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SLOW DISCONTINUOUS VENTILATION IN THE NAMIB DUNE-SEA ANT *CAMPONOTUS DETRITUS* (HYMENOPTERA, FORMICIDAE)

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Summary

Data on discontinuous ventilation phenomena in *Camponotus detritus* (Emery), an ant from the hyper-arid Namib Desert, are described and compared to equivalent data from two mesic insects, including *Camponotus vicinus* (Mayr). Although rate of CO_2 production ($\dot{V}_{CO_2}$) and body size were equivalent in *C. detritus* and *C. vicinus*, the ventilation rate of *C. detritus* was fourfold lower, significantly reducing predicted respiratory water loss rates. Ventilation rate was presumably modulated by $\dot{V}_{CO_2}$, and low ventilation frequency was maintained in part by significant gas exchange during the fluttering-spiracle phase of the ventilation cycle, which is generally characterized by low rates of respiratory water loss.

Introduction

We know little about short-term gas exchange phenomena (discontinuous ventilation) in adult insects while at rest, and nothing about equivalent phenomena in xeric insects. Yet a common thread running through the literature on discontinuous ventilation in insects has been the pivotal importance of water economy in the evolutionary development and ecophysiological significance of this remarkable ventilation system (Buck, 1958; Schneiderman and Schechter, 1966; Brockway and Schneiderman, 1967; Loveridge, 1968; Kestler, 1978, 1980, 1985; Lighton, 1988*a*; Corbet, 1988). Comparison of discontinuous ventilation phenomena in two congeneric, physiologically similar insects from very different ecological backgrounds, one mesic and the other hyper-arid, should therefore be useful. If considerations of respiratory water economy have indeed affected fitness as a correlate of ventilation strategy, the ventilation strategies of the two organisms can be expected to differ in ways that we can predict with reasonable confidence.

But comparisons need comparative data, and the only quantitative studies of gas exchange during discontinuous ventilation cycles (DVCs) in adult insects are of temperate-zone, mesic species; a tenebrionid beetle *Psammodes striatus* (Lighton, 1988*a*) and a formicine ant *Camponotus vicinus* (Lighton, 1988*b*). I describe here

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the first detailed discontinuous ventilation data obtained from an arid-adapted insect: the Namib Desert dune ant *Camponotus detritus* (Emery).

C. detritus is a large formicine ant (body mass about 45 mg) endemic to the dune-sea of the central Namib Desert, Namibia. The central Namib Desert is hyper-arid, with a mean annual rainfall of about 20 mm per year (Seely and Stuart, 1976) and additional moisture provided by occasional inland migration of advective fogs. High temperatures, hot winds and large water vapor saturation deficits combine to make the central Namib Desert dune-sea a singularly challenging environment for diurnal small-bodied insects.

C. detritus construct their nests beneath perennial vegetation on dune plinths. From their nests, they travel diurnally up to 200 m over bare sand with surface temperatures often exceeding 55°C (Curtis, 1985*a*), collecting honeydew from scale insects on perennial grasses (chiefly *Stipagrostis sabulicola*) or foraging opportunistically for dead or moribund insects (Curtis, 1985*b*). Thus, the environmental context of *C. detritus* provides a dramatic contrast to the mesic, montane habitat of *Camponotus vicinus* (San Jacinto mountains, California, pine and oak forests, elevation 1640 m; Lighton, 1988*b*).

The reader is referred to Miller (1981), Kestler (1985), Corbet (1988) and Slama (1988) for excellent reviews of our current understanding of insect ventilation phenomena. The following abbreviations are used in the text. C phase, closed phase: all spiracles are closed and no external respiratory gas exchange takes place; endotracheal P_{O_2} falls and hemolymph P_{CO_2} rises. F phase, flutter phase: triggered by falling P_{O_2}, the spiracle closer muscles are periodically inactivated and limited respiratory gas exchange takes place. B phase, burst phase [also referred to as the O (open) or V (ventilation) phase]: rising hemolymph P_{CO_2} inactivates the spiracle closer muscles, and CO_2 is expelled from the insect in a large 'burst', usually with ventilatory pulsations.

Respiratory water loss is zero in the C phase, very low in the F phase, and high in the B phase (Lighton, 1988*a*, and references therein; J. R. B. Lighton, in preparation), so one might expect the C phase to be elongated, and the contribution of the F phase to overall gas exchange to be emphasized, in arid-adapted insects. Consequently, one would expect the B phase, with its high rate of respiratory water loss, to occur less frequently; in other words, for the frequency of the DVC to be reduced.

Materials and methods

Location and animals

This investigation was carried out in December 1988 at the Namib Desert research station (Gobabeb, Namibia). *Camponotus detritus* workers were collected from an established laboratory colony (temperature 26±5°C, ambient photoperiod) or directly from two foraging colonies in the dune-sea. Larvae (last instar) and pupae (close to eclosion; eye-spots visibly darkened) were obtained from the laboratory colony only, which was in good condition, with a fertile queen,

plentiful larvae and pupae, and free-ranging workers that supplemented the colony diet of sugar-water and insects with extensive foraging around the station.

Respirometry

Air was taken from outside the building, scrubbed of H_2O and CO_2 by a Drierite/Ascarite/Drierite column, and drawn through a respirometer (volume 10 cm^3) at a flow rate of 50 ml min^{-1} regulated by a calibrated mass flow controller. I measured CO_2 concentration in this air stream with an infrared absorbance monitor tuned to respond to CO_2 only, and integrated with a data acquisition engine (Datacan Field, Sable Systems, Los Angeles, CA). Utilizing sample-cell temperature compensation, digital filtration and baseline correction, system resolution was 0.1 p.p.m. CO_2 and long-term drift was less than 0.2 p.p.m. h^{-1}. The temperature of the respirometer chamber and 50 cm of temperature equilibration tubing, through which the incoming air stream flowed, was maintained at 30±0.02 °C by a Peltier effect device under computer control. 30 °C is a reasonable 'consensus temperature' for most diurnal insects in the central Namib Desert and corresponds closely to the preferred temperature of *C. detritus* adults and brood (31.3±2.4 °C; Curtis, 1985*c*).

Prior to each run, I weighed a selected ant, larva or pupa to 0.1 mg and equilibrated it to 30 °C within the respirometer for at least 1 h. I then measured the zero CO_2 baseline of the flow-through system by bypassing the respirometer. After reconnecting the respirometer and flushing it of accumulated CO_2 for 5 min, I recorded CO_2 production for 45 min to 1 h, bypassed the respirometer, and recorded the baseline again. In the case of very low and continuous $\dot{V}_{CO_2}$, I sometimes measured baselines at one or two points within the recording itself to check for non-linear drift.

During analysis, I corrected drift in the CO_2 monitoring system by linear interpolation between beginning and end baseline readings. Any such drift was linear and less than 1 p.p.m. over the timescale of the recordings. STP-corrected rates or volumes of CO_2 production could then be determined over any part of the recording.

Statistics

Means are accompanied by standard deviation and sample size. Regression analysis was performed by least squares, with axis transformation where noted. Regressions were compared by analysis of covariance (ANCOVA), and means by Student's *t*-test. The significance level was set at $P<0.05$. Most of the statistical tests were performed with SYSTAT 4.0 (Wilkerson, 1988).

Results

Standard CO_2 production rate: adults

Rate of CO_2 production ($\dot{V}_{CO_2}$) was measured at 30 °C in 33 ants; 21 from two colonies in the dune-sea, and 12 from the laboratory colony. Ventilation was

always highly discontinuous when the ants were inactive (Fig. 1). Slight activity, such as slow creeping, increased DVC frequency without disrupting its cyclicity. In contrast, vigorous activity such as escape behavior caused apparently chaotic ventilatory patterns (Fig. 2) accompanied by high $\dot{V}_{CO_2}$. Such data were not analyzed further. Of the ants examined, nine from one colony in the dune-sea and seven from the laboratory colony maintained a low enough level of activity to

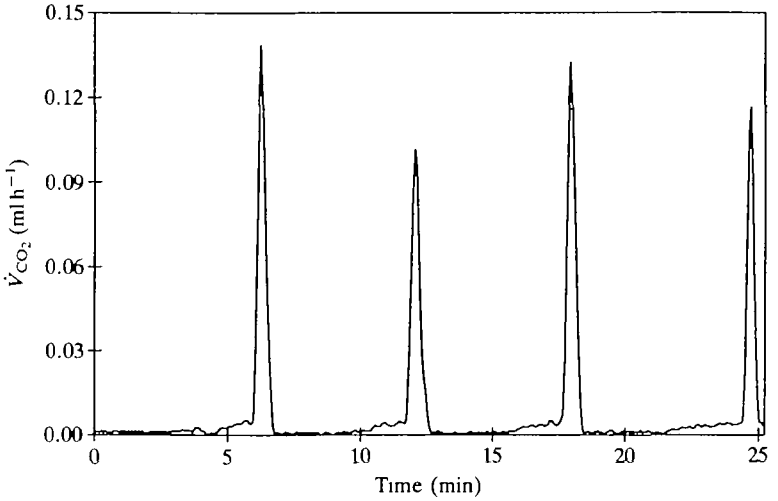

Fig. 1. Typical discontinuous CO_2 emission recording of inactive *Camponotus detritus*. Dune-sea colony ant, mass 0.0473 g, DVC periodicity=357±64 s (6 min), $\dot{V}_{CO_2}$=0.0105±0.0258 ml h^{-1}.

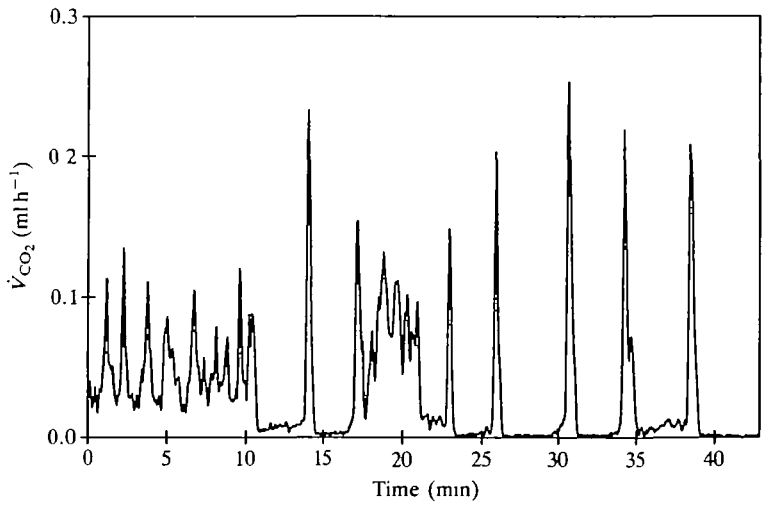

Fig. 2. The effect of activity on discontinuous ventilation in *Camponotus detritus* (mass 0.0692 g). During activity (0–10 min), $\dot{V}_{CO_2}$=0.0475±0.0246 ml h^{-1}; after activity (from 25 min), $\dot{V}_{CO_2}$=0.0187±0.0449 ml h^{-1}.

exhibit sustained, repetitive DVCs for more than 30 min. Ants from the laboratory colony tended to display continuous, low levels of activity; ants from the dune-sea tended to be either vigorously active or inactive. Mean masses did not differ significantly between the dune-sea and laboratory colony subsamples (0.0444±0.0119 g, N=9, and 0.0409±0.0098 g, N=7, respectively; t=0.6; df=14; P>0.3).

Standard $\dot{V}_{CO_2}$ ($s\dot{V}_{CO_2}$) of each ant was calculated from mean $\dot{V}_{CO_2}$ over 2–4 complete DVCs while the ant was minimally active or inactive. Mean $s\dot{V}_{CO_2}$ per ant in the laboratory colony (0.0148±0.0025 ml h^{-1}) was significantly higher than dune-sea colony $s\dot{V}_{CO_2}$ (0.0101±0.0049 ml h^{-1}; t=2.3; df=14; P<0.04), reflecting their slightly higher level of activity. Over the total mass range of 0.0206–0.0692 g, significant mass scaling of $s\dot{V}_{CO_2}$ was found. The two colonies shared a common mass scaling exponent of 0.832 [P(equal exponent)>0.2; F=1.7, df=1, 12], but the scaling coefficient of the laboratory colony was 68% higher [P(equal coefficient)<0.001; F=17.3, df=1, 13]. In laboratory colony ants,

$$s\dot{V}_{CO_2} = 0.215M^{0.832}, \quad (1)$$

where M is body mass in g and $s\dot{V}_{CO_2}$ is in ml h^{-1}. In dune-sea colony ants,

$$s\dot{V}_{CO_2}=0.128M^{0.832}. \quad (2)$$

Most measurements of '$s\dot{V}_{CO_2}$', or '$s\dot{V}_{O_2}$' in insects incorporate data from both inactive and slightly active insects (e.g. Jensen and Nielsen, 1975). Over the entire sample of 16 ants, mean mass-specific $s\dot{V}_{CO_2}$ was 0.290±0.099 ml g^{-1} h^{-1} at a mean mass of 0.0429±0.010 g. Converted to $s\dot{V}_{O_2}$ assuming an RQ of 0.828 (Lighton, 1988*b*), this figure becomes 0.351±0.119 ml g^{-1} h^{-1}.

$\dot{V}_{CO_2}$ *of larvae and pupae*

CO_2 production of *C. detritus* larvae was continuous (Fig. 3). $\dot{V}_{CO_2}$ of the larvae

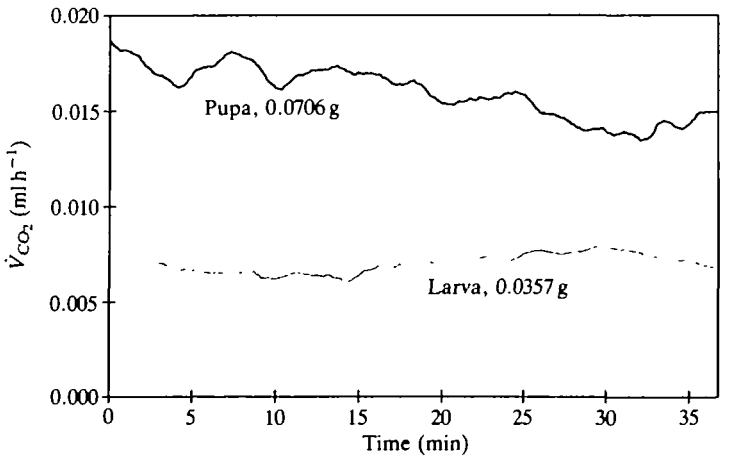

Fig. 3. Typical traces of CO_2 emission from a *Camponotus detritus* larva (mass 0.0357 g; bottom trace) and pupa (mass 0.0706 g; top trace).

was $0.0069\pm0.0011\,ml\,h^{-1}$ (mean mass=$0.0541\pm0.0226\,g$, $N=7$). In spite of the wide mass range investigated (0.0318– 0.0837 g), no significant mass scaling of $\dot{V}_{CO_2}$ was found ($F=0.1$, df=1, 5, $P>0.4$).

As with larvae, CO_2 production of *C. detritus* pupae was continuous (Fig. 3). Two pupae did exhibit slightly irregular and variable CO_2 emission, but the variability was only about 20% of the mean and so could not be described as discontinuous. Mean $\dot{V}_{CO_2}$ of the pupae was $0.0104\pm0.0037\,ml\,h^{-1}$ (mass $0.0499\pm0.0122\,g$, $N=9$). Pupal $\dot{V}_{CO_2}$ was significantly higher than larval $\dot{V}_{CO_2}$ ($t=2.4$, df=14, $P=0.03$), and significantly lower than $s\dot{V}_{CO_2}$ of laboratory colony (marginally active) adults ($t=2.74$, df=14, $P<0.02$) but equivalent to that of dune-sea colony (inactive) adults ($P>0.2$). Mass scaling of pupal $\dot{V}_{CO_2}$ was not significant ($F=1.7$, df=1, 7, $P>0.2$); however, with respect to mass scaling, the pupae formed a statistically homogeneous group with dune-sea colony adults [P(equal scaling exponent)>0.4; $F=0.4$, df=1, 14; P(equal scaling coefficient)>0.4; $F=0.2$, df=1, 15],

$$\dot{V}_{CO_2} = 0.166M^{0.925}, \tag{3}$$

where $\dot{V}_{CO_2}$ is in $cm^3\,CO_2\,h^{-1}$ and M is live body mass in g.

Discontinuous CO_2 emission

Discontinuous CO_2 emission in *C. detritus* was very marked in inactive to slightly active adults (Fig. 1). Following the B or V phase, CO_2 emission was insignificantly above baseline levels (C phase). There followed a rise to a measurable, steadily increasing rate of CO_2 emission (F phase), which presumably reflects intermittent partial openings of the spiracles, in DVCs lasting more than 180 s. In DVCs of shorter duration, no F phase was apparent. The C and F phases occupied tightly defined proportions of the complete DVC (Fig. 4). By regression analysis, the C phase occupied 71.4% (±3.3% S.E.) and the F phase 20.3% (±3.2% S.E.) of total DVC duration, with the B phase occupying the remaining 8.3%. Finally, accumulated CO_2 was released in a large burst (B phase). Active ventilation was not visible during this burst; however, ventilation that was not externally visible was presumably still occurring (see Slama, 1988).

DVC frequency in scarcely active or inactive ants was very low in both samples, ranging from $3.28\pm1.28\,mHz$ ($11.8\,h^{-1}$) in the dune-sea colony to a somewhat faster $4.83\pm1.13\,mHz$ ($17.4\,h^{-1}$) in the laboratory colony ($t=2.52$; df=14; $P<0.03$). Mean burst volumes did not differ significantly between colonies ($0.811\pm0.257\,\mu l$ in the dune sea colony *vs* $0.842\pm0.291\,\mu l$ in the laboratory colony; $P>0.4$). Burst volumes did, however, scale with mass:

$$BV = 0.00769M^{0.7166}, \tag{4}$$

where BV is burst phase CO_2 volume in cm^3 ($F=8.46$; df=1, 14; $P=0.01$). Mass scaling of burst volume did not differ between colonies ($P>0.3$).

The volume of CO_2 released during the F phase, expressed as a percentage of total CO_2 release, was twofold greater in the dune-sea colony [$13.9\pm2.8\%$ *vs*

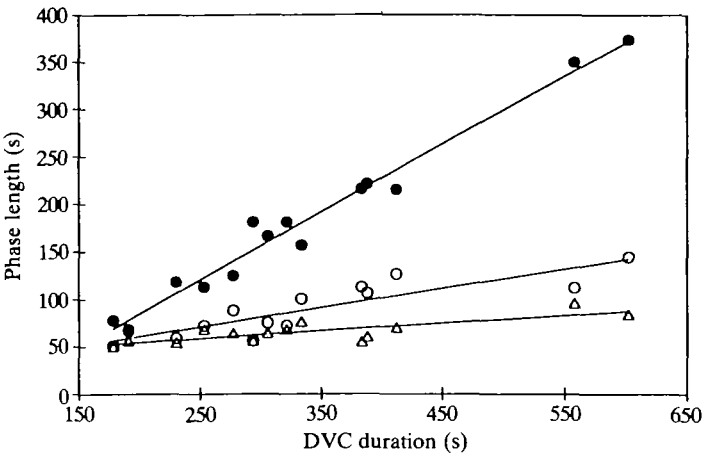

Fig. 4. Duration of the closed phase (closed circles), flutter phase (open circles) and burst phase (triangles) as a function of total DVC duration in 14 *Camponotus detritus* ants. Two ants from the laboratory colony are not included in this figure because they lacked an unambiguous F phase (DVC duration <180 s). Colonies did not differ in slope or intercept in any relationship (ANCOVA; $P>0.2$). For closed phase, CPD=−58.1+0.714(DVCD), $r^2=0.974$, $P<0.0001$, where CPD is C phase duration in s and DVCD is DVC duration in s. For flutter phase, FPD=20.4+0.203(DVCD), $r^2=0.771$, $P<0.0001$, where FPD is flutter phase duration in s. For burst phase, BPD=37.8+0.083(DVCD), $r^2=0.645$, $P<0.001$, where BPD is burst phase duration in s.

7.3±3.6 %; t(arcsine of square root transformed data)=4.0; df=14; $P<0.002$]. However, this is a consequence of the lower $\dot{V}_{CO_2}$ and lower DVC frequency of the dune-sea colony ants, which leads to a longer F phase (Fig. 4; and see Discussion). Neither the absolute volume nor the proportion of CO_2 released during the F phase scaled significantly with mass in either colony ($P=0.1$).

At low to zero activity levels at a given body mass and temperature, DVC frequency was determined by $\dot{V}_{CO_2}$, with higher $\dot{V}_{CO_2}$ corresponding to higher DVC frequencies (see Schneiderman, 1960; Lighton, 1988*b*). After the influence of body mass on $\dot{V}_{CO_2}$ had been accounted for by multiple regression, the influence of DVC frequency was highly significant ($t=10.1$; df=13; $P<0.0001$).

Discussion

Standard metabolic rate

A common adaptation to aridity is a reduction in metabolic rate (Snyder, 1971; Bartholomew *et al.* 1985; Peterson, 1990). This ameliorates the effect of scarce and unpredictable food resources, and reduces respiratory water loss rates. However, the $\dot{V}_{CO_2}$ of adult *C. detritus* (mean 0.290 ml $CO_2\,g^{-1}$, mean mass 0.0429 g) is typical for ants of their size. For example, the $\dot{V}_{CO_2}$ of *C. vicinus* at 30°C and a

body mass of 0.043 g is an equivalent 0.256 ml $CO_2\,g^{-1}$ (Lighton, 1988*b*); t=0.33, df=15, P>0.4. $\dot{V}_{CO_2}$ of a species very closely related to *C. detritus* (*C. fulvopilosus*; mean mass 0.043 g; Lighton, 1989) is an almost identical (P>0.4) 0.286 ml $CO_2\,g^{-1}$ at 30°C, estimated from $\dot{V}_{O_2}$ assuming an RQ of 0.828 (Lighton, 1988*b*). Plainly, if *C. detritus* exhibits respiratory adaptations to an arid environment, it is not in the direction of reduced metabolic rate. This is particularly interesting in view of the fact that *C. detritus* does not store food in its nests (Curtis, 1985*d*). If its physiology is similar to that of the very closely related *C. fulvopilosus*, it may be able to reduce its metabolic rate substantially as a response to starvation (Lighton, 1989).

What, however, of the possibility that rising hemolymph P_{CO_2} during the discontinuous ventilation cycle may in itself depress $\dot{V}_{CO_2}$ in a synergistic reaction, as Barnhart and McMahon (1987) documented in a mollusc? Plainly, this would allow the C phase and especially the F phase to lengthen significantly as a consequence of internal hypercapnia. However, were this effect to occur in *C. detritus*, the postulated modulation of $\dot{V}_{CO_2}$ would cause a non-linear inflection in the relationship between C and F phase duration and total DVC duration. Since no such inflection is evident (Fig. 4), such a downward modulation of $\dot{V}_{CO_2}$ is evidently not significant in *C. detritus*.

The fact that the $\dot{V}_{CO_2}$ of pupae near eclosion did not differ significantly from that of inactive adults is not surprising and has been reported before (e.g. Bartholomew *et al.* 1988), while the low metabolic rate of larvae has also been noted (e.g. MacKay, 1982). The absence of significant discontinuous ventilation in either larvae or pupae of *C. detritus* is much more surprising – particularly so because the DVC was originally discovered and described in the pupae of holometabolous insects (though the pupae were in diapause; see review by Miller, 1981). Because practically no comparative data exist in this area, however, it is impossible to say whether *C. detritus* is unusual in this respect. For example, it is possible that their larvae lack functional spiracular valves. It is worth noting that, unlike immobile immature forms of solitary species, the brood of social insects is subject to stringent environmental control of temperature and humidity. This may relax selective pressures imposed by very low humidity or high temperatures in an uncontrolled setting. The continuous ventilation of *C. detritus* larvae and pupae may reflect this relaxation of selection for reduced water loss; however, the benefits of their continuous ventilation are problematic.

Discontinuous ventilation – burst frequency and burst volume

C. detritus ventilates once per 5 min at 30°C. At that temperature, the DVC frequency of its comparably sized, mesic congener *C. vicinus* is three- to fourfold faster (Lighton, 1988*b*; P<0.0005) *in spite of the fact* that the $\dot{V}_{CO_2}$ values of *C. detritus* and *C. vicinus* are equivalent. Is the lower DVC frequency of *C. detritus* adaptive in reducing respiratory water loss? The fact that *C. detritus* and *C. vicinus* have similar $\dot{V}_{CO_2}$ values is critical, because $\dot{V}_{CO_2}$ itself affects

ventilation frequency (Schneiderman, 1960; Lighton, 1988*b*). Respiratory water loss is rapid during the B phase, in which convective ventilation usually occurs (Kestler, 1980; Lighton, 1988*a*, and references therein; J. R. B. Lighton, in preparation). If the B phase CO_2 emission volume of *C. detritus* were proportionately larger than that of *C. vicinus*, this would offset the water conservation benefit derived from reducing DVC frequency. However, the B phase CO_2 emission volumes of *C. detritus* are not significantly larger that those of *C. vicinus* at 30°C (Lighton, 1988*b*; $P=0.1$). From this it can be inferred that *C. detritus* emits more CO_2 during its F phase, when water loss rates are low, than does *C. vicinus*, allowing it to slow its DVC to the observed low rate.

Discontinuous ventilation – closed and flutter phases

In *C. detritus*, the C phase was very long (more than 70% of total DVC duration). During this period, no measurable external gas exchange, and hence no respiratory water loss, took place. By contrast, in the mesic beetle *P. striatus*, the C phase lasted only 6.7% of total DVC duration (Lighton, 1988*a*). Unfortunately, DVC data in *C. vicinus* (Lighton, 1988*b*) cannot be directly compared at C- and F-phase level with those in *C. detritus* because extreme sensitivity of CO_2 analysis was not available in the former investigation. However, an accentuated role of the F phase in CO_2 release in *C. detritus* can be inferred (see above).

The contribution of the F phase to total CO_2 release in *C. detritus* with low $\dot{V}_{CO_2}$ (dune-sea colony) was very similar to that found in *P. striatus* (Lighton, 1988*a*; 13.9% *vs* 13.0%). However, the proportional duration of the F phase was much less (20.3% *vs* 45.9% of the DVC; $P<0.001$), reflecting the much longer C phase of *C. detritus*.

The F phase is initiated when tracheal P_{O_2} falls below a critical value during the C phase (Schneiderman, 1960; Levy and Schneiderman, 1966). During this time, CO_2 accumulates in the hemolymph, and continues to accumulate during the F phase until the B phase is triggered. At a given $\dot{V}_{CO_2}$ within the range characterized by normal discontinuous ventilation, hypoxia and hypercapnia will initiate the F and B phases, respectively, at fixed intervals after the last B phase. The lengths of the C and F phases must therefore remain proportionately constant *relative to DVC duration* over a wide range of metabolic rates. This has never been documented in adult insects (an analogous situation in saturniid pupae can be inferred from data in Schneiderman, 1960), but is certainly the case in *C. detritus* (Fig. 4). It is worth noting that the apportionment between ventilation phases is identical in the laboratory and dune-sea colonies, which stresses that differences in their DVC characteristics reflect differing $\dot{V}_{CO_2}$ (and hence DVC frequencies) caused by differing activity levels, rather than different physiology.

From the data in Fig. 4, it is therefore possible to derive the partitioning of a normal DVC cycle (duration>180 s). Given that:

$$\mathrm{DVCD} = \mathrm{CD} + \mathrm{FD} + \mathrm{BD}\,, \tag{5}$$

where DVCD is the DVC duration, and CD, FD, and BD are closed, flutter and burst phase durations, respectively, DVCD can be expanded to:

$$\text{DVCD} = [-58.1 + 0.714(\text{DVCD})] + [20.4 + 0.203(\text{DVCD})] + [37.8 + 0.083(\text{DVCD})], \quad (6)$$

where the equations replacing CD, FD and BD are from Fig. 4 and units are in s. Because the constants sum is negligible, equation 6 can be simplified to:

$$\text{DVCD} = 0.714(\text{DVCD}) + 0.203(\text{DVCD}) + 0.083(\text{DVCD}), \quad (7)$$

from which it follows that the total DVC duration is apportioned as shown between the closed, flutter and burst phases, each of which has a unique proportionality coefficient. The coefficient of each phase, which can be referred to as its ventilation phase coefficient, is equal to the slope of its duration regressed against total DVC duration (Fig. 4). It should be noted that B phase duration may be slightly overestimated because of the wash-out time of the flowthrough respirometry apparatus. If so, the direction of the error relative to the other phases will be chiefly to decrease the measured length of the C phase. This error is small in the present study because of the relatively low respirometer volumes and high flow rates employed.

The C, F and B ventilation phase coefficients may be useful indices for interspecific comparisons. One would expect a xeric species to display larger C and F phase coefficients, and a lower B phase coefficient, than a mesic species. Comparing *C. detritus* with *P. striatus*, for example, we find that *C. detritus* has a far shorter B phase and a far longer C phase than *P. striatus*. Both differences are in the predicted direction for a comparison of a mesic with a xeric species. The extent to which other factors such as size and phylogeny interact with these proportionality coefficients is speculative, because the base of comparable data is limited to the two species mentioned.

Relative to mesic insects such as *P. striatus* or *C. vicinus*, then, the respiratory water conservation strategy of *C. detritus* is to increase C phase duration at a given $\dot{V}_{CO_2}$, and to allow significant quantities of CO_2 to escape during the F phase, thus reducing the volume of the next B phase with its high rate of respiratory water loss. The discontinuous ventilation characteristics of *C. detritus* therefore exhibit distinct adaptations to reduce respiratory water loss – plainly a positive correlate of overall fitness to a social insect with diurnal foragers in a hyper-arid environment.

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