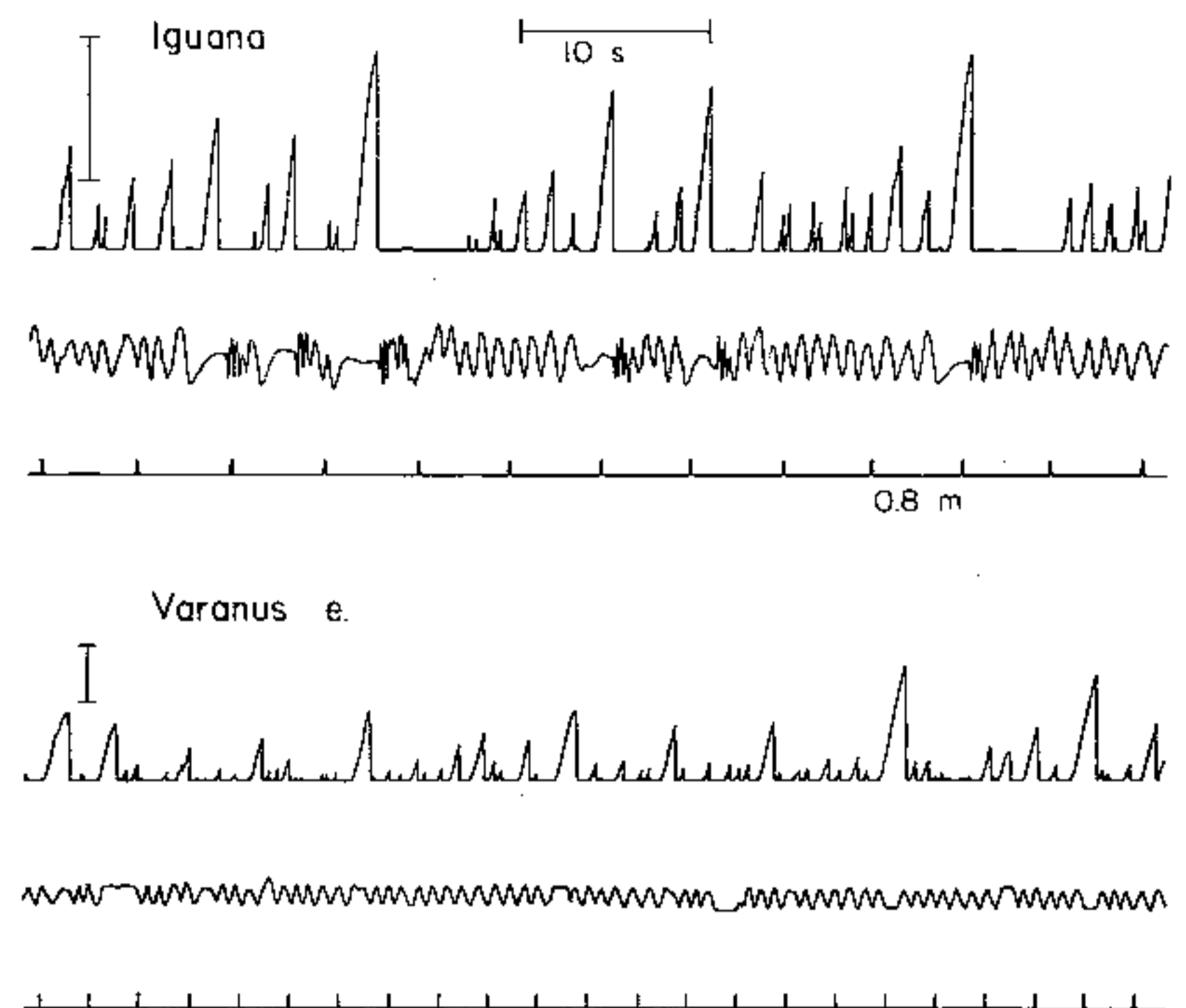


Fig. 7. Sample recording of breathing during the treadmill locomotion of *Iguana iguana* (mass = 355 g) and *Varanus exanthematicus* (mass = 813 g). The upper trace is a measure of inspiratory tidal volume. The vertical scale after the first breath equals 10 cm^3 . The second trace records lateral bending of the trunk. Each wave cycle of the trace equals one locomotor cycle. The third trace indicates the belt speed of the treadmill. Spikes occur at 0.80 m intervals so the belt speed of the iguana record is 0.16 m/s and 0.30 m/s for the varanid

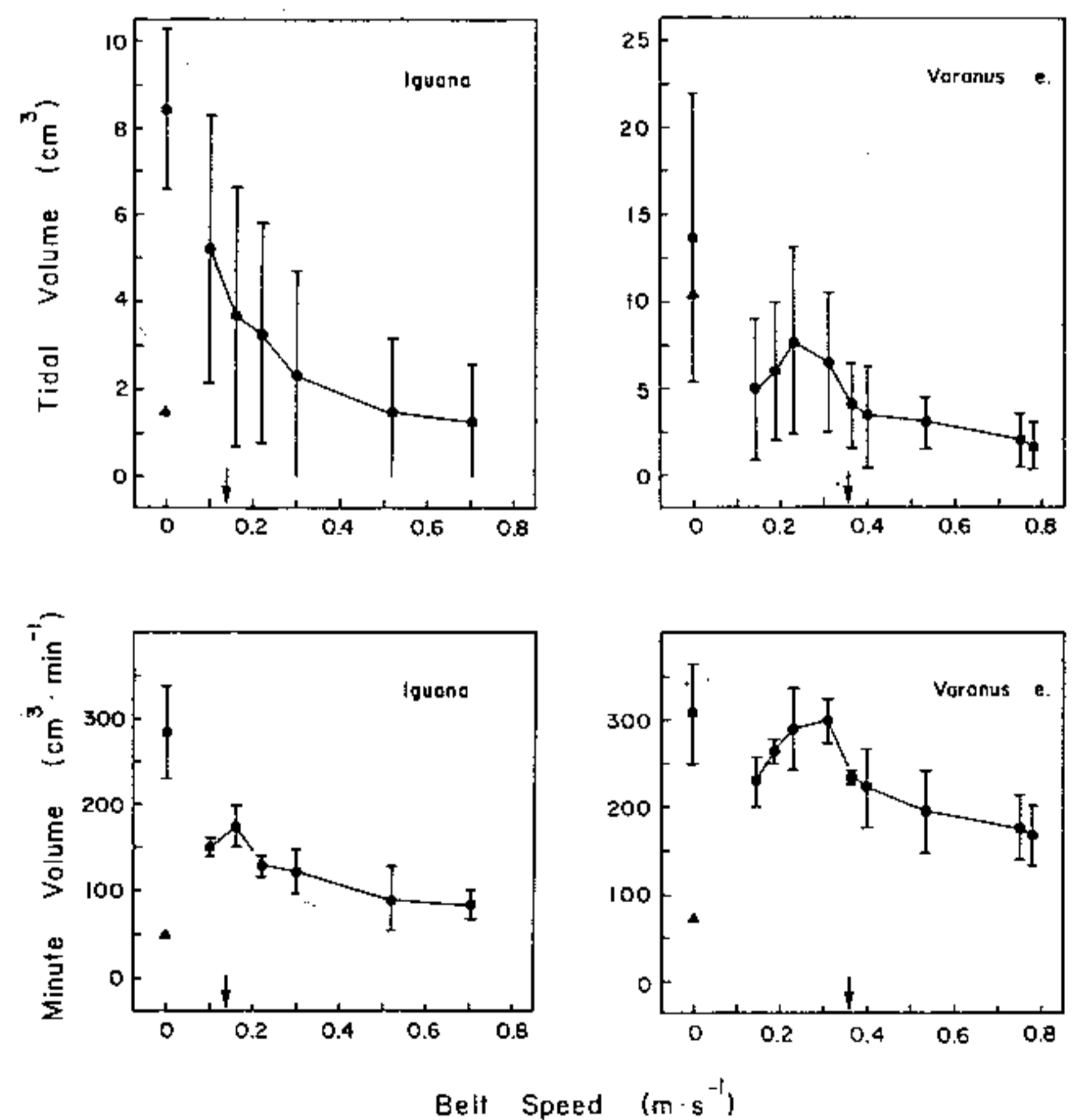


Fig. 8. Means and standard deviations of minute volume plotted against belt speed for single individuals of *Iguana iguana* (mass = 355 g) and *Varanus exanthematicus* (mass = 813 g). The dots and triangles at zero velocity represent recovery and pre-run ventilation respectively. The arrows on the ordinate indicate the reported maximum aerobic speed (Gleeson et al. 1981)

Table 2. Means and standard deviations of average tidal volume and minute volume of three *Varanus exanthematicus* (mean body mass, 744 g) and three *Iguana iguana* (mean body mass, 342 g) during walking (trial 1) and slow running (trial 2) on a treadmill

	Tidal volume (cm ³)					
	Pre-run		Run		Recovery	
	Trial 1	Trial 2	Trial 1	Trial 2	Trial 1	Trial 2
<i>Iguana iguana</i> N = 3	1.3 ± 0.2	1.5 ± 0.4	0.15 m/s 4.3 ± 1.3	0.70 m/s 1.8 ± 1.3	5.8 ± 1.3	6.9 ± 1.4
<i>Varanus exan.</i> N = 3	5.0 ± 3.3	5.1 ± 3.4	0.27 m/s 5.6 ± 0.8	0.80 m/s 1.7 ± 0.5	14.3 ± 10.4	28.3 ± 13.6
	Minute volume (cm ³ × min ⁻¹)					
	Pre-run		Run		Recovery	
	Trial 1	Trial 2	Trial 1	Trial 2	Trial 1	Trial 2
<i>Iguana iguana</i> N = 3	54 ± 13	50 ± 9	0.15 m/s 214 ± 76	0.70 m/s 111 ± 39	222 ± 37	237 ± 64
<i>Varanus exan.</i> N = 3	41 ± 19	64 ± 31	0.27 m/s 301 ± 6	0.80 m/s 186 ± 67	113 ± 47	294 ± 47

Ventilation of quail

Although the rate of travel influenced the breathing of quail, the effect was minimal compared to that observed in lizards (Fig. 1). In quail, tidal volume decreased as the animals ran faster, but the decline was gradual and only at the highest speeds did values fall below 50% of the average recovery tidal volume (Fig. 2). The frequency of ventilation increased with running speed. However, at the highest speeds it was only three times greater than during recovery ventilation (Fig. 4). Most importantly, quail ventilated more air during locomotion than during periods of recovery, although minute ventilation did decrease slightly at the higher speeds (Fig. 5).

Discussion

Lung ventilation declines as locomotor speed increases in the four species of lizards examined in this study. Tidal volume falls off rapidly at low speeds. At intermediate and high speeds, breath volume is generally much less than 10% of that during recovery ventilation. In *Varanus exanthematicus* and *Iguana iguana*, minute ventilation peaks at or below the maximum aerobic speed and decreases at speeds above this value.

It is reasonable to assume that ventilation recorded immediately upon the cessation of running (i. e., recovery ventilation) closely represents the gas exchange demands shortly before the ani-

mal stops moving. If this is true, then these lizards are not meeting their metabolic demands through lung ventilation over the greater part of the range of running speeds employed.

In mammals, the rate of oxygen consumption rises with running speed until a maximum is reached. At all speeds beyond the aerobic threshold, the energy that is made available through aerobic pathways is *supplemented* by anaerobic metabolism. In contrast, anaerobic metabolism must almost *replace* aerobic metabolism in animals in which breathing is largely curtailed during locomotion. The literature does provide limited evidence suggesting that lizards do have such a switch in metabolic pathways. *Varanus salvator* (Gleeson 1981; Gleeson and Bennett 1982) and *Varanus exanthematicus* (Gleeson et al. 1980) reach a maximum rate of oxygen consumption at very low speeds, and with subsequent increases in speed the rate of oxygen consumption is reduced. In *Amblyrhynchus cristatus*, oxygen consumption shows a transient elevation associated with deep ventilatory movements at the cessation of walking (Gleeson 1980). These observations are consistent with the finding that lung ventilation is reduced during locomotion.

One explanation for the reduced ventilation during locomotion is that lizards are so highly specialized for anaerobic metabolism that breathing during short bursts of intermediate and high intensity would not enhance running perform-

ance. However, it is hard to see why maintenance of high rates of lung ventilation during activity would not enhance stamina and quicken recovery. Even if oxygen transport does not limit the activity of lizards, these animals must still maintain tissue and plasma pH by buffering the high level of lactic acid and hydrogen ions produced through anaerobic metabolism (Mitchell et al. 1981 a). The immediate avenue for buffering the increased acid load is via acid titration of the blood bicarbonate system. This requires the elimination of CO_2 through the ventilatory gas. Consequently, reduced lung ventilation during extended locomotion will compromise the acid-base balance of the tissues, and therefore can be expected to limit anaerobic stamina.

Mechanical constraint?

The thorax of lizards is instrumental in producing both locomotion and lung ventilation. This raises the question of whether locomotion may interfere with breathing and vice versa. Lateral bending of the trunk and aspiration breathing seem to require discordant actions of this bone-muscle system. Aspiration of the lungs occurs by simultaneous lifting and depressing the ribs of the two sides. To effect axial bending, the dorsal and lateral trunk muscles (i. e., longissimus dorsi, iliocostalis, obliques, and intercostals) must actively shorten on one side and then on the other. The conflict between synchronous and alternate activation may make simultaneous aspiration and locomotion impossible.

The sprawling posture of lizards may also limit breathing during locomotion because of the lateral placement of the feet. Sprawling support results in a relatively large lateral component to the propulsive force (Gray 1968; p 98). Even in mammals, with more erect posture, these lateral forces can exceed 15% of body weight while walking (Jenkins and Weijs 1979; Kimura et al. 1979). Controlled forward progression requires that the lateral component be resisted by stiffening the trunk with the axial muscles. Because the majority of the axial muscles of lizards insert on the ribs, walking and trotting are expected to interfere with lung ventilation.

The observations reported here lend limited support to this hypothesis of a mechanical constraint. First, there is a strong temporal correlation between locomotor activity and the disruption of lung ventilation. Second, tidal volume is inversely related to stride frequency. The largest breaths that occur in a running sequence correspond to strides of relatively long duration or to

brief pauses in the locomotor movements. These consistent temporal correlations seem too rapid to invoke anything but a mechanical coupling. Third, minute ventilation is inversely related to running speed, suggesting that breathing may become more difficult as the locomotor effort increases. Finally, the minute ventilation of quail increases under the same experimental conditions that reduce the ventilation of lizards. Although terrestrial birds differ from lizards in many ways other than locomotor morphology, their upright posture, bipedal locomotion and relatively rigid trunk seem to exclude the kinds of mechanical restrictions on breathing that are postulated for lizards during locomotion.

At odds with the hypothesis of a mechanical constraint is the observation that lizards do breathe while walking. The gas exchange data of Mitchell et al. (1981 a, b), and Gleeson and Bennett (1982) clearly show that lizards ventilate their lungs effectively while walking on treadmills. However, this investigation shows that it is only at the slowest speeds (< 10% of maximum) that significant tidal ventilation occurs. It is well established that the forces exerted by muscles on bones and substrate rise rapidly as locomotor velocity increases (Cavagna et al. 1977; Biewener et al. 1983). As speed increases, loading of the respiratory system can be expected to become more pronounced. Therefore, if a mechanical constraint on simultaneous locomotion and breathing does exist, it should be least apparent at the lowest speeds. Also in support of a mechanical constraint is the observation that even when walking the largest breaths occur during brief pauses in the locomotor movements (Fig. 7).

One might also expect bipedal running to unload the anterior thorax and thereby facilitate breathing. Thus, the observation that lung ventilation is as low during bipedal as during quadrupedal running might be taken as evidence against the hypothesis of a locomotor constraint on breathing. However, the bipedal running of lizards is characterized by a vertical rotation of the body axis and by pronounced lateral bending of the trunk (Snyder 1949). Both of these movements might load the ribs in ways that limit lung ventilation.

At present, the evidence for a mechanical constraint is limited to assertions drawn from anatomical observations and the finding that ventilation is reduced during running. A detailed analysis of the activity of the thoracic musculature, to distinguish those muscles that are involved in locomotion from those involved in lung ventilation,

will be most helpful in resolving this issue. The hypothesis of a mechanical constraint would be strongly supported if the muscles that effect lung ventilation also turn out to play a role in locomotor movement. Further testing of the hypothesis should also include reptilian groups that differ from lizards in their locomotor and respiratory morphology. The observation that green sea turtles also curtail breathing during terrestrial locomotion (Jackson and Prange 1979) raises the possibility that a locomotor constraint on lung ventilation may be wide spread among ectothermic tetrapods.

Evolutionary implications

In many respects the locomotor and respiratory anatomy of the earliest tetrapods resembled that of modern lizards. The sprawling posture and aquatic heritage of the first tetrapods suggest that lateral bending of the vertebral column must have contributed significantly to stride length and propulsive force. These animals had poorly developed transverse processes on the trunk vertebrae (Romer 1956), indicating that much of the epaxial musculature attached to the ribs. They also had well developed ribs and dermal armor, which suggest that they probably ventilated their lungs with a thoracic (aspiration) pump, rather than the buccal pulse pump of modern amphibians (Gans 1970). Consequently, if the morphology of modern lizards limits breathing during locomotion, then this may also have been true for the earliest tetrapods (Carrier, 1987).

An inability of the original terrestrial vertebrates to breathe during locomotion would likely have had a profound effect on the evolution of tetrapods. The locomotor abilities of modern lizards may be the result of natural selection channeling the ancestors of lizards toward specialization in anaerobic metabolism and burst activity, because their morphology excluded the possibility of a high aerobic capacity during running. In contrast, development of a capacity for intense, sustainable aerobic activity in the lineages that gave rise to birds and mammals would have necessitated major anatomical reorganization in order to facilitate simultaneous running and breathing.

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