

# Discontinuous Gas-Exchange Cycles in *Scarabaeus* Dung Beetles (Coleoptera: Scarabaeidae): Mass-Scaling and Temperature Dependence

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## ABSTRACT

Although discontinuous gas exchange cycles (DGC) are known from many insects, the effects of body size and temperature on DGC have not been widely examined. Here, these effects are investigated in five *Scarabaeus* dung beetle species from mesic and xeric habitats. The investigation tests two hypotheses: that previous estimates of the scaling exponents for the DGC and its characteristics are more broadly applicable to insects, and that, in response to temperature, both DGC frequency and the quantity of CO<sub>2</sub> emitted during the open (O) phase (O-phase emission volume) are modulated. Like previous workers, we find that  $\dot{V}CO_2$  scaled as  $mass^{0.968}$  and that O-phase emission volume scaled as  $mass^{0.833}$ . However, temperature-associated increases in  $\dot{V}CO_2$  ( $Q_{10}$ 's of 2.19–2.65) were modulated mostly by increases in DGC frequency since O-phase volumes remained constant across temperature. Flutter (F)-phase and O-phase durations were closely coupled to DGC duration, although the relationship between closed (C)-phase duration and DGC duration was less pronounced. We show that ventilation phase coefficients, previously considered a measure of the proportional duration of each phase of the DGC, calculated from the slopes of these relationships are a measure of change in phase duration with change in DGC duration and not a measure of the way in which total DGC duration is apportioned among phases. We suggest that proportions be used to estimate the contribution of each of the phases to the total duration of the DGC.

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## Introduction

Discontinuous gas exchange cycles (DGCs) are characteristic of a variety of insect and noninsect arthropod species, both immature and adult. They appear to be most common among species that show long periods of immobility, undergo diapause (Levy and Schneiderman 1966a, 1966b; Lighton and Fielden 1995), or inhabit hypercapnic and/or hypoxic environments (Lighton 1996). Although the phases of the DGC (closed [C], flutter [F], and open [O]) have been reasonably well characterized in a variety of arthropod species (see Miller 1974; Kestler 1985; Lighton 1994; Wasserthal 1996), recent reviews have concluded that the taxonomic scope of this knowledge is limited and that certain key elements of the mechanistic basis of the DGC remain poorly understood (e.g., Lighton 1996).

DGCs have, to date, been documented in lepidopteran pupae (Punt 1950; Miller 1974), adult cockroaches (Wilkins 1960; Kestler 1985), adult Orthoptera (Hamilton 1964; Hadley and Quinlan 1993; Quinlan and Hadley 1993), adult Hemiptera (Punt 1950), adult tenebrionid and carabid beetles (Punt 1950, 1956; Lighton 1985, 1988b, 1991), a variety of ant species (Lighton 1988a, 1992; Lighton et al. 1993b; Lighton and Berrigan 1995; Lighton and Garrigan 1995), honeybees (Lighton and Lovegrove 1990), some ticks (Lighton et al. 1993a; Lighton and Fielden 1995), and solifuges (Lighton and Fielden 1996). However, the extent to which this phenomenon is consistently present within a given higher taxon (generally Order and Family levels) is not clear, except perhaps in the case of ants, in which it seems to be shown by the majority.

More significantly, the mechanistic basis of the DGC has been investigated in even fewer groups (Lighton 1996). For example, the extent to which the DGC and the characteristics of its phases are modulated by both body size and temperature have been investigated in few taxa. Lighton (1991) showed that metabolic rate scales as  $M^{0.979}$  in tenebrionid beetles, and this scaling relationship was subsequently borne out in a more extensive analysis (Lighton and Fielden 1995; see also Lighton and Wehner 1993). However, scaling of the duration, burst volume, and rate of CO<sub>2</sub> release of each of the phases of the DGC has to date been examined only for tenebrionid beetles and ants (Lighton 1991; Lighton and Berrigan 1995). Similarly,

Table 1: Collection localities for the five *Scarabaeus* species examined in this study

Species	Locality and Altitude (m)	Grid Reference	Mean Annual Rainfall (mm)	Mean Annual Temperature (°C)
<i>Scarabaeus westwoodi</i> Harold .....	Sani Pass 1,900	29°36.297'S, 29°21.191'E	1,185	11.8
<i>S. rusticus</i> (Boheman) .....	Rustenburg 1,260	25°35.674'S, 27°11.372'E	617	18.4
<i>S. galenus</i> (Westwood) .....	Crocodile Bridge 182	25°22.623'S, 31°46.739'E	554	22.0
<i>S. gariepinus</i> (Ferreira) .....	Kleinzee 190	29°34.090'S, 17°17.000'E	70	17.4
<i>S. striatum</i> (Castelnau) .....	Kleinzee 300	29°46.511'S, 17°22.555'E	105	17.0

the effects of temperature on the DGC and the characteristics of its phases have only been examined in a few ant species, with rather different results. In both *Camponotus vicinus* and *Pogonomyrmex* spp., O-phase CO<sub>2</sub> emission volumes decline and O-phase frequency increases with temperature, resulting in an overall Q<sub>10</sub> for metabolic rate of 1.86 (Lighton 1988a, 1996), a value realistic for most insects (Cossins and Bowler 1987). In sharp contrast, changes in metabolic rate caused by varying body temperature are associated with a modulation of

DGC frequency but not O-phase CO<sub>2</sub> emission volumes in *Cataglyphis bicolor* (Lighton and Wehner 1993). Such a pronounced dichotomy in the response of the DGC to extrinsic factors, and lack of information regarding the nature and extent of such responses in insects, stands in contrast to the extensive understanding of the modulation of vertebrate, and especially avian and mammalian, respiratory patterns (see, e.g., Schmidt-Nielsen 1997; and data compilations in Peters 1983).

In this study, we therefore use five species of dung beetles

Table 2: Results of least squares linear regression analyses of respirometry variables on log<sub>10</sub> body mass at 20°C

DGC Phases	Regression Statistics				
	Slope ± SE	Intercept ± SE	R <sup>2</sup>	F <sup>a</sup>	P
Log <sub>10</sub> CO <sub>2</sub> emission volume (mL):					
Closed .....	.845 ± .546	-2.835 ± .096	.07	2.40	.131
Flutter .....	.825 ± .668	-2.506 ± .114	.04	1.53	.225
Open .....	.833 ± .230	-1.268 ± .041	.28	13.09	.001
Log <sub>10</sub> DGC phase duration (h):					
Closed .....	-.535 ± .399	-.473 ± .070	.05	1.80	.189
Flutter .....	-.588 ± .688	-.536 ± .117	.02	.73	.399
Open .....	-.207 ± .191	-.332 ± .034	.03	1.17	.288
All phases .....	-.563 ± .263	.115 ± .046	.12	4.57	.040
Log <sub>10</sub> CO <sub>2</sub> emission rate (mL h <sup>-1</sup> ):					
Closed .....	1.409 ± .294	-2.367 ± .052	.40	22.99	<.001
Flutter .....	1.374 ± .294	-1.998 ± .056	.38	17.59	<.001
Open .....	1.047 ± .232	-.934 ± .041	.37	20.31	<.001
All phases .....	.968 ± .229	-1.261 ± .041	.34	17.79	<.001
Log <sub>10</sub> DGC frequency (mHz):					
Closed .....	.535 ± .399	-.084 ± .070	.05	1.80	.189
Flutter .....	.534 ± .655	-.019 ± .116	.02	.67	.420
Open .....	.207 ± .192	-.225 ± .034	.03	1.17	.288
All phases .....	.563 ± .263	-.671 ± .046	.12	4.57	.040

Note. Data from the five species were pooled to generate the regressions.

<sup>a</sup> df = 1, 34.

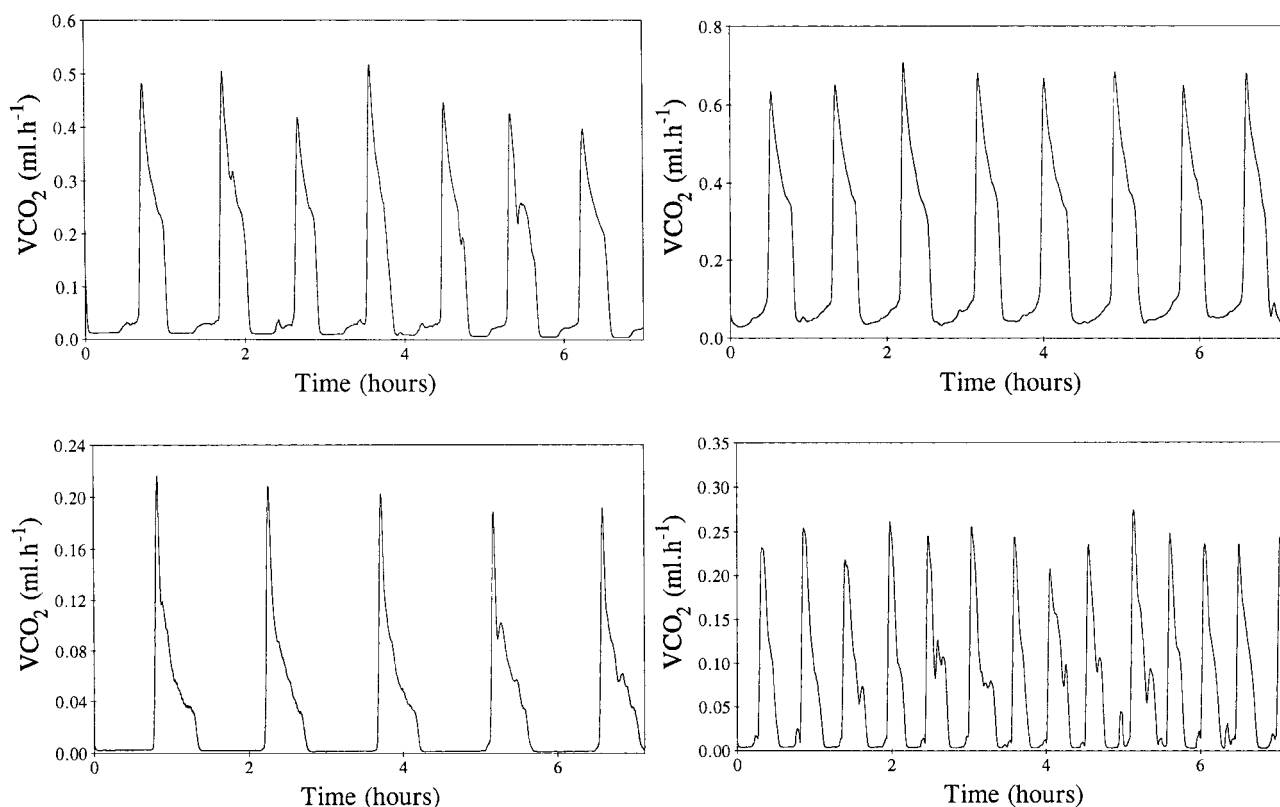


Figure 1. Discontinuous gas exchange cycles recorded over 7.1 h in *top left*, *Scarabaeus rusticus* at 24°C; *top right*, *Scarabaeus westwoodi* at 24°C; *bottom left*, *Scarabaeus striatum* at 20°C; and *bottom right*, *Scarabaeus garipeinus* at 32°C.

in the genus *Scarabaeus* (Coleoptera, Scarabaeidae) to test two major hypotheses concerning the modulation of the DGC in insects. First, that the allometry (or lack thereof) of the duration, burst volume, and rate of CO<sub>2</sub> release of each of the DGC phases determined by Lighton (1991) and Lighton and Berrigan (1995) for tenebrionid beetles and ants applies more broadly to other insect taxa. Second, that temperature-related changes in metabolic rate are associated with a modulation of both O-phase frequency and O-phase CO<sub>2</sub> emission volumes.

### Material and Methods

The five *Scarabaeus* species examined in this study were each collected from a single locality (Table 1). Beetles were kept at 25°C (12L : 12D) for a minimum of 5 d before respirometry. Because the species investigated here are all diurnal, ball-rolling dung beetles, respirometry was conducted at night, when these species are generally inactive (see Edwards 1988). For each measurement, a single individual (starved for 24–48 h) was weighed (to 0.1 mg; Sartorius R 200 D digital balance) and then placed into a cuvette located within a water jacket connected to a Grant LTD20 water bath that controlled the temperature in the

cuvette to within 0.2°C. Beetles were placed into the cuvette during midmorning ( $\pm 1000$  hours) and settled for approximately 6 h in still air at the temperature of interest in the darkened laboratory. Thereafter, measurements were made in moving air for approximately 8–10 h, during which time disturbance was minimized, although observations were occasionally made through the reddened cuvette wall. Following respirometry, beetles were weighed again.

Flow-through CO<sub>2</sub>-based respirometry was undertaken using a Sable Systems respirometry system (Sable Systems, Henderson, Nev.). Air was passed through Drierite and Soda Lime columns to remove water vapor and CO<sub>2</sub>. It was then passed through an automated baselining system, the 340-mL cuvette containing the beetle, and finally through a Li-Cor CO<sub>2</sub>/H<sub>2</sub>O Analyzer Model Li 6262 at a flow rate of 150 mL min<sup>-1</sup> (suggesting an equilibration time of ca. 4 min, which may have influenced estimates of DGC parameters; see “Discussion”). DATACAN V software was used for data capture and analysis. All measurements were corrected to standard temperature and pressure and are expressed as mL CO<sub>2</sub> h<sup>-1</sup>.

In four of the five *Scarabaeus* species, temperature-related

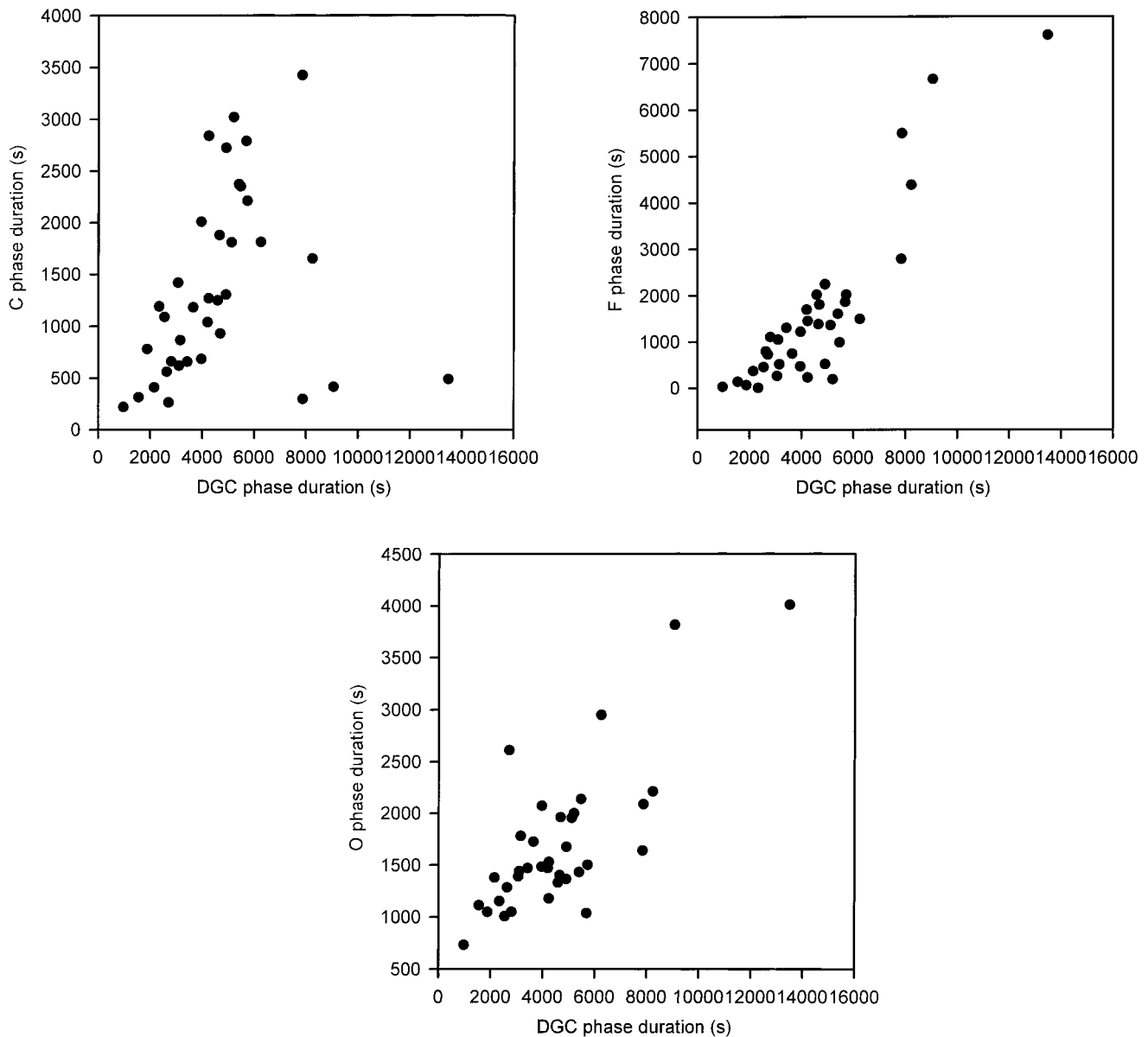


Figure 2. Relationships between DGC duration and C-phase duration (C-phase duration =  $0.089$  [DGC duration] +  $946.5$ ,  $F_{(1,34)} = 2.10$ ,  $P > 0.15$ ,  $R^2 = 0.06$ ; excluding *Scarabaeus gariiepinus*, C-phase duration =  $0.385$  [DGC duration] -  $115.4$ ,  $F_{(1,30)} = 36.13$ ,  $P < 0.00001$ ,  $R^2 = 0.546$ ; top left); F-phase duration (F-phase duration =  $0.660$  [DGC duration] -  $1449.9$ ,  $F_{(1,34)} = 136.7$ ,  $P < 0.00001$ ,  $R^2 = 0.800$ ; excluding *Scarabaeus gariiepinus*, F-phase duration =  $0.455$  [DGC duration] -  $725.4$ ,  $F_{(1,30)} = 52.42$ ,  $P < 0.00001$ ,  $R^2 = 0.636$ ; top right); and O-phase duration (O-phase duration =  $0.224$  [DGC duration] +  $671.9$ ,  $F_{(1,34)} = 47.51$ ,  $P < 0.00001$ ,  $R^2 = 0.582$ ; excluding *Scarabaeus gariiepinus*, O-phase duration =  $0.165$  [DGC duration] +  $725.4$ ,  $F_{(1,30)} = 19.02$ ,  $P < 0.00014$ ,  $R^2 = 0.388$ ; bottom).

changes in patterns of  $\text{CO}_2$  and water vapor release (to be reported elsewhere) were recorded at  $4^\circ\text{C}$  intervals across a temperature range from  $16^\circ$  to  $32^\circ\text{C}$  (treatment temperatures were randomized). In *Scarabaeus westwoodi* and *Scarabaeus rusticus*, measurements were made for 10 or more different individuals at each temperature, while in the remaining species, fewer individuals were available. In consequence, there were

some repeated measures in *Scarabaeus gariiepinus* and *S. rusticus*, but multiple regression showed these to have little influence on the outcome of the analyses. DGC phase data were used only for those individuals where at least more than two, but generally more than four, DGCs were recorded. Means of phase volumes, durations, and rate of  $\text{CO}_2$  release were calculated from these data for each individual, using DATACAN

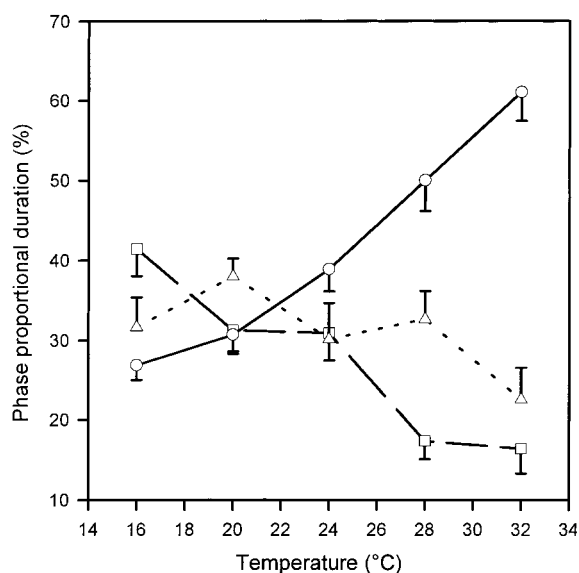


Figure 3. Changes in the proportional duration of the phases of the DGC (mean  $\pm$  SE) with temperature (C phase = squares, F phase = triangles, O phase = circles) in *Scarabaeus rusticus*. Compare the estimates here with the ventilation phase coefficients provided for this species in the text.

V. In addition, this software was also used to calculate O-phase trigger points (i.e.,  $\dot{V}_{CO_2}$  at which the O phase was initiated).

Individuals subsequently constituted the units of analysis. Therefore, means and standard errors describe the amount of variation between individuals unless stated otherwise. Least-squares regression was used to examine relationships between mass and gas exchange variables at 20°C across individuals of all species and between temperature and gas exchange variables within each species. Significance was set at  $P = 0.05$  throughout. Following Lighton (1990, 1991), ventilation phase coefficients were derived from the slopes of the relationships of phase durations on DGC duration. Cossins and Bowler's (1987) formula was used for the calculation of  $Q_{10}$  from the regression of  $\log_{10} \dot{V}_{CO_2}$  on temperature. A  $t$ -test was used to compare the slopes of the allometric relationships derived in this study with those reported previously (see Sokal and Rohlf 1995, p. 470).

## Results

All of the species examined here showed discontinuous gas exchange cycles when at rest, but these cycles were disrupted if the beetles moved. Characteristics of the DGC varied both with temperature and between species (Fig. 1). Standard  $\dot{V}_{CO_2}$  scaled allometrically with an exponent of 0.968. O-phase, F-phase, and C-phase  $CO_2$  emission rates showed similar relationships with body mass (Table 2). Relationships between mass and duration of the DGC phases were not significant. Neither were the regressions of C- and F-phase  $CO_2$  emission

volumes on mass (Table 2). However, O-phase emission volume scaled as mass<sup>0.833</sup>. Although there were no significant relationships between mass and frequency of any of the DGC phases, there was a positive but marginally significant relationship between mass and overall DGC frequency (Table 2). In contrast, a significant and strong positive relationship was found between F-phase duration and DGC duration and between O-phase duration and DGC duration, whereas the relationship between C-phase duration and DGC duration was not significant (Fig. 2). By regression, F-phase and O-phase ventilation coefficients were therefore 66% and 22%, respectively. However, because *Scarabaeus garipepinus* appeared to be such a significant outlier, especially where C-phase duration was concerned, the ventilation-phase coefficients were calculated excluding this species. Thus, the ventilation-phase coefficients were DGC = 0.385 (C phase) + 0.455 (F phase) + 0.165 (O phase).

When ventilation phase coefficients were calculated for each species based on temperature modulation of the DGC, considerable variation between species was found. For *Scarabaeus rusticus*, the ventilation phase coefficients were DGC = 0.421 (C phase) + 0.452 (F phase) + 0.127 (O phase); for *Scarabaeus westwoodi*, DGC = 0.421 (C phase) + 0.275 (F phase) + 0.304 (O phase); for *Scarabaeus striatum*, DGC = 0.560 (C phase) + 0.089 (F phase) + 0.351 (O phase); and for *S. garipepinus*, DGC = 0.01 (C phase) + 0.710 (F phase) + 0.240 (O phase), with a major difference in the contribution of the C phase to total DGC duration in this latter species. Proportional durations (as a percentage) of each of the phases at each temperature are illustrated for *S. rusticus* for comparison with these values (Fig. 3).

For  $\dot{V}_{CO_2}$ ,  $Q_{10}$ 's of 2.65, 2.42, 2.25, and 2.19 were found in *S. rusticus*, *S. garipepinus*, *S. westwoodi*, and *S. striatum*, respectively (see Table 3 for means at each temperature). This temperature-related increase in metabolic rate was modulated mostly by increases in DGC frequency, with temperature either having no effect on  $CO_2$  emission volumes of all phases (*S. garipepinus*) or having a significant, negative effect on C-phase  $CO_2$  emission volume, but no effect on F- or O-phase emission volumes (Tables 4, 5; Fig. 4). With regard to O-phase trigger points (i.e., the  $\dot{V}_{CO_2}$  at which O phase is initiated), it is clear that there is a significant increase in trigger point with temperature in all of the species examined (Fig. 5).

## Discussion

### Metabolic Rate, DGCs, and Their Allometry

This study demonstrates that, across a variety of temperatures, discontinuous gas exchange cycles are the characteristic pattern of gas exchange in resting adult dung beetles of the genus *Scarabaeus*. Based on an examination of  $\dot{V}_{O_2}$  ventilatory patterns, Lighton (1985) obtained a similar result for *Scarabaeus (Pachysoma) hippocrates*. However, unlike *P. hippocrates*, and tenebrionid beetles in the 1.0-g range, which showed DGC

frequencies of 2.7–6.5 mHz (Lighton 1991), DGC frequencies in the *Scarabaeus* species examined here were lower (0.323–0.451 mHz at 24°C), especially in the case of *Scarabaeus garipepinus* (0.189 mHz at 24°C). Nonetheless, they compared well with those found in lubber grasshoppers (ca. 2.9 g, 0.669 mHz; Hadley and Quinlan 1993) and the tenebrionid *Onymacris unguicularis* (ca. 0.737 g, 0.624 mHz; Louw et al. 1986; all comparisons for measurements made at ca. 25°C).

*Scarabaeus westwoodi*, *Scarabaeus rusticus*, and *Scarabaeus striatum*  $\dot{V}CO_2$  values were well within the range found for insects of a similar size examined using flow-through respirometry at similar temperatures (Louw et al. 1986; Lighton 1991). However,  $\dot{V}CO_2$  for *S. garipepinus* was low, given its large body size. For a beetle of a mean mass of 1.13 g, such as *S. garipepinus*, Lighton's (1991) equation predicts a  $\dot{V}CO_2$  of 0.179 mL h<sup>-1</sup>, whereas at both 28°C and 32°C,  $\dot{V}CO_2$  measured here was considerably lower (0.0554 and 0.0686 mL h<sup>-1</sup>, respectively).

Despite this interspecific variation, across all the species,  $\dot{V}CO_2$  scaled allometrically with an exponent indistinguishable from that reported by Lighton (1991) and by Lighton and Fielden (1995;  $t = -0.480$ ,  $P > 0.1$  and  $t = -0.625$ ,  $P > 0.1$ , respectively; see also Lighton and Wehner 1993; Hack 1997). Likewise, O-phase and F-phase CO<sub>2</sub> emission volumes showed

scaling exponents statistically similar to those obtained for tenebrionid beetles by Lighton (1991;  $t = 0.661$ ,  $P > 0.1$  and  $t = 0.555$ ,  $P > 0.1$ , respectively), as did the scaling exponents for O- and F-phase CO<sub>2</sub> emission rates ( $t = 0.211$ ,  $P > 0.1$  and  $t = 1.585$ ,  $P > 0.05$ , respectively). F-phase frequency in the dung beetles did not covary with body mass, a situation unlike that reported by Lighton (1991) for tenebrionid beetles, where F-phase frequency showed a significant negative relationship with mass. This may well have been the consequence of the fact that the beetles examined here showed a conventional F phase, whereas the tenebrionid beetles exhibited a quantum-like F phase, termed an intermittent single pulse phase by Lighton (1991). Nonetheless, as was the case in Lighton's (1991) study, no significant relationships were found between O-phase and C-phase frequencies and mass in the species examined here.

In summary, Lighton's (1996) generalizations concerning the allometry of the DGC appear to be upheld for another group of insects, thus lending weight to the validity of his generalizations. Likewise, his conclusion that similar scaling exponents for CO<sub>2</sub> emission volumes, and for  $\dot{V}CO_2$ , result in the independence of DGC frequency from body mass in insects also appears to be more widely applicable than the original, single study of tenebrionid beetles (Lighton 1991) would perhaps have suggested. In this study, although DGC frequency was margin-

Table 3: Mean  $\pm$  SE of body mass and  $\dot{V}CO_2$  for each species at each temperature

Species and Temperature (°C)	Mean $\dot{V}CO_2 \pm$ SE (mL h <sup>-1</sup> )	Mean Body Mass $\pm$ SE (g)
<i>Scarabaeus westwoodi</i> :		
16 .....	.0873 $\pm$ .0062	1.905 $\pm$ .095
20 .....	.1169 $\pm$ .0073	1.741 $\pm$ .101
24 .....	.1704 $\pm$ .0083	1.758 $\pm$ .082
28 .....	.2197 $\pm$ .0110	1.689 $\pm$ .091
32 .....	.3172 $\pm$ .0161	1.890 $\pm$ .107
<i>S. rusticus</i> :		
16 .....	.0386 $\pm$ .0027	1.057 $\pm$ .052
20 .....	.0580 $\pm$ .0035	1.051 $\pm$ .047
24 .....	.0887 $\pm$ .0074	1.061 $\pm$ .048
28 .....	.1411 $\pm$ .0129	1.081 $\pm$ .046
32 .....	.1962 $\pm$ .0126	1.073 $\pm$ .042
<i>S. garipepinus</i> :		
16 .....	.0180 $\pm$ .0007	1.186 $\pm$ .060
20 .....	.0234 $\pm$ .0009	1.158 $\pm$ .056
24 .....	.0389 $\pm$ .0006	1.130 $\pm$ .053
28 .....	.0554 $\pm$ .0021	1.097 $\pm$ .051
32 .....	.0686 $\pm$ .0028	1.055 $\pm$ .051
<i>S. striatum</i> :		
16 .....	.0167 $\pm$ .0017	.885 $\pm$ .145
20 .....	.0285 $\pm$ .0013	.0849 $\pm$ .096
24 .....	.0382 $\pm$ .0028	.753 $\pm$ .053
28 .....	.0498 $\pm$ .0022	.685 $\pm$ .040
32 .....	.0499	.517

Table 4: Relationships between temperature and DGC characteristics ( $\log_{10}$ ) for *Scarabaeus rusticus* and *Scarabaeus westwoodi*

Parameter	<i>Scarabaeus rusticus</i> <sup>a</sup>			<i>Scarabaeus westwoodi</i> <sup>b</sup>		
	Slope $\pm$ SE	Intercept $\pm$ SE	$R^2$	Slope $\pm$ SE	Intercept $\pm$ SE	$R^2$
DGC rate .....	.0423 $\pm$ .0030	-2.090 $\pm$ .073	.808 <sup>***</sup>	.0353 $\pm$ .0022	-1.640 $\pm$ .053	.840 <sup>***</sup>
C-phase rate .....	.0321 $\pm$ .0034	-2.905 $\pm$ .084	.647 <sup>***</sup>	.0395 $\pm$ .0051	-2.702 $\pm$ .125	.542 <sup>***</sup>
F-phase rate .....	.0472 $\pm$ .0042	-2.792 $\pm$ .103	.727 <sup>***</sup>	.0391 $\pm$ .0037	-2.292 $\pm$ .091	.691 <sup>***</sup>
O-phase rate .....	.0202 $\pm$ .0031	-1.193 $\pm$ .076	.471 <sup>***</sup>	.0252 $\pm$ .0021	-1.112 $\pm$ .056	.708 <sup>***</sup>
DGC volume .....	...	...	...	...	...	...
C-phase volume .....	-.0376 $\pm$ .0072	-1.921 $\pm$ .177	.364 <sup>***</sup>	-.0139 $\pm$ .0069	-2.173 $\pm$ .169	.074 <sup>*</sup>
F-phase volume .....	...	...	...	...	...	...
O-phase volume .....	...	...	...	...	...	...
DGC frequency .....	.0381 $\pm$ .0039	-1.426 $\pm$ .096	.668 <sup>***</sup>	.0356 $\pm$ .0029	-1.245 $\pm$ .072	.741 <sup>***</sup>
C-phase frequency .....	.0697 $\pm$ .0060	-1.551 $\pm$ .146	.741 <sup>***</sup>	.0547 $\pm$ .0050	-1.113 $\pm$ .124	.698 <sup>***</sup>
F-phase frequency .....	.0493 $\pm$ .0094	-1.136 $\pm$ .232	.364 <sup>***</sup>	.0397 $\pm$ .0057	-.707 $\pm$ .139	.497 <sup>***</sup>
O-phase frequency .....	.0145 $\pm$ .0027	-.442 $\pm$ .066	.381 <sup>***</sup>	.0253 $\pm$ .0030	-.669 $\pm$ .073	.587 <sup>***</sup>

<sup>a</sup> df = 52.<sup>b</sup> df = 49.\*  $P < 0.05$ .\*\*\*  $P < 0.001$ .

ally significant across all phases, the coefficient of determination of the relationship was low (12%), suggesting that if it exists at all, the relationship is weak. Thus, we have been unable to disprove the first of our major hypotheses.

#### Duration of the DGC and Its Phases

In tenebrionid beetles (Lighton 1991) and ants (Lighton 1990; Lighton and Wehner 1993), C-phase duration is only loosely

related to DGC duration, and this was clearly the case for the dung beetles examined here. Bearing in mind that O-phase durations may be overestimates caused by the nature of the flow-through system used, the close coupling between O- and F-phase durations and DGC duration is nonetheless similar to the situation found in most other insects (Lighton 1994). Examination of the ventilation phase coefficients derived both from the mass scaling data and from the temperature modulation data thus suggest, for example, that O-phase duration

Table 5: Relationships between temperature and DGC characteristics ( $\log_{10}$ ) for *Scarabaeus garipepinus* and *Scarabaeus striatum*

Parameter	<i>Scarabaeus garipepinus</i> <sup>a</sup>			<i>Scarabaeus striatum</i> <sup>b</sup>		
	Slope $\pm$ SE	Intercept $\pm$ SE	$R^2$	Slope $\pm$ SE	Intercept $\pm$ SE	$R^2$
DGC rate .....	.0384 $\pm$ .0018	-2.365 $\pm$ .044	.963 <sup>***</sup>	.0340 $\pm$ .0041	-2.267 $\pm$ .095	.835 <sup>***</sup>
C-phase rate .....	.0160 $\pm$ .0051	-2.944 $\pm$ .125	.355 <sup>**</sup>	...	...	...
F-phase rate .....	.0391 $\pm$ .0038	-3.102 $\pm$ .093	.858 <sup>***</sup>	.0441 $\pm$ .0063	-3.090 $\pm$ .148	.778 <sup>***</sup>
O-phase rate .....	.0305 $\pm$ .0048	-1.839 $\pm$ .056	.695 <sup>***</sup>	.0236 $\pm$ .0076	-1.720 $\pm$ .178	.410 <sup>**</sup>
DGC volume .....	...	...	...	...	...	...
C-phase volume .....	...	...	...	-.086 $\pm$ .0181	-1.174 $\pm$ .425	.615 <sup>**</sup>
F-phase volume .....	...	...	...	...	...	...
O-phase volume .....	...	...	...	...	...	...
DGC frequency .....	.0349 $\pm$ .0087	-1.502 $\pm$ .214	.475 <sup>***</sup>	.0497 $\pm$ .0085	-1.630 $\pm$ .199	.710 <sup>***</sup>
C-phase frequency .....	...	...	...	.0787 $\pm$ .0192	-1.758 $\pm$ .453	.543 <sup>**</sup>
F-phase frequency .....	.0504 $\pm$ .0165	-1.442 $\pm$ .408	.340 <sup>**</sup>	...	...	...
O-phase frequency .....	.0258 $\pm$ .0065	-.909 $\pm$ .159	.469 <sup>***</sup>	.0388 $\pm$ .0102	-1.032 $\pm$ .240	.507 <sup>**</sup>

<sup>a</sup> df = 19.<sup>b</sup> df = 15.\*\*  $P < 0.01$ .\*\*\*  $P < 0.001$ .

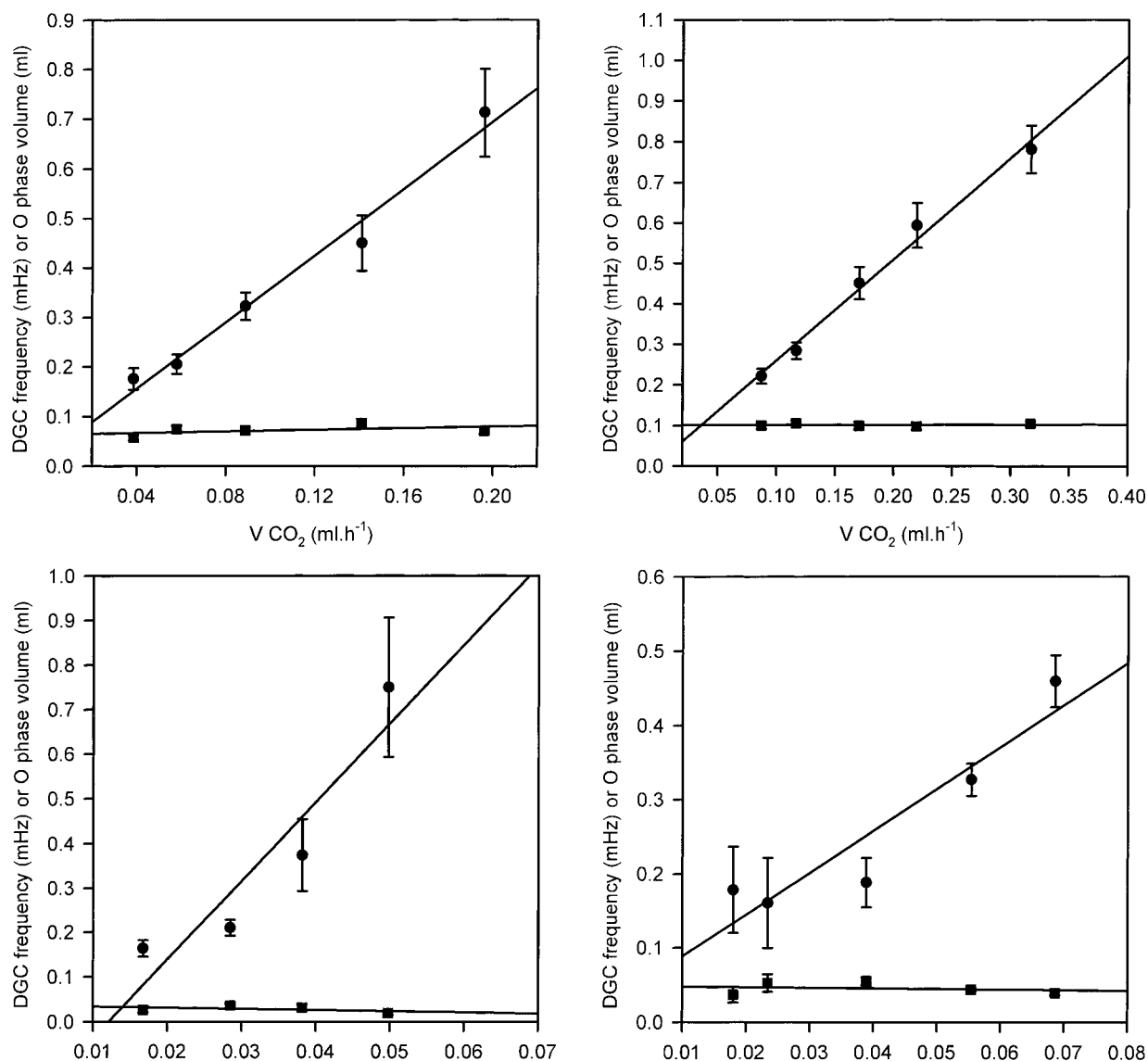


Figure 4. Relationships between  $\dot{V}CO_2$  and DGC frequency (mean  $\pm$  SE; circles) and O-phase volume (mean  $\pm$  SE; squares) in *Scarabaeus rusticus* (top left); *Scarabaeus westwoodi* (top right); *Scarabaeus striatum* (bottom left); and *Scarabaeus garipepinus* (bottom right).

in *S. rusticus* constitutes approximately 12.7% of the DGC. However, the data in Figure 3, and the illustration of the DGC in this species in Figure 1, suggest that this cannot be the case. Rather, the O phase should contribute more than 30% to the DGC. Similar discrepancies are clear for the other phases and species examined here. Likewise, these problems are clear in Lighton's (1990) analysis. In his Figure 1, closed phase constitutes approximately 0.50 of the DGC, whereas the ventilation phase coefficient analysis suggests that the value is 0.714. Thus,

the concept of ventilation-phase coefficients requires reinvestigation.

Lighton (1990) first developed the concept of ventilation-phase coefficients and argued that these provide an indication of the way in which "the total DVC duration is apportioned ... between the closed, flutter and burst phases" (Lighton 1990, p. 80). His reasoning was as follows:

$$DGCD = CD + FD + BD, \quad (1)$$



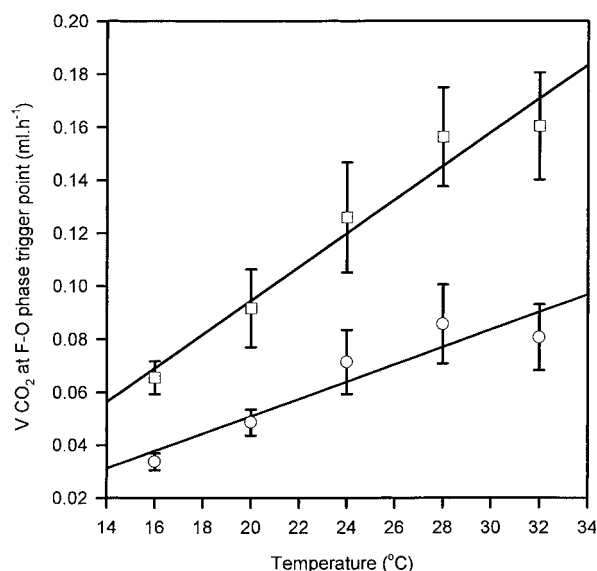


Figure 5. Relationships between temperature and the O-phase  $\dot{V}_{CO_2}$  trigger point in *Scarabaeus rusticus* (circles), and *Scarabaeus westwoodi* (means  $\pm$  SE; squares).

where DGCD is DGC duration and CD, FD, and BD are closed-, flutter-, and open-phase durations, respectively. He subsequently argued that equation (1) can be expanded to

$$DGCD = [a_1 + b_1(DGCD)] + [a_2 + b_2(DGCD)] + [a_3 + b_3(DGCD)], \quad (2)$$

where  $a_i$  and  $b_i$  are the intercepts and slopes, respectively, of the linear regression equations relating phase duration to DGC duration in each of the three phases. Because the duration of the three phases must sum to DGCD, the solution to equation (2) must yield

$$DGCD = [0 + 1(DGCD)]. \quad (3)$$

Consequently, Lighton (1990, 1991) argued that  $b_i$  provides a measure of the proportional length of each phase, which assumes that

$$b_i = y/x, \quad (4)$$

where  $y$  is the duration of the phase in question and  $x$  is the total duration of the DGC. This is the major source of interpretational error. The slope of each regression line does not provide a measure of the proportional duration of each phase. Rather,

$$b_i = \Delta y / \Delta x, \quad (5)$$

and

$$y/x = b_i + a_i/x. \quad (6)$$

Thus, the ventilation phase coefficients proposed by Lighton (1990, 1991, see also 1994) do not indicate the way in which the DGC is apportioned among the three phases. Rather, they provide a measure of the change in phase duration with a change in the total DGC duration. Thus, the partitioning of a normal DGC can be calculated more simply as

$$DGCD = CD/DGCD + FD/DGCD + OD/DGCD. \quad (7)$$

Of course, this does not imply that ventilation-phase coefficients are not useful. Indeed, they are an important measure of the way in which the duration of the phases change as DGC duration changes and may yet provide a useful means for demonstrating how the DGC is modulated by species living under different environmental conditions (see Lighton 1990, 1991, 1994; Lighton and Wehner 1993; Duncan and Lighton 1997).

#### Temperature Modulation of the DGC

In the beetles examined here, O-phase  $CO_2$  emission volumes did not change as temperature changed. Rather, the increase in  $\dot{V}_{CO_2}$  with temperature was modulated almost entirely by an increase in DGC frequency (accompanied by changes in proportional duration of the phases). In consequence, we do not find support for the second major hypothesis we set out to test; that is, that temperature-related changes in  $\dot{V}_{CO_2}$  are modulated by changes in both DGC frequency and O-phase emission volumes.

In a similar context, Lighton and Wehner (1993) suggested that the temperature independence of O-phase  $CO_2$  emission volumes and a reduction in O-phase duration with increasing temperature minimizes convective water loss and can be considered an adaptation to xeric conditions because this phenomenon occurs in the xeric ant *Cataglyphis bicolor* but not in the more mesic species, *Camponotus vicinus* (Lighton 1988a). Our data do not support this interpretation. The species we examined occur in a wide variety of habitats, ranging from mesic montane environments (*S. westwoodi*) to highly xeric west coast deserts (*S. gariiepinus*). Nonetheless, all of them showed both pronounced alterations in DGC frequency with changes in  $\dot{V}_{CO_2}$  and  $\dot{V}_{CO_2}$ -independent O-phase  $CO_2$  emission volumes. However, the slopes of the regressions of O-phase frequency on temperature were different among species. Therefore, modulation of the proportional contribution of the phases to the DGC may be a more likely response to differences in water availability, a subject that requires further investigation.

We currently have no synthetic explanation for the differences in DGC modulation with temperature found so far among ants, tenebrionid beetles, and the dung beetles examined

here; too few species have been examined to allow for this. However, we note that constant O-phase CO<sub>2</sub> emission volumes across a range of temperatures have now been recorded in at least half of the species examined to date (see Buck and Keister 1955; Schneiderman and Williams 1955; Lighton 1988a, 1996 for contrary examples). This implies that many insects must be capable either of altering the hypercapnic setpoint of the O phase (see Lighton 1994) or compensating for the reduced buffering capacity of the haemolymph, associated with a temperature increase, in some other way. Given that the trigger point for the F-phase/O-phase switch increased significantly with temperature in the species examined here (Fig. 5), it appears that the former mechanism may be of greatest significance. However, without an investigation of endotracheal gas concentrations, such as those undertaken by Levy and Schneiderman (1966a, 1966b) and Kanwisher (1966), or of haemolymph gas concentrations, the mechanistic basis of these temperature-associated changes in gas exchange cannot be resolved. Nonetheless, it does appear that in insects, two pronounced strategies are involved.

In conclusion, we have shown that *Scarabaeus* dung beetles have a pronounced DGC while at rest and that the allometry of both metabolic rate and the characteristics of the DGC is similar to that found for other species, thus supporting previous hypotheses concerning the scaling of the DGC. We have also shown that variation in the DGC associated with temperature changes is modulated mostly by changes in DGC frequency and not by changes in O-phase emission volumes. Finally, and importantly, we have demonstrated that allometric changes and temperature-related changes in the DGC and its characteristics are dissimilar, at least in *Scarabaeus* dung beetles. In so doing, we have highlighted the merits of broadening the scope of investigations of the DGC in insects.

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