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Respiratory cycles of *Chelifer cancroides* (Pseudoscorpiones) and *Galeodes* sp. (Solifugae)

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Abstract. Respiratory functions have been monitored by microrespirographic scanning method in immature and adults of *Chelifer cancroides* (L.) (Pseudoscorpiones) and male adults of wind scorpions *Galeodes* sp. (Solifugae). Both species exhibited a more or less continuous respiratory pattern with relatively constant, acyclic CO_2 output and CO_2/O_2 ratio of 0.72–0.73 under conditions of high relative humidity, and during feeding or intensive locomotion. Conversely, under dry environmental conditions, during starvation or arrested locomotion while watching for prey, both pseudoscorpions and much larger wind scorpions exhibited a wide range of respiratory cycles with various frequencies and amplitudes. These cycles are characterized by discontinuous emissions of free, gaseous CO_2 from haemolymph or tissue buffers. During emissions, CO_2 is released at rates surpassing several times the rate of O_2 consumption. It is similar to the Prague respiratory cycles found in some insects.

In starved adult *Chelifer* (3 mg body mass, 25°C, dry environment), O_2 consumption rate was 5.7 nl per min (136 µl $O_2.g^{-1}.h^{-1}$) with regular Prague respiratory cycles in CO_2 release. Duration of each cycle was 4.93 min; the emissions of CO_2 lasted 0.9 min, the amount of CO_2 released in one emission was 22.8 nl (corrected for simultaneous O_2 uptake). Total average rate of CO_2 release was 4.16 nl per min (99.8 µl $CO_2.g^{-1}.h^{-1}$); R.Q. 0.729. The emissions of gaseous CO_2 were limited only to bursts; the initial rate of CO_2 emission exceeded four times the rate of O_2 consumption.

In starved adult *Galeodes* sp. (200 mg, 27°C, dry environment, motionless position) the rate of O_2 consumption was relatively low (105 µl $O_2.g^{-1}.h^{-1}$); the emissions of 3.9 µl CO_2 lasted 4 min with 16 min duration of the whole respiratory cycle. During emissions; gaseous CO_2 was produced at 5-times faster rate than that of O_2 consumption.

Both the investigated tracheate arachnids can actively regulate breathing by adjusting frequency and amplitude of the respiratory cycles to external or internal physiological conditions. Possible involvement of a special nervous mechanism, similar to the autonomic, parasympathetic-like, nervous system (coelopulse) of insects is indicated.

INTRODUCTION

A distinctive characteristic of arachnids is the large variation in structure and function of the respiratory system. A special feature of spiders and other arachnids is the book lungs, that other arthropods lack (Strazny & Perry, 1987). The number of book lungs varies in different orders: in scorpions, four pairs; in Uropygi and orthognath spiders, two pairs; in Amblypygi, Schizomida and most labidognath spiders, one pair. Other orders have only tracheae: the small pseudoscorpions; the very active wind scorpions (Solifugae); the harvestmen (Opiliones), and the Ricinulei and mites (Levi, 1967).

Compared with insects (see reviews by Mill, 1985 and Kestler, 1985), the ventilatory and respiratory physiology of arachnids is less understood. Most knowledge has been

related to functions of the book lungs in large spiders or scorpions (Paul et al., 1989; Paul & Fincke, 1989; Fincke & Paul, 1989). Babák (1921) when describing the functional morphology and physiology of respiratory systems in invertebrates, pointed out that arachnids do not exhibit any apparent ventilatory movements, unlike insects. The discovery of discontinuous CO_2 release in diapausing ixodid ticks introduced new insights into the respiratory physiology of tracheate arachnids (Sláma, 1991). According to this, the acidaemia caused by respiratory CO_2 in diapausing adult *Dermacentor* appeared to be periodically counterbalanced by sudden emissions of 20–60 nl of gaseous CO_2, once every 8–12 min. The amplitudes and frequencies of these respiratory cycles in *Dermacentor* were regulated by a neurochemical mechanism that was quite similar to the autonomic, parasympathetic-like, nervous system (coelopulse) of insects (Sláma, 1991).

More recently Fielden et al. (1993) and Lighton et al. (1993) confirmed the presence of discontinuous CO_2 release in other species of ixodid ticks; *Rhipicephalus* and *Amblyomma*. They found discontinuous respiratory cycles in CO_2 release, that were stereotypically interpreted as the "DVC" (discontinuous ventilation cycles) previously known from large, diapausing insect pupae (Lighton et al., 1993). They did not find any evidence for active, neurohormonal control of the DVC. New evidence, however, for active physiological control of discontinuous respiratory patterns was provided in *Ixodes* (Acari: Ixodidae) and *Chrysopa* (Insecta: Neuroptera) by Sláma (1994). These cycles had little in common with the stereotypic "DVC" of immobile insect pupae. The rapid emissions of CO_2 from the body were clearly controlled by a nervous system showing great similarity to the autonomic coelopulse system first found in small, diapausing Bruchid beetles (Coquillaud et al., 1990). To make a distinction between the purely diffusive, ventilatory outputs of CO_2 which remain unnoticed by the respirographic method, and the actively regulated emissions of gaseous CO_2 from tissue buffers, Sláma & Coquillaud (1992) proposed describing the latter as the Prague respiratory cycles (PRC).

PRC are found in xerophilic, terrestrial insects or ticks, with high resistance against desiccation. We extended further respirographic investigations to certain other groups of arachnids, which are also xerophilic and resistant to water loss, of which the common European species, *Chelifer cancroides* (L.) (Pseudoscorpiones), indicated as a xerophilic species, can survive a long time in dry environmental conditions at increased temperature (Heurtault & Vannier, 1990).

The second group, solpugids, is represented by a xerophilic species from Southern Europe, *Galeodes* sp. (Solifugae). The body mass of *Galeodes* is almost 100-times larger than that of pseudoscorpions or ticks. Pseudoscorpions have two pairs of tracheae which are equipped with functional spiracles that can open and close; solpugids of the family Galeodidae have one pair of functional spiracles on the prosoma and two pairs on the opisthosoma (Babák, 1921).

MATERIAL AND METHODS

Immature stages and adults of *Chelifer cancroides* (L.) were collected in bee hives in Dožice, South-West Bohemia. They were kept on folded paper, inside small plastic containers, with a cotton plugged vial with water to supply moisture, at 25°C in darkness, and occasionally fed psocopteran insects. The wind scorpions, *Galeodes* sp., were obtained by the courtesy of Dr V. Růžicka, and the genus was determined by Prof. J. Buchar of Faculty of Sciences, Charles University in Prague. They were collected in Turkey. In our laboratory they were kept in a sand-filled terrarium at room temperature and fed small insects occasionally.

The respirographic recording was realized on a 4-channel tensiometric electronic unit M-1000 by Mikrotechna in Prague, Czech Republic. The basic principles of the respirographic scanning method were the same as described previously by Sláma (1984, 1991; see also Sláma & Denlinger, 1992). DC voltage output signals from the respirographic transducers were recorded on a battery of linear recorders or, alternatively, were monitored on PC by using the data acquisition hardware/software system DATACAN (Sable Systems, Salt Lake City, Utah, USA).

Respiratory compartments of 2 ml capacity for *Chelifer* or 20 ml capacity for *Galeodes*, at 25–27°C, in darkness, were used for recordings. The special technical arrangement used to replace O_2 consumed by the animal with equal amounts of the electrolytically produced O_2 inside the respiratory compartment, made it possible to obtain long-term uninterrupted recordings of respiratory patterns throughout several days. In *Chelifer cancroides* (L.), these long-term recordings were obtained with 8 adult specimens (2 to 3 mg body mass); short-term, several-hour duration recordings were completed with an additional 12 specimens of immature or adult stages (1.5 to 2 mg body mass). Only two specimens of adult wind scorpions, *Galeodes* sp. were available for all respirometric recordings. *Galeodes* sp. #1 (210–235 mg body mass) was periodically fed small insects; *Galeodes* sp. #2 (198–200 mg) fasted for the whole period of the recordings (5-day recording in both specimens).

RESULTS

When measured by a constant volume respirographic technique, small terrestrial arthropods usually exhibit a continuous or "purely diffusive" type of CO_2 release. This common type of respiration can be easily recognized by a straight-line respirographic relationship which corresponds to the rate of O_2 consumption with CO_2 absorption or, conversely, to the ratio of CO_2–O_2 in the absence of CO_2 absorption. The difference between the two measurements indicates indirectly the actual rate of CO_2 release, which is used for calculation of the respiratory quotient (R.Q.; CO_2/O_2).

The adult specimens of *Chelifer*, which were placed on a moistened filter paper during the recordings (i.e. conditions of high humidity), almost invariably exhibited the above-described type of acyclic, "purely diffusive" respiration. This was usually characterized by a rather constant rate of O_2 consumption (100–200 µl $O_2.g^{-1}.h^{-1}$) and a constant CO_2 release (70–140 µl $CO_2.g^{-1}.h^{-1}$), with a very narrow range of R.Q. (0.72–0.73). It must be emphasized that under these conditions of high relative humidity, with a minimal risk of water loss, the spiracular valves would be opened for free diffusion of respiratory gases in- and outside the tracheal system.

The pattern found in pseudoscorpions exposed to dry conditions was substantially different. The continuous type of respiration was replaced by a wide range of cyclic changes, suggesting alteration of openings of the spiracles or the liberation of CO_2 from liquid carbonate buffers. It appears that a small tracheate arachnid can exhibit a range of respiratory changes characteristic of the "concert" of PRC of insects.

The basic pattern of these respiratory regulations in a small fragment of the scanning microrespirographic record is shown in Fig. 1. Examination of the curve (CO_2–O_2; without CO_2 absorption) reveals essential respirometric data, which is generally common to all starved adult *Chelifer*. The duration of the PRC or periodicity of the CO_2 emissions was 2.6–3.15 min, with 2.93 min average for the whole 4-h period. The rate of O_2 consumption, indicated by the slope of the curves between the separate CO_2 emissions, was 6.0 nl per min (120 µl $O_2.g^{-1}.h^{-1}$). The rate of CO_2 release, calculated from the average CO_2–O_2 ratio, was 4.4 nl of CO_2 per min (88 µl $CO_2.g^{-1}.h^{-1}$), which resulted in the R.Q. of 0.733. One CO_2 emission lasted on average 0.66 min, when 12.8 nl of CO_2 was produced. No CO_2 was

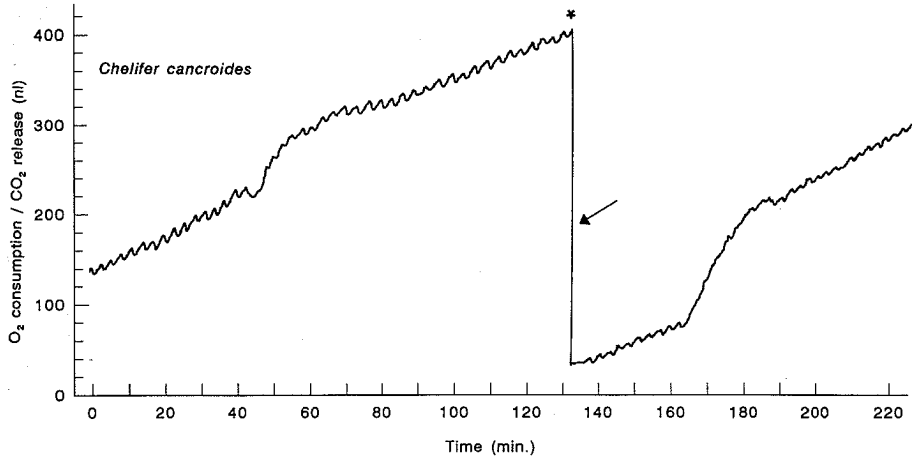

Fig. 1. Scanning microrespirographic record showing O_2 consumption and CO_2 release in adult pseudoscorpion *Ch. cancroides* (3 mg body mass, 27.5°C, measured without CO_2 absorption; the arrow indicates automatic zero control setting).

liberated from carbonate buffers during the period of 2.26 min, that is not between two consecutive emissions.

Further observations revealed that the most uniform PRC were produced only when the pseudoscorpions remained motionless. Locomotion was associated with the disturbed rhythm and increased rate of O_2 consumption observed in Fig. 1 close to min 50 and min 170 of the recording time. Part of a high resolution, microrespirographic record showing 4 Prague cycles with another starved *Ch. cancroides* is shown in Fig. 2. The ascending curve

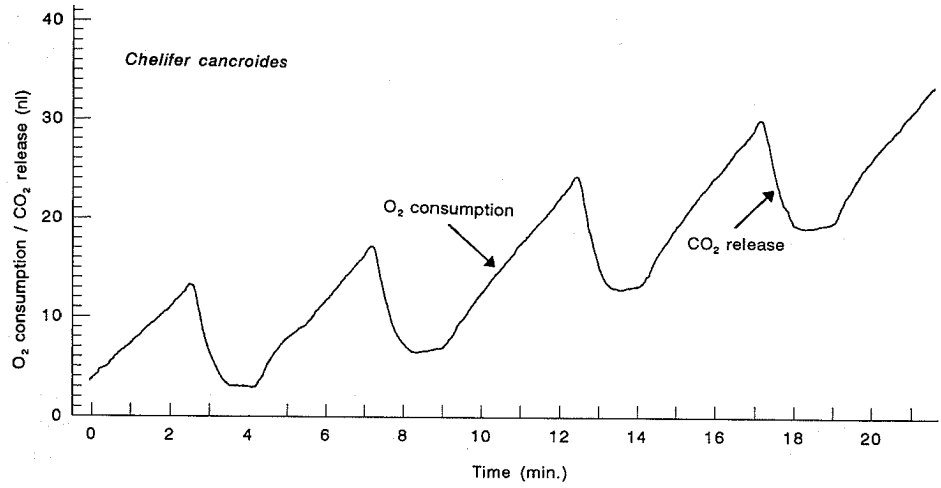

Fig. 2. Microrespirographic record of O_2/CO_2 exchange in adult pseudoscorpion, *Ch. cancroides* (2.5 mg body mass, 25°C, recorded without CO_2 absorption). The trace shows a series of 4 Prague respiratory cycles. The ascending trace corresponds to O_2 consumption, the periodic deflections of the curve in opposite direction correspond to CO_2 emissions.

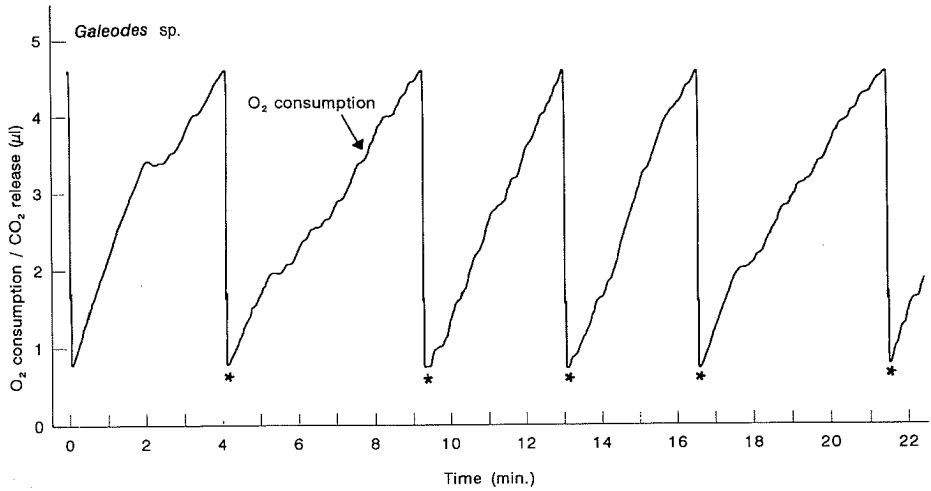

Fig. 3. O_2 consumption in fed adult wind scorpion *Galeodes* sp. (specimen #1, 230 mg body mass; 27°C), one day after feeding. The CO_2 emissions are very frequent, almost invisible on the trace, which is partly due to the concurrent CO_2 absorption (asterisks show the moments of automatic zero control settings).

corresponds to O_2 consumption; an artificial line connecting the tops or bottoms of the cycles indicates the CO_2–O_2 ratio; and the descending deflections indicate a volumetric increase associated with CO_2 emissions.

Fig. 2 shows a relatively constant O_2 consumption of 5.7 nl per min (136 µl $O_2.g^{-1}.h^{-1}$) with average duration of one cycle 4.93 min, and 0.9 min lasting emissions of 22.8 nl CO_2 (corrections had to be made for simultaneous O_2 consumption). From these data we can further calculate average total output of CO_2 would be 4.16 nl per min (99.8 µl $CO_2.g^{-1}.h^{-1}$), giving the R.Q. ratio of 0.729. In this case, the perfect correlation of the R.Q.

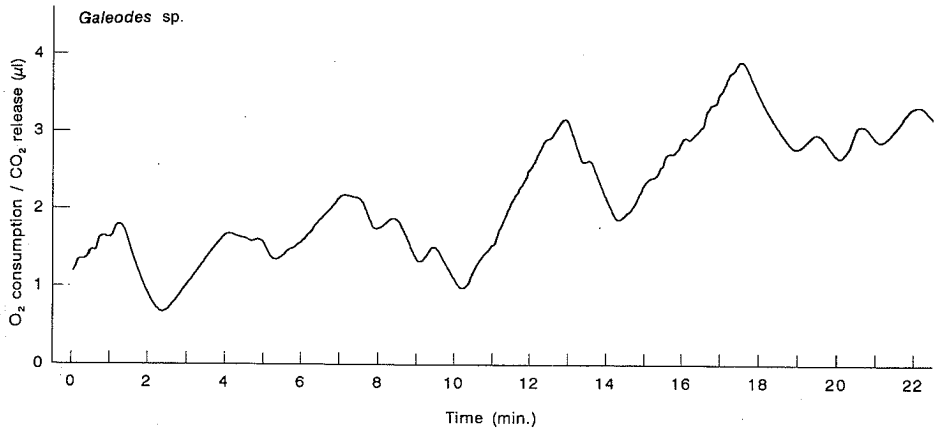

Fig. 4. O_2 consumption and CO_2 release in starved adult wind scorpion *Galeodes* sp. (specimen #2, 200 mg body mass; 27°C, recorded without CO_2 absorption). The animal was moving slowly within the respiratory vessel, its O_2 consumption rate was 300 µl.$g^{-1}.h^{-1}$, intervals between large and small CO_2 emissions were 5 and 1 min, respectively.

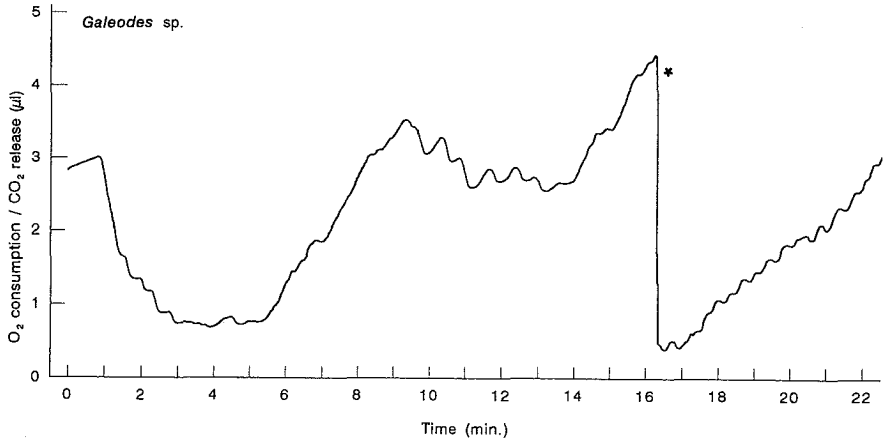

Fig. 5. The same as in Fig. 4, showing a different respiratory pattern in the slow-moving wind scorpion with O_2 consumption rate close to 300 µl.g^{-1}.h^{-1}. Note a large, 4.5 µl CO_2 burst between min 1 and 4, followed by very small or no bursts, as between min 5 and 8, and numerous small, 0.5 µl CO_2 outputs with a periodicity of 3 or more per min, when the animal started moving around (asterisk shows zero setting point).

ratio with expected 0.73 average value confirms that CO_2 was not liberated between the emissions. The initial speed of CO_2 emission was four times faster than O_2 consumption.

The results presented in Figs 1 and 2 were characteristic for starved nymphs and adults of *Chelifer* under dry conditions. Well fed specimens gave less interesting, acyclic and more variable results in recordings, which can be briefly described as: a) considerably increased metabolic rate (up to 440 µl of O_2.g^{-1}.h^{-1}); b) mostly continuous or "diffusive" type of respiration and, c) very frequent, irregular, or completely indiscernible PRC. It appears that the relationships between ingestion, digestion and respiration have general value. They apply to insects, ticks and pseudoscorpions, as well as to much larger wind scorpions. Data, which were obtained from the fully-fed wind scorpion, *Galeodes* sp. #1, corroborate these conclusions (see Fig. 3). There are very frequent, almost continuous emissions of CO_2, which can only be discerned by this microrespirographic method. The increased rate of O_2 consumption shows some temporary variations (391 µl.g^{-1}.h^{-1} in average) without any larger CO_2 emission. Small deformities on the curves suggest that the metabolic CO_2 was also released discontinuously at a higher rate than O_2 consumption. During the 5-day period of continuous recordings, the unfed wind scorpion, *Galeodes* sp. #2, exhibited a range of respiratory patterns. Changes were dependent on specific time of day or night; locomotive activity; behavioural patterns, e.g. occasional movements of the "antennae-like" first pair of legs. Although only one starved solpugid specimen existed, the recordings showed evidence for active regulation of the CO_2 emissions (see Figs 4 to 7). This indicates indirectly that these invertebrate animals could also actively control the respiratory acidaemia.

The respirographic record of the starved, sluggish adult *Galeodes* sp. (Fig. 4) oscillated in O_2 consumption around 60 µl.h^{-1} (300 µl.g^{-1}.h^{-1}), from larger to smaller PRC (periodicity 5 min, release approx. 2 µl CO_2 – periodicity 1 min, release 0.5–1.0 µl CO_2).

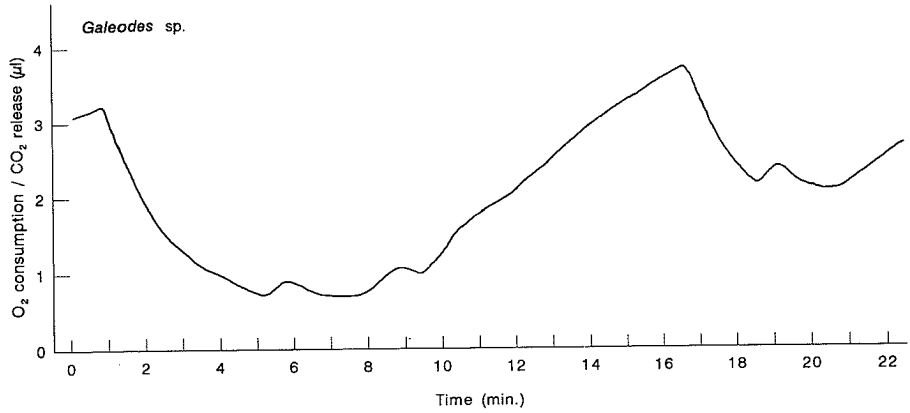

Fig. 6. O_2 consumption and CO_2 release in starved adult wind scorpion *Galeodes* sp. (specimen #2, 200 mg body mass; 27°C, recorded without CO_2 absorption). The animal was immobile, with O_2 consumption rate of 105 $\mu l.g^{-1}.h^{-1}$, large CO_2 bursts with a periodicity of 16 min and a few, occasional small bursts.

The rate of CO_2 emission was constantly at least two times faster than O_2 consumption. Another type of respirographic pattern in a *Galeodes* which started to move slowly around the respiratory vessel is shown in Fig. 5. Initially it made one large 4.5 µl burst of CO_2 lasting 4 min, which was then followed by periods of arrested emissions or some rapid microcycles: 3 or more emissions per min. This suggests that the animal can actively regulate or adjust the frequency and amplitude of the emissions according to the prevailing physiological conditions. These microcycles have not been detected by any other flow-through or constant volume respirometric method.

The commonest respirographic pattern occurs in the immobile predator watching for prey. The rate of total metabolism is lowered to one third of its usual value (105 µl $O_2.g^{-1}.h^{-1}$), the emissions of CO_2 lasting 4 min with a periodicity of 16 min, and formation of 3.9 µl CO_2 per cycle. During the emission, gaseous CO_2 was released at an initial rate five times greater than the rate of O_2 consumption (Fig. 6).

Fig. 7 shows basically the same patterns as in Fig. 6, with a reduced scale. A series of Prague cycles in the same motionless *Galeodes* adult demonstrates that during certain determined periods of time, the animal could release considerably larger amounts of CO_2 compared with O_2 consumption. Conversely, other parts of the record, not shown here, revealed that under certain circumstances (mechanical irritation, stress) the animal could temporarily conserve large amounts of the respiratory CO_2 in the buffered form within haemolymph or tissues. Then, after a delay of several minutes, came the postponed compensation for the respiratory acidaemia (see Fig. 7). The postponed emissions may also indicate that the output of metabolic CO_2 cannot depend solely on its passive gaseous diffusion. The regularity of O_2 consumption in the course of successive PRC is not constant. The rates of O_2 consumption were higher after the emissions of CO_2 (48 µl $O_2.g^{-1}.h^{-1}$), falling to only half of these values before the next emission (24 $\mu l.g^{-1}.h^{-1}$).

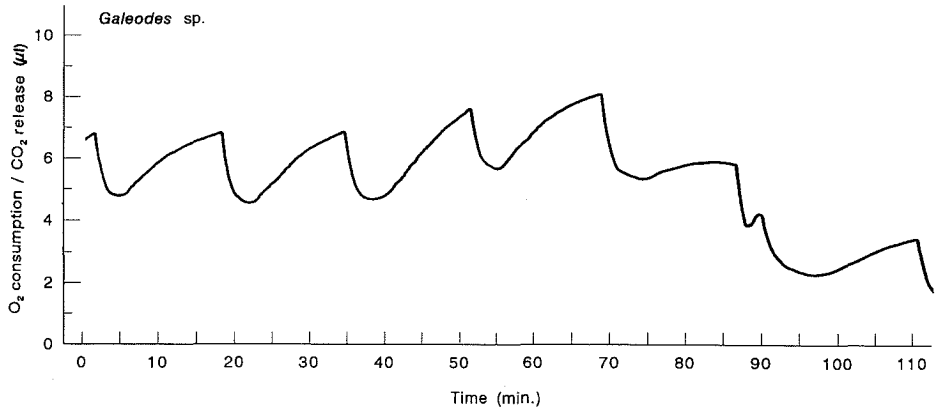

Fig. 7. The same as in Fig. 6, after several hours of complete locomotive immobility. Note 7 complete, regular emissions of CO_2 (PRC), with periodicity 16, 16, 16.5, 17, 17 and 20 min; duration 2.5, 3, 3, 3, 5, 1, 5 min; and release of 2.3, 2.76, 2.56, 2.36, 3.4, 2.12 and 2.4 µl of CO_2, respectively. The respirometric trace clearly shows that the rate of O_2 consumption is about two times higher shortly after each burst (48 $\mu l.g^{-1}.h^{-1}$) than before the burst (24 $\mu l.g^{-1}.h^{-1}$).

DISCUSSION

In most spiders and scorpions, the respiratory gases are transported from tissues by circulating haemolymph to the epithelium of the book lungs where O_2 enters and CO_2 leaves the body. This type of respiration shows certain physiological, though not chemical, analogies with respiration of large, vertebrate animals (Strazny & Perry, 1987). A substantially different perception of respiration in tracheate arachnids has been introduced by recent findings that diapausing ixodid ticks exhibit actively regulated, cyclic emissions of CO_2 (Sláma, 1991). These cycles, known as Prague respiratory cycles (PRC), were originally discovered in small diapausing beetles that were resistant to water loss (Coquillaud et al., 1990; Sláma & Coquillaud, 1992). The described findings with arachnids suggest that physiological mechanisms associated with PRC may be used by other non-insect terrestrial arthropods for successful reduction of respiratory water loss and increased survival under dry conditions. These conclusions are confirmed by earlier reports of the presence of cyclic CO_2 emissions in other species of ixodid (Lighton et al., 1993; Sláma, 1994) as well as argassid ticks (*Ornithodoros moubata, Argas persicus*, Sláma 1995, unpublished).

These present data extend the number of arthropod groups exhibiting active regulation of CO_2 emissions (PRC) to Pseudoscorpiones and Solifugae. In contrast to spiders possessing book lungs (which do not show PRC), in all these animals, including ticks and adult coleopteran or neuropteran insects (Sláma, 1994), the anatomical structure of the respiratory system involves functional spiracles or spiracular sieves at the orifice of branched tracheal tubes that carry oxygen directly to the tissues and even to cells. This seems to be the most efficient way of breathing in small terrestrial organisms. The transport of gas in air is 500 million times faster than in liquid, and CO_2 is 36 times more soluble in tissues than O_2 or N_2 (Buck, 1962). The limitations are evidently connected with water retention during the release of CO_2. This conclusion is in agreement with our findings that both *Chelifer*

and *Galeodes* exhibited a "free running", acyclic or continuous CO_2 output under high relative humidity, when the danger of respiratory water loss is minimized, or when the animals ingested some additional water with food.

Comparison of the discontinuous respiration between ticks and insects revealed special features concerning the role of spiracles, differences in metabolic rate, water retention and other physiological conditions, as concluded by Lighton et al. (1993). The cycles have been interpreted in terms of the stereotypic DVC (discontinuous ventilation cycles) composed of three phases: opened, closed and fluttering phase (Kestler, 1985; Lighton, 1991; Lighton et al., 1993). Physical factors are emphasized in regulation of the DVC.

These results regarding *Chelifer* and *Galeodes* indicate that the conventional DVC respiratory cycle is reduced to two essential phases in arachnids: a shorter phase of CO_2 emission and a longer phase of decreased or no CO_2 emission. Such a simplified bi-phasic respiratory cycle without the fluttering period seems to be characteristic of Prague cycles in general. Previous experiments with *Bruchus affinis* (Coleoptera; Sláma & Coquillaud, 1992) provided evidence for an active, neuromuscular, ventilatory expulsion of CO_2 through some opened spiracles. So far, there is no evidence that this would also apply to the PRC of *Chelifer* and *Galeodes*, because according to Babák (1921) there are no ventilatory movements in arachnids.

In previous experiments on *Ixodes*, PRC were occasionally combined with a small but constant proportion of continuously produced CO_2. The mechanism of PRC achieved only a homeostatic compensation for restraining the acidaemia, while some small proportion of total CO_2 was released by simple diffusion (Sláma, 1994). Combination of all these data suggests that some terrestrial invertebrate animals, insects and arachnids, possess a mechanism similar to an electronic microprocessor, which is collecting a number of input signals from the periphery, transforming these signals into the most economic respiratory output for successful survival and reproduction.

There are principally two different methods for recording CO_2 emissions: A) the flow-through, infra-red technique, which detects nonspecifically all kinds of CO_2 release from the body, including ventilatory outbursts of intratracheal CO_2 – and B) the constant volume, respirographic method, which does not properly record CO_2 released by continuous diffusion, but accurately records CO_2 evaporated from the liquids, even when this takes a fraction of a second and the CO_2 stays inside the body. To be accurate, the flow-through method uses absolutely dry air streams deprived of all CO_2 (i.e., conditions favouring cyclic respiration; Lighton, 1991; Lighton et al., 1993). Due to longer retention time of the instruments the method does not record the microcycles as described in Fig. 5. Some physiologists still believe the "diffusion theory of insect respiration", thus ignoring the possibility that an invertebrate animal can also actively regulate the respiratory acidaemia. These results provide evidence that not only insects, but also tracheate arachnids, can actively regulate the emissions of CO_2 which are responsible for homeostatic control of respiratory acidaemia. This is demonstrated by specific changes in frequency and amplitude of the respiratory cycles in response to food ingestion, temperature, humidity and locomotory activity. The results for *Chelifer* and *Galeodes* confirm our previous findings obtained from ticks (Sláma, 1991, 1994), that respiration of arachnids may be controlled by a nervous mechanism residing in the prosomal ganglionic mass, similar to the autonomic nervous mechanism (coelopulse) located in the thoracic ganglia of the ventral nerve cord in

insects (Sláma, 1988, 1991, 1994). The selective advantage of the actively regulated cyclic respiration in invertebrate evolution is undoubtedly water retention.

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