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VENTILATION IN NAMIB DESERT TENEBRIONID BEETLES: MASS SCALING AND EVIDENCE OF A NOVEL QUANTIZED FLUTTER-PHASE

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Summary

The mass scaling of discontinuous ventilation (DV) phenomena in adult motionless insects is currently unknown. I present DV phenomena from 10 species of Namib Desert tenebrionid beetles; four from the dune-sea habitat, five from the river-bed habitat and one from the gravel plain habitat, which is characterized by very low and patchy resource availability. This species differed from the others in many respects. However, all species exhibited a previously undescribed, convective and quantized F phase ventilation (ISP, or intermittent serial pulsation, phase). For dune-sea and river-bed habitat species, all DV characteristics except DV frequency (V phase CO_2 emission volume and rate, total and per-burst ISP phase CO_2 emission volume, and total rate) scaled tightly with body mass with a scaling exponent close to 1.0 (typical r^2>0.95–0.98), as did overall rate of CO_2 production and hence metabolic rate (MR). Consequently these parameters were independent of body mass when expressed on a mass-specific basis, explaining the independence of body mass and DV frequency. These findings are compatible with published DV data in other species and orders of insects, suggesting that these scaling phenomena may be widespread. The gravel plain species (*Epiphysa arenicola*) had an MR of 38%, V phase CO_2 volume of 41% and V phase CO_2 emission rate of 23% of those predicted on the basis of its body mass, and it emitted a greater proportion of CO_2 during its ISP phase (47% *vs* 24% of total CO_2 output per DV cycle in the other species). It is suggested that these discrepancies are respiratory and ventilatory adaptations to scarce and patchy energy and water availability.

Introduction

Several investigations have documented discontinuous ventilation cycles (DVCs) in motionless adult insects (e.g. Punt *et al.* 1957; Kestler, 1978, 1980; Bartholomew *et al.* 1985; Louw *et al.* 1986; Lighton, 1987, 1988*a*,*b*, 1990; Lighton and Lovegrove, 1990). These DVCs are usually detected as cyclic CO_2 emissions by sensitive flow-through respirometry, and have largely been compatible with the now-classic pupal insect ventilation theories advanced by Schneiderman and

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others (see Miller, 1981; Kestler, 1985; Slama, 1988; and Corbet, 1988, for reviews and discussions).

Briefly, it has been found that adult insects, when in a quiescent state, proceed cyclically through a closed-spiracle (C) phase during which external gas exchange is minimal, followed by a fluttering-spiracle (F) phase during which low endotracheal P_{O_2} triggers the rapid periodic inactivation of spiracular closer muscles, allowing ingress of significant O_2 and some egress of CO_2 and presumably H_2O. Finally, rising haemolymph P_{CO_2} triggers an open-spiracle (O) phase which may be accompanied by convective ventilation (in which case it is referred to as the V phase). In all insects monitored with sufficiently sensitive apparatus, the three phases of the DVC can be clearly distinguished. The C phase is marked by very low gas exchange rates; the F phase by a small increase in CO_2 emission rate ($\dot{V}_{CO_2}$) and a much larger increase in O_2 consumption rate ($\dot{V}_{O_2}$), approximating tissue $\dot{V}_{O_2}$ and yielding a respiratory exchange ratio (RER) of about 0.2; and the V phase by a large, sustained output of CO_2 and a rapid ingress of O_2, which quickly declines to a plateau level while CO_2 output continues at a high rate, yielding an RER of about 1.2 (see Lighton, 1988*a*). The F phase is, of course, not continuous with respect to O_2 and CO_2 exchange but appears as a smooth plateau in flow-through respirometry recordings, because limited temporal resolution precludes the separation of very rapid events (e.g. the F phase in the ant *Cataglyphis bicolor* consists of rapid spiracular flutterings at about 5 Hz; J. R. B. Lighton, T. Fukushi and R. Wehner, in preparation).

However, we still lack data in areas essential to realistic biophysical modelling of the DVC in adult insects; for example, the detailed and *quantitative* time course of spiracular movements, gas exchange rates and intratracheal and haemolymph pressure fluctuations during the C, F and V phases. At a less rigorous level, our knowledge of externally measurable ventilation phenomena in adult, motionless insects remains scarce and patchy.

Consequently, a number of basic questions in insect ventilatory physiology remain unanswered. Considering interspecific comparisons only, is DVC frequency related to body mass, as ventilation frequency is in mammals? Or is ventilation modulated by volume rather than frequency, or by both, across a range of body masses? What are the mass scaling characteristics, if any, of discontinuous ventilation phenomena in adult insects, and how do they compare to the mass scaling characteristics of metabolic phenomena? If an insect species has unusually low energy metabolism, and/or is adapted to an arid habitat, how do its ventilation characteristics differ from those of more 'normal' insects? Is the F phase invariably a rapid spiracular fluttering, not easily amenable to detailed analysis with present technology, or is it replaced in some species by other phenomena that may be more readily quantified?

It is clear that comparative data are required to resolve these questions and facilitate the selection of model animals, differing perhaps in certain key aspects of their ventilation strategy, for detailed biophysical study. To provide some preliminary answers I investigated 10 species of tenebrionid beetles from the

Namib Desert, Namibia (see Seely, 1978, for an introduction to the Namib Desert ecosystem). The 10 species cover a 40-fold range of body masses and occur in the three distinct habitats that comprise the Namib Desert. Four species are endemic to the dune-sea habitat [*Onymacris plana* Peringuey, *O. unguicularis* Haag, *O. laeviceps* Gebien and *Zoophosis* (*Cardiosis*) *fairmarei* Peringuey], five to the river-bed habitat [*Physadesmia globosa* Haag, *Zophosis orbicularis* Deyrolle, *Stenocara gracilipes* Solier and two subspecies of *O. rugatipennis rugatipennis* (Haag) and *albotesselata* (Schulze)], and one species occurs in the particularly harsh environment of the gravel plain and its associated rock outcrops (*Epiphysa arenicola* Penrith), although it can also occur in rocky areas of the river-bed habitat (Wharton and Seely, 1982).

The hot and hyper-arid Namib Desert was chosen as a study site because it is a challenging environment for small-bodied ectotherms. It is reasonable to assume that this has placed significant selective pressure on water economy, *inter alia* on control of respiratory water loss, in the endemic insect species. Paradoxically, the Namib Desert is singularly rich in insect species relative to other deserts. For example, the Sahara supports 63 species of tenebrionid beetles, none endemic to its dune-sea. The Namib, in contrast, boasts approximately 200 species, 17 endemic to its dune-sea (Koch, 1962). This diversity is an *a posteriori* indicator of successful adaptation to this environment, and the ventilatory adaptations, if any, that may contribute to colonization of the hyper-arid Namib Desert habitat are not without interest.

Materials and methods

Nine of the 10 beetle species were collected in the vicinity of Gobabeb research station (Desert Ecology Research Unit, Namibia): *Onymacris plana*, *O. unguicularis*, *O. laeviceps* and *Cardiosis fairmarei* from the dune sea; *Physadesmia globosa*, *Zophosis orbicularis*, *Stenocara gracilipes* and *O. rugatipennis rugatipennis* from the Kuiseb river bed; and *Epiphysa arenicola* from rock outcrops on the gravel plain. *Onymacris rugatipennis albotesselata* were collected from thorn scrub near the Kuiseb River in the far East of the Namib Desert. Only male beetles of the 10 species were collected to avoid possible artefacts from oogenesis or low egg metabolism in females.

I made measurements on the beetles 4–8 h after collection or, in the case of *O. rugatipennis albotesselata*, after about 2 weeks of captivity on a diet of lettuce and oat flakes, at an ambient temperature 26±5 °C. Beetles collected at Gobabeb were released at their collection site after measurements.

Ventilation was measured by flow-through CO_2 respirometry using a stable, high-resolution (0.1 p.p.m. CO_2), field-portable system described elsewhere (Lighton, 1990). DATACAN IV software (Sable Systems, 1015 Gayley Avenue, Suite 155, Los Angeles, CA 90024) was used for data acquisition and analysis, and for controlling the Peltier-effect constant-temperature cabinet in which the respirometer chamber was placed.

Air entering the respirometer chamber was dried and scrubbed of CO_2 with a Drierite/Ascarite/Drierite scrubber. Excurrent air was dried with a low-volume magnesium perchlorate scrubber; unlike conventional desiccants, magnesium perchlorate neither reacts with nor adsorbs CO_2. Flow rate ($100\,ml\,min^{-1}$) was regulated downstream from the respirometer chamber and CO_2 analyzer by a calibrated mass flow meter/controller.

In a typical recording, I weighed a beetle to 0.001 g and placed it in the respirometer chamber where it equilibrated to the measurement temperature (30±0.1°C) for 1 h. 30°C is a reasonable 'consensus temperature' for Namib Desert ectotherms (Lighton, 1990). I then bypassed the respirometer chamber, measured the system baseline, reconnected the respirometer chamber, allowed it to equilibrate for 5–10 min, and recorded the CO_2 output of the beetle for about 1 h. Data on flow rate and respirometer chamber temperature were simultaneously acquired. At the end of the recording I measured the system baseline again. If the beetle was motionless and yielding good ventilation data, I sometimes repeated the recording up to two more times. During analysis, I subtracted the beginning and end baseline readings (assuming linear drift; generally <0.2 p.p.m. CO_2), then converted the voltage record into CO_2 concentration and STP-corrected rate of CO_2 release ($\dot{V}_{CO_2}$), from which I could determine rates or absolute volumes of CO_2 release over any section of the recording.

To examine the relationship between abdominal ventilation pulsations and CO_2 output, I fenestrated the elytra of two *O. plana* beetles by cutting approximately 3 mm×6 mm rectangles through the elytral cuticle, taking care not to puncture the thin abdominal tergites, and visually monitored the abdomen while recording CO_2 output. No bleeding or other adverse effects were noted, and the beetles behaved normally. These data were collected at 26±5°C (room temperature) to facilitate continuous observation and, in terms of ventilation patterns, were very similar to those collected at 30°C. However, because of the difference in temperature, I did not include these ventilation data in the data set described below.

Means are accompanied by standard deviations (S.D.) and number of observations (N). Regressions were calculated by the least-squares method, and their significance was tested by analysis of variance. Regressions were compared using analysis of covariance (ANCOVA), and means were compared using Student's t-test after testing for homogeneity of variance. Correlations were assessed with Pearson's product-moment correlation coefficient, r. The significance level for all tests was $P<=0.05$.

Results

All of the species ventilated discontinuously while motionless. Sustained activity, such as escape behaviour, elevated mean $\dot{V}_{CO_2}$ and yielded distorted or apparently chaotic ventilation data, which were not further analyzed. As a corollary, stereotyped discontinuous ventilation could itself be used as a sensitive *a posteriori* indicator of motionlessness or very low activity. Hence, standard $\dot{V}_{CO_2}$ in

Table 1. *Mass (grams), S.D. $\dot{V}_{CO_2}$ (ml h^{-1}) S.D., N and the number of discontinuous ventilation cycles (DVCs) used to calculate $\dot{V}_{CO_2}$ of the 10 beetle taxa investigated*

Species	Mass (g)	S.D.	$\dot{V}_{CO_2}$ (ml h^{-1})	S.D.	*N*	DVCs
Onymacris plana	0.767	0.150	0.1876	0.0907	7	132
O. unguicularis	0.585	0.097	0.1266	0.0655	7	71
O. rugatipennis r.	0.496	0.085	0.0904	0.0205	5	32
O. rugatipennis a.	0.573	0.039	0.1173	0.0429	4	25
O. laeviceps	0.525	0.033	0.0867	0.0307	3	17
Epiphysa arenicola	1.237	0.149	0.0951	0.0341	5	25
Cardiosis fairmarei	0.032	–	0.0060	0.0015	1	6
Stenocara gracilipes	0.268	0.059	0.0965	0.0036	6	63
Zophosis orbicularis	0.103	0.016	0.0246	0.0053	3	19
Physadesmia globosa	0.516	0.118	0.1215	0.0785	13	110

In the case of *Onymacris rugatipennis*, *r.* denotes subspecies *rugatipennis* Haag and *a.* denotes subspecies *albotesselata* Schulze.

beetles known to be motionless could be accurately measured as the mean of an integral number of complete ventilation cycles (Table 1).

Standard $\dot{V}_{CO_2}$

The standard $\dot{V}_{CO_2}$ of the 10 beetle species scaled allometrically with mass (Fig. 1), with a scaling exponent of 0.858. Body mass explained 87% of $\dot{V}_{CO_2}$ variance. The only species differing markedly from this relationship was *Epiphysa arenicola*, with a $\dot{V}_{CO_2}$ only 38% of that predicted, based on the other species in the data set. This difference is significant (residuals analysis on the all-species regression, $t=10.1$; $P<0.001$). Hence *Epiphysa arenicola* is an outlier. If *Epiphysa arenicola* is excluded from the regression calculation, the mass scaling exponent becomes 0.979 (see Fig. 1 legend), and mass alone explains 95% of the variance in $\dot{V}_{CO_2}$.

$\dot{V}_{CO_2}$ can be converted to $\dot{V}_{O_2}$ if the respiratory quotient (RQ) is known. I could not determine RQ values in this investigation, but if a reasonable 'consensus' RQ of 0.8 is assumed, the scaling of $\dot{V}_{O_2}$ on mass becomes;

$$\dot{V}_{O_2} = 0.2812M^{1.005}, \quad (1)$$

where $\dot{V}_{O_2}$ is in ml h^{-1} and M is body mass in grams (*Epiphysa arenicola* excluded; the standard error of the exponent is 0.085).

Discontinuous ventilation

A typical record of discontinuous ventilation is shown in Fig. 2. All of the species ventilated with this characteristic pattern when motionless. CO_2 output was very low at the start of the DVC, and remained low until a variable number of approximately equally spaced, small emissions of CO_2 occurred (these were not

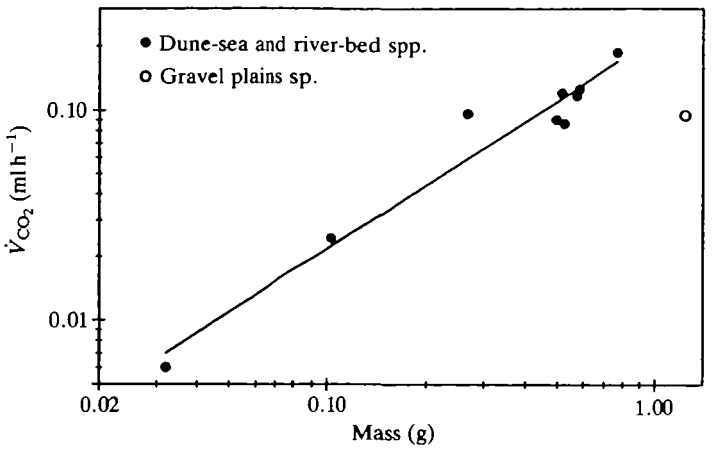

Fig. 1. The relationship between mean standard $\dot{V}_{CO_2}$ and mean body mass in 10 species of Namib Desert adesmiine tenebrionids. The regression line excludes *Epiphysa arenicola* (open circle: see below and text). The equation relating $\dot{V}_{CO_2}$ to mass in all species is $\dot{V}_{CO_2}=0.1615M^{0.858}$, where $\dot{V}_{CO_2}$ is in ml h^{-1} and M is body mass in grams ($F=52.4$, $P<0.0001$). The standard error of the exponent is 0.118. If *Epiphysa arenicola* is excluded from the data set (outlier; see text), the equation (as shown above) becomes $\dot{V}_{CO_2}=0.2024M^{0.979}$, where units are as before ($F=149$, $P<0.0001$).

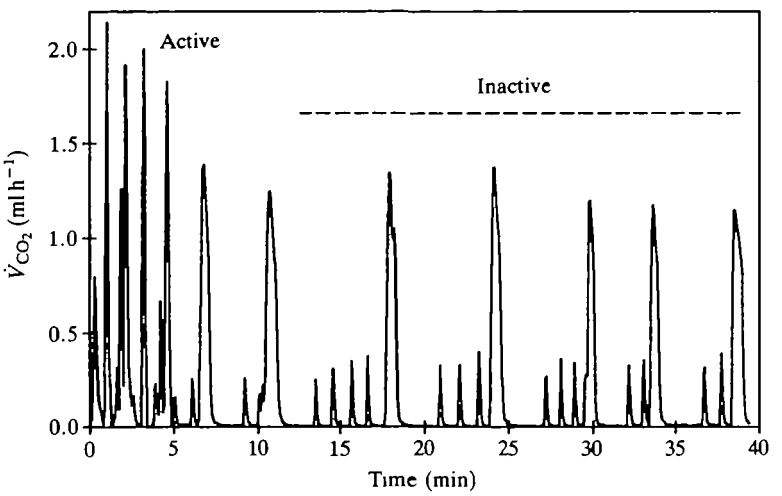

Fig. 2. A typical ventilation pattern of the kind displayed by all of the species investigated, which differed chiefly in terms of CO_2 emission volumes. Species, *Onymacris plana*; mass 0.639 g, at 30°C. The transition from activity to motionlessness can be plainly seen from the ventilation patterns. When motionless, mean $\dot{V}_{CO_2}$ was 0.143 ml h^{-1}; the mean discontinuous ventilation cycle period was 5.1 min (3.3 mHz).

invariably present in short DVCs). CO_2 output remained low between these emissions. Finally, an unambiguous V phase occurred, and the cycle repeated.

The DVCs reported here have some novel characteristics, the most striking of which is the absence of marginally elevated $\dot{V}_{CO_2}$ after the C phase and prior to the V phase that characteristically accompanies the F phase in other adult insects (e.g. Punt *et al.* 1957; Lighton, 1988*a*, 1990). Instead, the 'F phase' consisted of discrete, small, widely but regularly spaced CO_2 emissions ('F bursts') followed by an unambiguous V phase ('V burst'), with very little measurable CO_2 output in between and with no measurable tendency for the inter-emission CO_2 output to increase as the cycle proceeded towards the V phase. This may, therefore, constitute a new form of insect ventilation, or at least a novel modulation of a previously described ventilation phase. (Louw *et al.* 1986, reported cyclic CO_2 emission in *Onymacris unguicularis*, but did not report any F bursts. However, the resolution of their data acquisition system – a chart recorder – was only sufficient to resolve the V bursts; see Fig. 1 of that paper.)

The V phase

V bursts could be unambiguously distinguished from F bursts in all species investigated. Fig. 3 shows the bimodal distribution of the CO_2 emissions (F bursts *vs* bursts). Compared to V bursts, the volume of F bursts was always lower and much less variable. The DVC frequencies, V burst volumes, V burst durations and C phase durations of the 10 species investigated are summarized in Table 2. In the fenestrated *O. plana*, the V phase was always accompanied by several visible abdominal pulsations (usually more than 10). This was probably the case with all

Table 2. *Ventilation characteristics (V and C phases) of the 10 beetle species investigated*

Species	DVF (mHz)	S.D.	VBV (μl)	S.D.	VPD (s)	S.D.	CPD (s)	S.D.	*N*
Onymacris plana	3.7	2.9	15.2	6.1	69.0	18.0	145	76	132
O. unguicularis	3.2	2.1	10.1	3.5	80.5	19.2	139	101	71
O. rugatipennis r.	2.7	1.4	9.4	4.1	75.4	10.7	155	63	32
O. rugatipennis a.	3.3	1.9	9.7	3.5	71.6	10.8	134	52	25
O. laeviceps	3.0	1.5	7.3	1.3	65.2	10.9	166	38	17
Epiphysa arenicola	2.9	1.6	7.8	2.5	101.5	32.8	196	121	25
Cardiosis fairmaryii	2.7	0.6	0.52	0.07	96.4	23.1	137	35	6
Stenocara gracilipes	4.1	2.1	5.2	1.4	63.3	10.7	52	32	63
Zophosis orbicularis	4.0	2.1	1.8	1.0	81.6	19.5	71	30	19
Physadesmia globosa	6.5	5.7	5.7	3.1	55.9	12.7	110	63	110

DVF, discontinuous ventilation frequency (measured from the end of the previous V phase to the end of the current V phase); VBV, V phase burst volume; VPD, V phase duration (note that, because of the nature of flow-through respirometry and its associated response distortions, this figure is probably a slight over-estimate); CPD, closed phase duration (measured from the end of the previous V phase to the start of the first F burst).

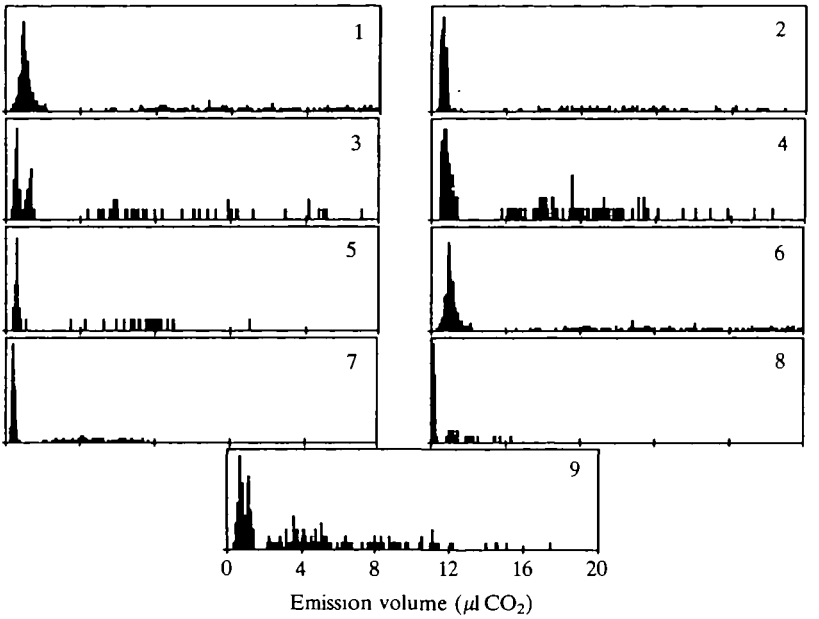

Fig. 3. Histogram distributions of CO_2 emission volumes in nine of the 10 species investigated, showing the markedly bimodal distribution of ventilation volumes. Each set of histograms consists of 600 bins, each 0.033 μl wide. *Cardiosis fairmaryii* is not included because its tiny emission volumes compress its distribution into the first few bins, but the bimodal distribution was equally evident in that species (see text). Species code (with number of F and V phase ventilation events analyzed): 1, *Onymacris plana* (574); 2, *O. unguicularis* (430); 3, *O. rugatipennis rugatipennis* (126); 4, *O. rugatipennis albotesselata* (188); 5, *O. laeviceps* (54); 6, *Epiphysa arenicola* (97); 7, *Stenocara gracilipes* (355); 8, *Zophosis orbicularis* (87); 9, *Physadesmia globosa* (271). *Cardiosis fairmaryii* [(not shown) 24].

species (see also Bartholomew *et al.* 1985; Lighton, 1988*a*; *E. arenicola*, see Discussion).

V phase CO_2 emission volumes scaled allometrically with body mass (Fig. 4). Once again, *E. arenicola* was an outlier in this relationship, with a lower than expected V burst volume (residuals analysis; $t=10.5$; $P<0.001$). If *E. arenicola* is excluded from the data set, the scaling exponent of V burst volume on mass is 0.985, and mass alone explains 96% of the variance in mean V burst volume. V burst volume and standard $\dot{V}_{CO_2}$ scaled identically with mass (ANCOVA: $F=0.03$, $P>0.4$, shared slope=0.982).

DVC frequency, unlike V burst volume, did not scale with mass (Fig. 5; $r^2=0.005$, $F=0.04$, $P>0.4$); indeed, a species of intermediate mass had the highest DVC frequency (Table 2).

The approximate *rate* of CO_2 emission during the V phase could be calculated by dividing V burst volumes by measured V burst durations (see below for a discussion of V phase length measurement). V burst emission rates scaled

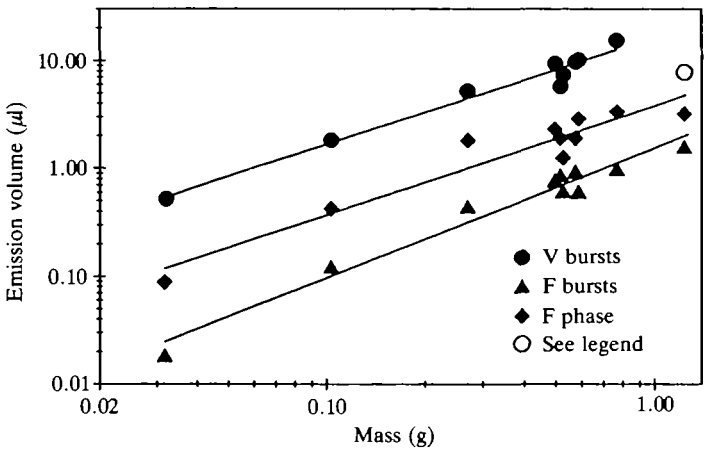

Fig. 4. V and F burst, and F phase, CO_2 emission volumes in relation to body mass in the 10 beetle species investigated. V burst volumes scaled with body mass as $VBV=0.0153M^{0.985}$, where VBV is V burst volume in ml and M is body mass in grams ($r^2=0.96$, $F=190$, $P<0.0001$, the standard error of the exponent is 0.071). *Epiphysa arenicola* (open circle) was an outlier in this relationship (residuals analysis: $t=10.5$, $P<0.001$). F burst volumes in all species scaled with body mass as $FBV=0.00151M^{1.196}$, where FBV is F burst volume in ml and M is body mass in grams ($r^2=0.97$, $F=241$, $P<0.0001$, the standard error of the exponent is 0.077). F phase volumes in all species scaled with body mass as $FPV=0.00380M^{1.004}$, where FPV is F phase volume in ml and M is body mass in grams ($r^2=0.91$, $F=84$, $P<0.0001$, the standard error of the exponent is 0.109). All lines are parallel with a shared exponent of 1.067 (ANCOVA: $P=0.8$).

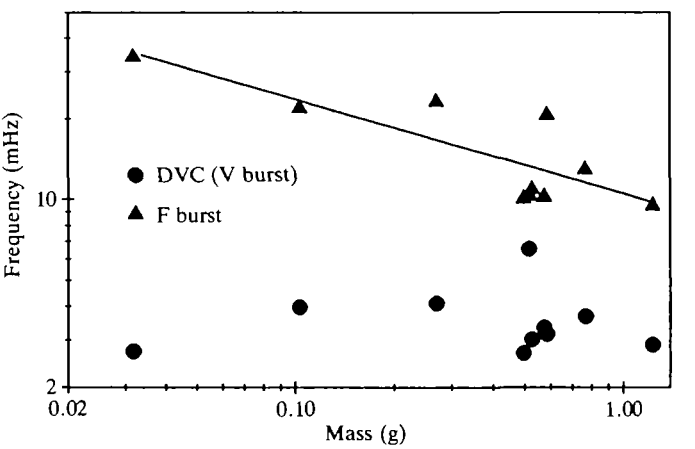

Fig. 5. The frequency of V and F bursts in relation to body mass in the 10 beetle species investigated. F burst frequency declined significantly with body mass ($FBF=10.42M^{-0.354}$, where FBF is F burst frequency in mHz and M is body mass in grams; $r^2=0.69$, $F=18$, $P<0.001$, the standard error of the exponent is 0.077). In contrast, there was no relationship between body mass and V burst (=DVC) frequency in the species investigated ($r^2=0.01$, $P>0.3$).

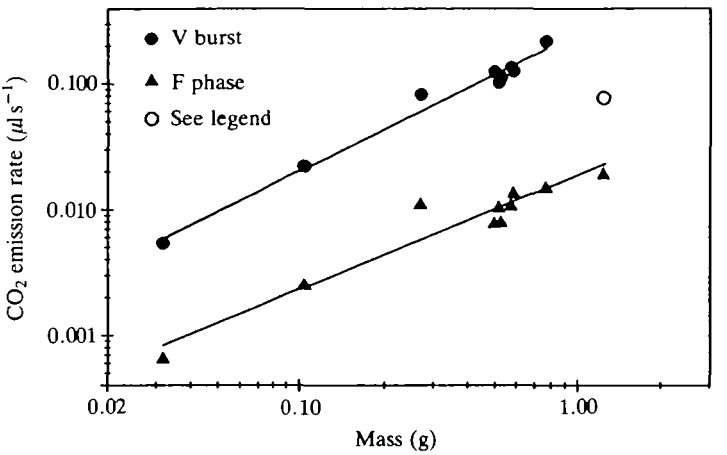

Fig. 6. V burst and F phase CO_2 emission *rates* as a function of body mass in the 10 beetle species investigated. *Epiphysa arenicola* (open circle) was a marked outlier in terms of the V phase, with a CO_2 emission rate only 24% of that predicted (residuals analysis: $t=23$, $P<0.0001$). For the other nine species, $VER=0.00026M^{1.096}$, where VER is V burst emission rate in $\mu l\,s^{-1}$ and M is body mass in grams ($r^2=0.98$, $F=366$, $P<0.0001$, the standard error of the exponent is 0.057). For all species, $FER=0.0000191M^{0.908}$, where FER is F phase emission rate in $\mu l\,s^{-1}$ and M is body mass in grams ($r^2=0.92$, $F=95$, $P<0.0001$, the standard error of the exponent is 0.093). The two lines share an exponent of 0.989 (ANCOVA: $P=0.1$).

allometrically with mass, with smaller species emitting CO_2 more slowly (Fig. 6). The mass scaling exponent was 1.096 (standard error 0.057), with mass explaining 98% of V burst CO_2 emission rate variance. Again, *E. arenicola* departed significantly from this relationship, emitting CO_2 at only 23% of the predicted rate.

The F phase

Like V burst volumes, F burst and F phase volumes increased allometrically with body mass, this time with no outliers (Fig. 4, Table 3).

Nine of the 10 species emitted very similar proportions of CO_2 in their F phases (F/V phase volume ratio). 24±7% of total CO_2 release occurred in the F phase in all species except *E. arenicola*, which emitted 47% in this phase, a significantly larger amount ($t=10.3$, $P<0.001$).

F burst frequency, unlike V burst frequency (=DVC frequency), scaled allometrically with mass (Fig. 5), with larger species showing lower F burst frequencies. There were no significant outliers.

Each F burst corresponded to a single, brief abdominal pulsation in the fenestrated *O. plana*. Clearly, the F burst has a substantial convective component which is induced by actual ventilation movements, unlike other F phases described in the literature, where any convective component arises from the passive bulk flow of air down a trans-spiracular pressure gradient.

DVC phase lengths

The C phase increased in length with increasing DVC duration (Fig. 7), up to a C phase length of about 350 s, at or before which point the F phase was generally triggered. Essentially all DVCs longer than 250 s, however, contained an F phase.

Table 3. *Ventilation characteristics (F phase only) of the 10 beetle species investigated*

Species	FBF (mHz)	S.D.	*N*	FBV (μl)	S.D.	*N*	FBN	S.D.	FPD (s)	S.D.
Onymacris plana	13.1	5.4	96	0.99	0.24	113	3.29	1.75	254	67
O. unguicularis	20.9	10.4	65	0.61	0.11	69	4.57	2.07	282	242
O. rugatipennis r.	10.2	3.8	22	0.77	0.31	30	2.60	1.71	268	220
O. rugatipennis a.	10.3	3.5	14	0.93	0.23	23	1.96	1.11	186	135
O. laeviceps	11.0	1.7	10	0.61	0.08	16	2.00	0.89	169	94
Epiphysa arenicola	9.6	6.5	12	1.58	0.29	20	2.00	1.08	196	137
Cardiosis fairmaryii	34.6	3.7	6	0.018	0.003	6	5.17	3.13	149	105
Stenocara gracilipes	23.5	6.6	60	0.44	0.06	62	4.06	1.64	181	97
Zophosis orbicularis	22.3	10.4	15	0.012	0.003	17	3.41	1.62	190	135
Physadesmia globosa	10.5	3.6	37	0.86	0.24	63	2.03	1.27	188	145

Sample numbers refer to discontinuous ventilation cycles (DVCs) in which F bursts occurred.

FBF, F phase burst frequency (note that the sample number of this variable may be less than the total number of DVCs in which F bursts occurred, because two or more F bursts are required to characterize frequency); FBV, F burst volume; FBN, number of F bursts per DVC; FPD, F phase duration (measured from the start of the first F burst to the start of the V phase).

The sample sizes for FBV, FBN and FPD are equivalent, and are usually less than the total number of DVCs (Table 2) because some short DVCs did not contain an F phase.

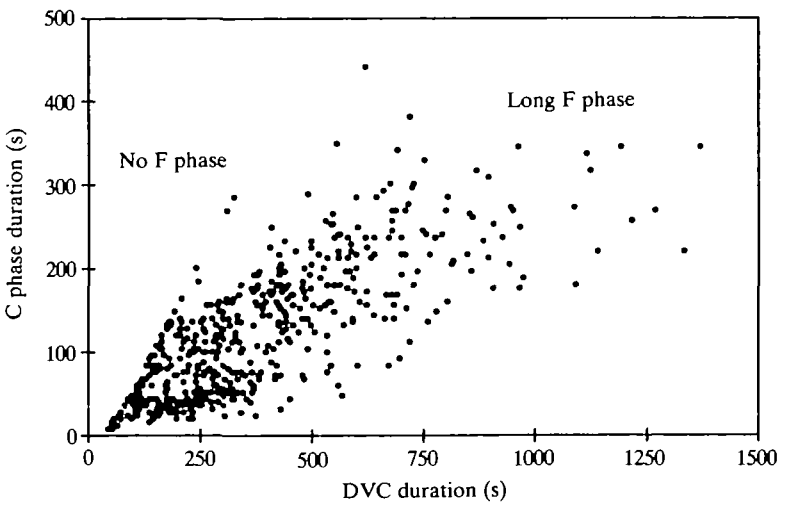

Fig. 7. C phase duration is correlated with total discontinuous ventilation cycle (DVC) duration (r=0.69, N=504, P<0.0001). The sharply defined line at $x=y$ corresponds to DVCs in which no F phase occurred.

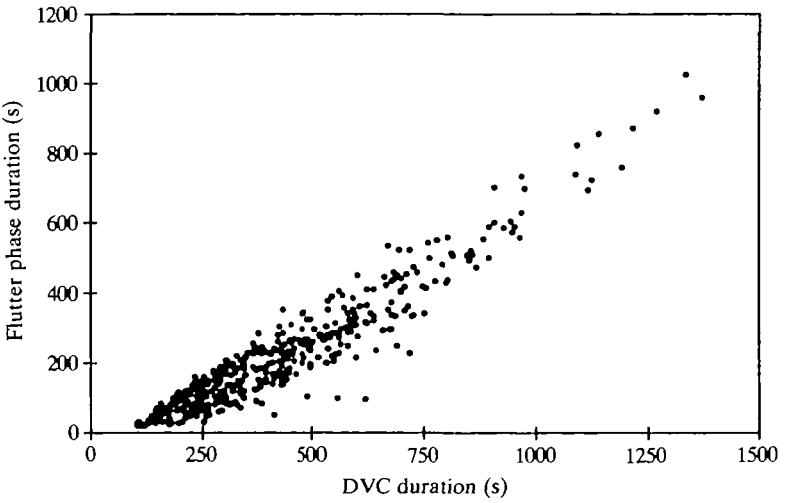

Fig. 8. F phase duration is linearly related to total discontinuous ventilation cycle (DVC) duration in all species investigated, which form a single data set. FPL=−77.7+0.702DVCD, where FPL is F phase length in seconds and DVCD is DVC duration in seconds (r^2=0.90, F=3771, P<0.0001).

The range of termination time of the C phase, relative to DVC duration, is quite wide and shows no apparent difference between species. Because of the slightly non-linear C phase length *vs* DVC length relationship, a linear regression model is not appropriate to these data.

In contrast to the C phase, the length of the F phase was very tightly controlled relative to DVC duration, with the proportional length of the F phase for all DVCs and all species forming one coherent linear data set (Fig. 8). The slope of this relationship (the 'F ventilation phase coefficient'; Lighton, 1990) is 0.702 (S.E.=0.011, N=419, r^2=0.90).

The length of the V phase is not easy to characterize accurately in a flow-through system because of temporal response distortions. These were corrected, as far as possible, with the single-order response correction technique described by Bartholomew *et al.* (1981), but V phase lengths should nevertheless be regarded as slight overestimates. At a constant flow rate and respirometer volume this does not significantly affect the *slope* of regressions (e.g. the V ventilation phase coefficient), merely the intercept of the relationship. In the 10 species investigated, the V ventilation phase coefficient was 0.066 (S.E.=0.011).

Discussion

Standard $\dot{V}_{CO_2}$

Considerable uncertainty exists in the literature on the subject of insect standard metabolic rate (SMR), chiefly because the SMR of most insects is low, making

constant-volume or constant-pressure, closed-system respirometry the only practical measurement system until very recently. Both techniques integrate measurements over long periods. Further, visual observation of animals within respirometers submerged in temperature-regulated waterbaths is often difficult or impossible. It is therefore likely that many or most measurements of insect SMR in the literature are significant overestimates because active and inactive MR could not be accurately separated.

The technique described here, in contrast, affords excellent temporal resolution, so that active and inactive periods can be distinguished and analyzed separately. Further, in the case of insects that ventilate discontinuously, and in which the ventilation patterns corresponding to inactivity are known, SMR can be determined by averaging gas exchange rates over an integral number of 'characteristic-inactive' DVCs. SMR can either be directly determined if simultaneous measurement of $\dot{V}_{CO_2}$ and $\dot{V}_{O_2}$ is feasible (body mass $\geqslant 1$ g; Lighton, 1988*a*), or, as here, it can be calculated in the desired units by measuring, or assuming, an RQ. The RQ can, if necessary and practical, be measured separately using a closed-system technique subject to the usual *caveats* concerning the effect of activity on RQ (see, for example, Lighton, 1988*b*).

The SMR of very few insects has been measured by flow-through respirometry under conditions where the ventilation patterns corresponding to inactivity are known. The relationship between body mass and $\dot{V}_{CO_2}$ in nine species of beetles and two species of ants is shown in Fig. 9. Again, *E. arenicola* is an outlier in this regression (t=9.5; P<0.001), with lower than predicted $\dot{V}_{CO_2}$. Because the shared slope of the relationship does not differ significantly from 1.0, $\dot{V}_{CO_2}$ is constant when expressed on a mass-specific basis at 0.233 ml $CO_2\,g^{-1}\,h^{-1}$, corresponding to a $\dot{V}_{O_2}$ of 0.292 ml $g^{-1}\,h^{-1}$ and an SMR of 1.63 W kg^{-1} at an RQ of 0.8 and body temperature of 30°C.

This equation yields significantly lower $\dot{V}_{O_2}$ values than do other equations relating body mass to insect $\dot{V}_{O_2}$ in the literature, after temperature correction (e.g. Kittel, 1941; Bartholomew and Casey, 1977; Lighton *et al.* 1987; although the $\dot{V}_{CO_2}$ reported by Louw *et al.* 1986 for *Onymacris unguicularis* while motionless and ventilating discontinuously is similar to that reported here). Part of this discrepancy may be due to the disproportionate representation of arid-region species in this data set; arid-region species are commonly considered to exhibit atypically low $\dot{V}_{O_2}$, a possible adaptation to low and patchy energy and water availability (see Snyder, 1971). However, it is also possible that the lower predictions of equation 1 stem from the fact that insects *known* to be motionless provided the data. This is perhaps a more feasible explanation, which should be considered by investigators wishing to measure insect $\dot{V}_{O_2}$ accurately and/or collect allometric data sets relating insect mass to standard $\dot{V}_{O_2}$.

Surprisingly, in view of the probable differences in energy and water availability between the dune-sea and river-bed habitats in the Namib Desert, no differences in standard $\dot{V}_{CO_2}$ were found between beetle species endemic to these very different habitats. This argues either that energy and water availability are roughly

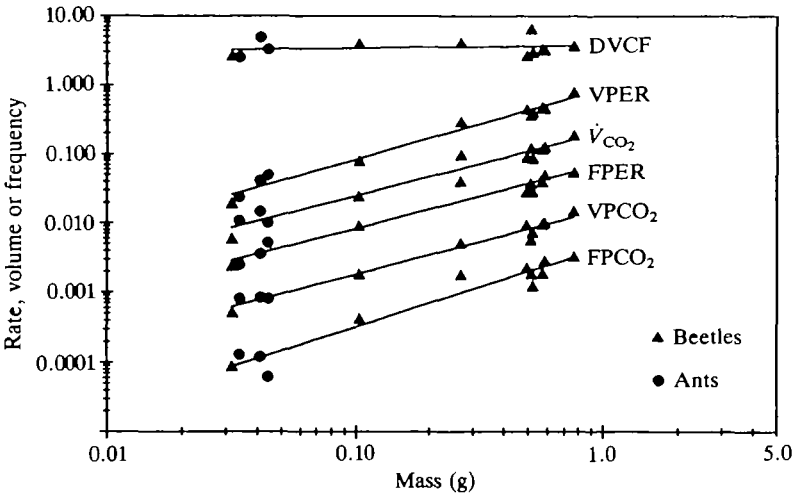

Fig. 9. DVC frequency (DVCF: mHz), V phase CO_2 emission rate (VPER: $ml\,h^{-1}$), overall rate of CO_2 emission ($\dot{V}_{CO_2}$: $ml\,h^{-1}$), F phase CO_2 emission rate (FPER: $ml\,h^{-1}$), V phase CO_2 emission volume ($VPCO_2$: ml) and F phase emission volume ($FPCO_2$: ml) in nine species of tenebrionid beetles, excluding *Epiphysa arenicola*. Ant data (filled circles) are from Lighton (1990) and J. R. B. Lighton and R. Wehner (in preparation). Body temperature is 30°C. Raw data regression lines are plotted; however, all regressions shared a common slope of 0.99 (ANCOVA: $P=0.1$), not significantly different from 1.0 ($P>0.3$). On a mass-specific basis, V and F phase CO_2 emission rates are 0.832 and $0.078\,ml\,g^{-1}\,h^{-1}$, respectively, V and F phase CO_2 emission volumes are 17.2 and $3.42\,\mu l\,g^{-1}$, respectively, and overall rate of CO_2 emission is $0.233\,ml\,g^{-1}\,h^{-1}$. Similar values can be inferred from other studies conducted at different temperatures, but are not included in this data set because temperature affects DVC variables (Lighton, 1988*b*).

equivalent between the two habitats, given the hypothesis that reduced energy and water availability are generally reflected in reduced rates of energy metabolism, or that energy metabolism is independent of energy and water availability in the dune-sea and river-bed beetle species investigated. Given the substantial energy input to the Namib Desert dune-sea from allochthonous wind-blown plant and insect detritus, which is efficiently trapped by the dune slip-faces in which the dune-sea species live, the first explanation is perhaps more likely, especially because water input from dew and advective fogs, absorbed by hygroscopic detritus and even harvested directly by some beetle species (Hamilton and Seely, 1976), is significant in the dune-sea habitat.

The gravel plain habitat in the Namib Desert is, in spite of occasional fluxes of abundant vegetation following rare and unpredictable rains, indisputably marked by extremely low resource availability for much of the year, and sometimes for several years in succession (Seely, 1978; Wharton and Seely, 1982). *Epiphysa arenicola* is common in that habitat, and can often be found beneath rocks in areas that otherwise appear utterly devoid of macroscopic animal life, with the

exception of a few thysanurans (J. R. B. Lighton, personal observations). Its low SMR, 38% of that predicted for its body mass from the dune-sea and river-bed beetle data set (Fig. 1), does not disprove the hypothesis that low resource availability and low SMR are correlated. The resolution of how general this correlation and other possible correlations between environment and SMR may be awaits collection of further suitable data sets derived from truly inactive insects.

It is of some interest that the scaling exponents of insect SMR on mass presented here do not differ significantly from 1.0, the value calculated by Kittel (1941) in her epic and meticulous survey of insect $\dot{V}_{O_2}$. Much ingenuity has been expended on explanations of the famous Kleiber exponent (approximately 0.75) of interspecific mass scaling of BMR or SMR in tetrapods, and most of these explanations (and their refutations and counter-explanations) are equally relevant to arthropods. I do not wish to enter the fray here, but I would wish merely to point out that the SMR of insects and tetrapods may scale differently with respect to body mass, and that this difference might profitably be borne in mind when formulating general scaling theories.

Discontinuous ventilation

The data presented above finally allow the tentative resolution of some long-standing questions regarding the occurrence and scaling of discontinuous ventilation phenomena in adult insects, and are combined with those of two species of ants, *Camponotus detritus* and *Cataglyphis bicolor*, in Fig. 9 (because *Epiphysa arenicola* has very low $\dot{V}_{CO_2}$ and departs significantly from many of the relationships discussed below, it is considered as a separate case).

V burst CO_2 emission volumes and rates

The volume of CO_2 emitted during the V phase scales strongly with mass in two different orders of insects (Fig. 9), with a shared mass scaling exponent of 0.99, which does not disprove mass-specific independence of V burst volume. Given the independence of DVC frequency on mass in the available data, the hypothesis that interspecific differences in $\dot{V}_{CO_2}$ are expressed chiefly in differences in V burst volume cannot be disproved.

As with V burst volume, V burst CO_2 emission rate scaled against mass with an exponent not significantly different from 1.0 (Figs 6, 9). Hence V burst CO_2 emission rate, *on a mass-specific basis*, is independent of body mass in the insect species investigated.

Data from one species of ant (*Camponotus vicinus*; Lighton, 1988*b*) show that V phase CO_2 volume and DVC frequency were inversely co-modulated by $\dot{V}_{CO_2}$, which is not incompatible with a constant rate of V phase CO_2 emission. In contrast, modulation of V phase emission rate with increasing $\dot{V}_{CO_2}$ would allow the maintenance of a constant V phase CO_2 emission volume while DVC frequency is increased (and hence V phase duration is decreased). Whether this strategy occurs in any insect is currently unknown.

F phase CO_2 emission volumes and rates

F phase emission volumes and rates again scale against mass with a shared slope not significantly different from 1.0. In the nine dune-sea and river-bed beetle species investigated, a mean of 24 % of total CO_2 output occurred in the F phase. This is rather more than that in other species investigated (e.g. 13 % and 7 % in dune-sea and laboratory colonies, respectively, of the Namib dune-sea ant *Camponotus detritus*; Lighton, 1990, and 6 % in the more mesic beetle species *Psammodes striatus*; Lighton, 1988*a*). These latter insects employ a more conventional, rapid-flutter F phase and this may be responsible for part of the difference. However, I have suggested (Lighton, 1990) that xeric species may display a tendency to shift more of their total CO_2 output to the F phase relative to mesic species and the current findings do not disprove that hypothesis. Given that F-phase $\dot{V}_{CO_2}$ presumably cannot be increased indefinitely without reducing water vapour retention, such a 'shift' may take one of two forms: either an increase in F phase duration relative to DVC length, or a reduction in V phase volume. Underlying that hypothesis is another: that H_2O loss rates *as a proportion of* CO_2 emission rates may be lower in the F than in the V phase. The requirement to remove CO_2 rapidly and effectively from the haemolymph across moist respiratory surfaces in the V phase may increase water loss rates per unit CO_2 released relative to the F phase, especially because the V phase depends (in many species at least) on prolonged convective ventilation that must affect a large proportion of the entire tracheal system. In contrast, the primary purpose of the F phase is to obtain oxygen for tissue respiration, in most species through bulk flow and diffusion. This hypothesis has not yet been tested, and so the validity of hypotheses based on it must remain speculative. Nevertheless, a pattern of increased CO_2 output in the F phase in arid-adapted insects is beginning to emerge. More data are needed in this area.

DVC frequency

DVC frequency is not related to insect mass in the species for which data exist (Fig. 9). There is not even a marginal but non-significant trend in the data. Within insect species, DVC frequency may be modulated by $\dot{V}_{CO_2}$ (Lighton, 1988*b*; J. R. B. Lighton and R. Wehner, in preparation), but this modulation does not hold in interspecific comparisons. Given the data available, the hypothesis that insect DVC frequency scales with body mass is therefore disproved.

It is not surprising that DVC frequency is independent of body mass in the species for which data are available. This is a corollary of the mass-independence of major DVC characteristics (Fig. 9). A constant mass-specific volume and rate of CO_2 emission, presumably caused by constant efficiency of the enzymatic, diffusional and convective mechanisms for removing CO_2 from the haemolymph and tissues, would necessarily reduce or eliminate the dependence of DVC frequency on body mass. A simple model of CO_2 exchange makes this point clearer. Let us define $FPCO_2$ and $VPCO_2$ as the F and V phase CO_2 emission volumes, and

DVCD as the DVC duration. Assuming that the mass scaling exponent for rates and volumes is 1.0 (Fig. 9) and that CO_2 release during the C phase is negligible, then at any mass $DVCD=(FPCO_2+VPCO_2)/\dot{V}_{CO_2}$. Using the values in the legend to Fig. 9, DVCD is 318.6 s or 3.14 mHz, a *mass-independent* value well within the measured range (Fig. 9, Table 2).

F phase dynamics

The F phases of all 10 species of Namib Desert beetles investigated here differed fundamentally from any F phases previously described in the literature, whether for pupal or adult insects. In fact the term 'F phase' is a misnomer because each 'flutter' was a single, short cycle of convective ventilation caused by an abdominal pulsation. Hence the terms 'ISP (intermittent single pulsation) phase' and 'ISP burst' (for a single event in the ISP phase) might be more appropriate.

It is interesting to speculate on the dynamics of O_2 and CO_2 exchange revealed in the V phase of the beetle *Psammodes striatus* (Lighton, 1988*a*); CO_2 output is quite low, and O_2 ingress very high, during the initial few abdominal ventilation movements. So much so that a *single* convective ventilation event may have many of the characteristics of a more conventional, passive F phase. In fact the CO_2 and O_2 exchange characteristics of F and ISP phases appear to be identical; for example, it can be calculated from data in Fig. 9 that the estimated RER during the ISP phase is 0.27, assuming an overall RQ of 0.8. This value is well within the range expected for the F phase (see Lighton, 1988*a*) and has been verified by direct measurement (J. R. B. Lighton, in preparation).

The comparative merits, as far as respiratory water loss rates are concerned, of F and ISP phases remain to be determined. However, because progress in this field depends in large measure on instrumentation, and because current H_2O sensors are notoriously noisy and unreliable at the levels of sensitivity required to resolve water loss during ventilation in small inactive insects, the ISP phase offers substantial measurement advantages compared to the F phase, because it is quantized. In other words, CO_2, O_2 and H_2O exchange are confined to brief events that are potentially resolvable (particularly for H_2O) with the sensors currently available, rather than maintained at low levels over long periods. This property may allow resolution of the question of respiratory H_2O loss per unit of CO_2 emitted in the ISP *vs* V phases (see also Kestler 1980, 1985, for a different approach). The interesting pressure-pulse theories of Corbet (1988) may have application here.

Relative durations of phases in the DVC

In contrast to the C phase duration, which is only loosely correlated with DVC length in the species investigated here (Fig. 7), F phase duration is very tightly coupled with DVC length (Fig. 8). The C phase starts at the end of the last V phase, during which the endotracheal space has reached approximately atmospheric P_{O_2}, and lasts until endotracheal O_2 concentration reaches a critical

threshold (Levy and Schneiderman, 1966; Burkett and Schneiderman, 1974). Once this threshold is reached, the flutter phase begins, and it continues until haemolymph CO_2 levels reach a critical threshold (both thresholds are subject to some modulation). Judging by the observed close interdependence of F phase and DVC durations, it seems probable that any modulatory influences co-modulate the two setpoints very closely (and/or that the V phase termination setpoint is very variable compared to the others). Although the species investigated here all show an F ventilation phase coefficient of 0.70, some other insect species do not, although they do exhibit similarly tight phase-length coupling (e.g. *Camponotus detritus* and *Cataglyphis bicolor* F phase ventilation coefficients are 0.20 and 0.52, respectively; Lighton, 1990; J. R. B. Lighton and R. Wehner, in preparation). Whether these differences reflect different F or V phase initiation setpoints (or both) remains to be determined. In the absence of a reduction in V phase volume, however, increasing the F phase ventilation coefficient offers a way to increase the relative contribution of the F phase to CO_2 loss.

Low SMR: effects on discontinuous ventilation

The SMR of the gravel plain beetle *Epiphysa arenicola* is significantly lower than predicted on the basis of its body mass (Fig. 1). It is also a prominent outlier in most other relationships described in this paper. Table 4 summarizes these differences.

The primary effect of low $\dot{V}_{CO_2}$ on the ventilation characteristics of *E. arenicola* is an atypically low V phase CO_2 emission volume. Coupled to this is a very low V phase CO_2 emission rate. The former factor explains how *E. arenicola* has emphasized the F phase in terms of CO_2 emission relative to the other species. Clearly, *E. arenicola* shifts far more of its total CO_2 output (47 %) into its F (ISP) phase than do the other species. However, note that the F phase CO_2 output of

Table 4. *A summary of the chief differences between the gravel plain beetle species* Epiphysa arenicola *and the dune-sea/river-bed beetle species data set*

	Difference (%)	Significance
Metabolic rate (as $\dot{V}_{CO_2}$)	−62	***
V burst CO_2 volume	−59	***
F burst CO_2 volume	−19	NS
F/V phase CO_2 output	+96	***
V burst CO_2 emission rate	−77	***
F phase CO_2 emission rate	−16	NS

Differences are expressed as a percentage of the predicted value, given the mean mass of *E. arenicola*, for mass-dependent variables (all except F/V phase CO_2 output ratio).

Significance (***=$P<0.001$, NS=$P>0.05$) is calculated from residuals analysis about the regression line if *E. arenicola* is included in the regression, or by a *t*-test of the square root of arcsine-transformed data in the case of F/V phase output ratio.

Because the other species formed very coherent data sets, significance is frequently high.

E. arenicola is normal for its body mass (Figs 4, 6), and this 'shift' has occurred passively as the result of a diminished V phase CO_2 output. If the hypothesis is correct that respiratory H_2O loss per unit CO_2 emission is lower in the F than in the V phase, this may be a water-conserving measure that acts in tandem with a lowered metabolic rate, lowering tissue O_2 requirements and reducing net throughput of dry air through the respiratory system (see Lighton, 1990). In this respect, *E. arenicola*'s very low V phase CO_2 emission rate may be relevant. Judging by the fourfold shortfall in *E. arenicola*'s V phase CO_2 emission rate compared to that of the other species, it appears likely that the convective component of its V phase has been reduced, or even possibly eliminated. The reduced V phase emission volume in *E. arenicola* may make diffusion, perhaps aided by some convection, a viable strategy for eliminating CO_2. Whether a chiefly diffusive *vs* chiefly convective V phase offers any advantages in terms of water loss rates in *E. arenicola* must await further study, but it should be noted that the energy saved by reducing, or dispensing with, abdominal ventilatory pulsations may be significant (Lighton, 1988*a*).

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