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Energetics of locomotion and patterns of respiration in tenebrionid beetles from the Namib Desert

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Summary. 1. Rates of oxygen consumption ($\dot{V}_{O_2}$) were measured in 4 species of flightless tenebrionids ranging in mass from 0.6 to 1.3 g. Three were fast-moving day-active species (*Onymacris plana, Physadesmia globosa, Physosterna cribripes*), and one was slow-moving and crepuscular (*Epiphysa arenicola*).

2. For motionless animals at 22–24 °C during the inactive phase of their daily cycle, the regression of log $\dot{V}_{O_2}$ (ml O_2/h) on mass (g) is described by $Y = 0.105X^{0.796}$.

3. In male *O. plana* $\dot{V}_{O_2}$ increased with running speed up to 13 cm/s. From 13 to 22 cm/s the slope of the regression of $\dot{V}_{O_2}$ on speed did not differ significantly from zero. We hypothesize that the independence of $\dot{V}_{O_2}$ and high running speeds in *O. plana* results from the generation of aerodynamic lift by its flattened and laterally expanded body which acts as an airfoil. In *P. globosa* and *P. cribripes* $\dot{V}_{O_2}$ increased linearly with running speed at all speeds measured.

4. $\dot{V}_{O_2}$ was strongly cyclical. The periodicity was most conspicuous in motionless animals but was also apparent during locomotion. The cycles corresponded with periods of ventilation associated with episodes of pumping by the abdomen which lies within a space inclosed in a rigid chitinous capsule formed by the fused elytra and fused abdominal sternites.

5. Factorial metabolic scope was greatest in *O. plana*, the most cursorial of the species studied.

Introduction

Little information is available on the energy cost of terrestrial locomotion in insects. To our knowledge, direct measurements of oxygen consumption in insects during walking or running have been published only for a flightless cockroach (Herreid et al. 1981a; Herreid et al. 1981b), and for three ant species (Jensen and Holm-Jensen 1980; Nielsen et al. 1982).

We present here the physiological parts of a combined field and laboratory study of locomotion in several species of the flightless tenebrionid beetles that are the most conspicuous arthropod inhabitants of the Namib Desert of southern Africa. Aspects of the ecology, distribution, water economy, and thermal biology of these Namib tenebrionids have been documented (see for example, Edney 1971; Hamilton 1975; Seely 1979; Nicolson 1980; Louw and Seely 1982), but their energy metabolism has not previously been measured.

Materials and methods

Species studied

All of the species dealt with in the present study belong to the tribe Adesmiini of the family Tenebrionidae (Koch 1962; Penrith 1979). Three of them (*Onymacris plana, Physadesmia globosa*, and *Physosterna cribripes*) are day-active, and one (*Epiphysa arenicola*) is crepuscular. In all four species the elytra are fused and form a chamber into which the abdominal spiracles open. None has flight muscles. All are omnivorous scavengers and feeders on detritus.

Onymacris plana is endemic to the Namib dune sea. It is a "sand swimmer" and spends more than half of its time beneath the surface. It is associated with isolated perennial plants, particularly *Stipagrostis sabulicola* and *Trianthema hereroensis*. It is active on the surface throughout the year at sand temperatures of 20 to 50 °C. During surface activity its body temperature is usually above 35 °C (Hamilton 1975), but it will emerge from beneath the sand when the temperature is less than 10 °C to drink condensed fog droplets from plants. It is highly resistant to desiccation. The body of the male is dorsoventrally compressed and the fused elytra are flared out laterally giving the animal a discoid shape (Fig. 2). The females of *O. plana*, and both sexes of the other species studied, have body forms of a more generalized beetle type. *O. plana* is by far the swiftest runner of the beetles of the Namib Desert. When surface tempe-

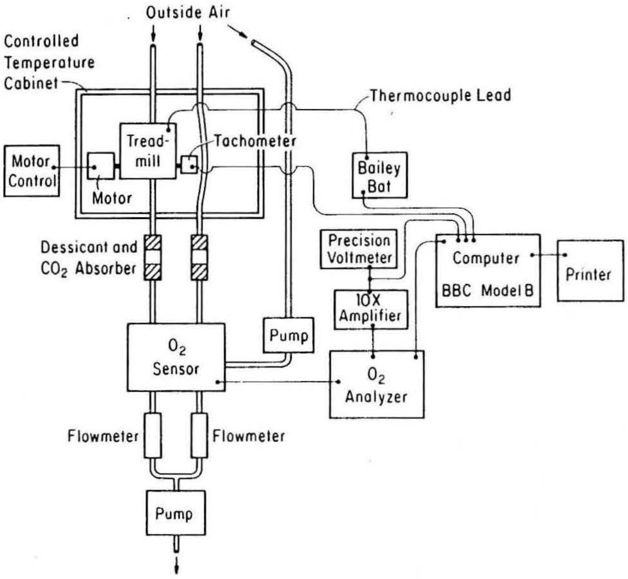

Fig. 1. Diagram of the respirometry system used to measure the oxygen consumption of running beetles

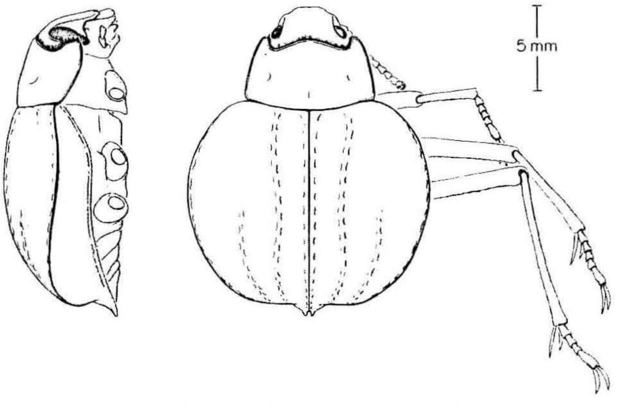

Fig. 2. Dorsal and lateral views of a male *O. plana*

ratures are high (35 to 50 °C) it often runs rapidly for distances of more than 20 m from one isolated plant to another.

Physosterna cribripes occurs throughout the Namib Desert in sandy washes and sandy dry river courses. It often seeks shade and its body temperature during activity is much lower than that of *O. plana*.

Physadesmia globosa occurs in sandy, dry river beds that support perennial plants, and on vegetated dunes where shrubs provide shade. It feeds extensively on fallen *Acacia* flowers.

Epiphysa arenicola differs from the above species, not only in being crepuscular, but because of its extremely low speed of locomotion.

The experimental animals were captured in the Namib Desert near the Gobabeb Research Station and taken to the University of Cape Town, where they were kept on Namib sand in glass terraria in a constant temperature room (28 °C) on a 12 h photoperiod. Heat lamps above the terraria were switched on during the day, so that the beetles could maintain body temperature near 35 °C. Food, consisting of rolled oats and lettuce, was always available.

Oxygen consumption

Rates of oxygen consumption ($\dot{V}_{O_2}$) of individual beetles either at rest or running on a treadmill were measured with an Applied Electrochemistry S3A two-channel oxygen analyser. Rates of oxygen consumption of motionless beetles at rest were measured using both a closed system and an open-flow system. All measurements of running beetles were made with the open-flow system.

Open-flow system. Outdoor air (flow rate, 72 cm^3/min) was drawn through a respirometry system arranged as shown in Fig. 1. Ambient temperature (T_a) was controlled to within 0.5 °C. Two different techniques were used; both allowed determination of the fractional concentration of oxygen in the excurrent air stream with a resolution of 0.001%. Initially both channels of the analyzer were employed, air from the respirometer going to one, and outside air to the other. $\dot{V}_{O_2}$ was computed from the difference between the fractional concentrations of O_2 in the two channels. During the second half of the study only a single channel was used. The output of the analyzer was inverted and amplified 10-fold. The amplified output was connected to a Hewlett Packard 3468A multimeter and to a computer. The output voltage from the amplifier, when dry, CO_2-free outside air was going through the sensor, was offset to zero. When an insect was put in the respirometer, it reduced the oxygen concentration in the air stream and the resultant change in the amplifier output was processed by the computer.

The treadmill respirometer was made of Lucite. It was housed in a temperature control cabinet maintained at 35 °C. The canvas belt on which the beetles ran was driven by a variable speed electric motor. One shaft of the belt drive was attached to a small electric motor that acted as a generator. The output from the motor was integrated using a RC network with a time constant of 1.0 s. The resultant voltage was converted to belt speed (cm/s) by the computer. Belt speed could be varied from 6 to 50 cm/s. The working chamber of the treadmill had a floor measuring 4.9 by 4.1 cm, and a volume of approximately 54.9 cm^3.

Open flow determinations of resting $\dot{V}_{O_2}$ values at 35 °C were usually made in the treadmill respirometer with the belt motionless. However, in some instances the treadmill was replaced by a Lucite vessel with a volume of 25.5 cm^3.

To measure $\dot{V}_{O_2}$ of a beetle in the treadmill respirometer, we placed it in the working chamber of the treadmill and allowed it to explore the area for several minutes and to come to a body temperature of 35 °C. After the animal settled down and became motionless we monitored its $\dot{V}_{O_2}$ for 20 to 40 min to obtain resting values. Thereafter, we tried to measure its running $\dot{V}_{O_2}$ by starting the treadmill. It was difficult to get the beetles to run in synchrony with the speed of the treadmill. To guide their movements, we used a thin, wooden prod controlled by hand and inserted into the treadmill chamber through an air-tight flexible fitting.

Instantaneous rates of $\dot{V}_{O_2}$ were determined every 15 s by the computer using a method of calculation based on the washout characteristics of the respirometry system. These characteristics, of course, vary with the flow rate of the air and volume of the system (see Bartholomew et al. 1981, for details and computations).

The behavior of the beetles on the treadmill, or in the small respirometer chamber, was monitored continuously. A coded entry was made from the keyboard of the computer describing the behavior during each 15 s interval while the treadmill was running and as appropriate when it was not. Every 15 s the computer printed out time, instantaneous $\dot{V}_{O_2}$ corrected to STP, ambient temperature in the respirometer chamber, tread-

Table 1. $\dot{V}_{O_2}$ at rest in relation to time of day, maximum $\dot{V}_{O_2}$ and factorial metabolic scope in some African tenebrionid beetles

		$\dot{V}_{O_2}$ at rest (ml/g h)			Maximum $\dot{V}_{O_2}$ (ml/g h)	Factorial metabolic scope		
		10–1530 h 35 °C A	17–1930 h 35 °C B	20–2200 h 22 °C C	10–1530 h 35 °C D	D/A	D/B	D/C
Onymacris plana	Mean	0.670	–	0.122	7.782	11.6	–	63.8
	SD	±0.073	–	±0.023	±1.407			
	n	(6)	–	(12)	(12)			
	Mass (g)	0.691	–	0.687	0.698			
Physadesmia globosa	Mean	0.362	–	0.123	3.846	10.6	–	31.3
	SD	±0.093	–	±0.024	±0.757			
	n	(8)	–	(13)	(11)			
	Mass (g)	0.652	–	0.743	0.676			
Physosterna cribripes	Mean	0.382	0.287	0.093	2.602	6.8	9.1	27.9
	SD	±0.237	±0.063	±0.034	±0.352			
	n	(9)	(8)	(13)	(6)			
	Mass (g)	1.226	1.285	1.226	1.189			
Epiphysa arenicola	Mean	–	–	0.111				
	SD	–	–	±0.042				
	n	–	–	13				
	Mass (g)	–	–	1.187				

mill belt speed, a statement about the behavior of the beetle, and a specification of whether or not the beetle was running in synchrony with the treadmill.

Closed system. An individual beetle was placed in a 60 cm^3 syringe equipped with a 3-way valve. The syringe was placed in a vertical position in the constant temperature chamber. After the beetle settled down and became motionless, the plunger was introduced into the syringe and pumped several times slowly to flush out the air. The volume of the syringe was then adjusted to 35 cm^3 and the valve was closed. After a period of 10 to 30 min depending on the temperature and mass of the beetle, the syringe was removed from the constant temperature chamber, and a 20 cm^3 sample of the air it contained was transferred to a second syringe also equipped with a 3-way valve. The three-way valve of the transfer syringe was connected to a hypodermic needle inserted near the middle of a 1 m length of Tygon tubing (inside diameter, 3 mm). One end of the tube was connected to a 10 ml pipette open at its opposite end to room air; the other end was connected, via a H_2O and CO_2 scrubber with an internal volume of about 5 cm^3, to the input of the oxygen analyzer through which air was drawn at a rate of about 40 cm^3/min. The 20 cm^3 air sample was then injected from the syringe at a rate of about 5 cm^3/s, filling the Tygon tube and open-ended pipette with a bolus of air which was then drawn through the scrubber and then through the analyzer.

The computer was programmed to monitor the fractional concentration of oxygen once per second. When a minimum value was obtained, the computer calculated and printed out the beetle's rate of oxygen consumption using the following formula and correcting to STP:

$$\dot{V}_{O_2}=(((V_a-V_b-V_w)\times(F_IO_2-F_EO_2))/t)/(1-F_EO_2)$$

where $\dot{V}_{O_2}$ is cm^3/min; V_a is the volume of air in the test syringe during the run; V_b is the volume of the beetle (mass in g × density which was assumed to be 1.01); V_w is the volume of water vapor in the air (calculated from air temperature, relative humidity, and barometric pressure); t is in minutes and F_IO_2 and F_EO_2 are the initial and end fractional concentrations of oxygen.

Results

$\dot{V}_{O_2}$ *when motionless*

In the laboratory the day-active species were much more alert and responsive during the middle of the day than at dusk. This behavioral difference is also apparent in their rates of oxygen consumption when at rest. For example, in *P. cribripes* $\dot{V}_{O_2}$ at 35 °C was 75% higher during midday than at dusk, even though the lighting conditions were the same (Table 1). At 35 °C the daytime values for *O. plana* were almost twice as high as those for the other two diurnal species, but its nighttime values at 22 °C were indistinguishable from those of *P. globosa.* The nighttime values at 22 °C for both *O. plana* and *P. globosa* were significantly higher than those for *P. cribripes* ($P<0.05$, two-tailed *t*-test). The nighttime values at 22 °C for *E. arenicola* fell near the center of the range of the others.

The $\dot{V}_{O_2}$ of resting Namib tenebrionids during the inactive phase of their daily cycle at ambient temperatures of 22–24 °C increased with increasing mass (Fig. 3). To improve our understanding of this relationship we have employed analysis of covariance, using the data for the individuals of the four tenebrionid species and also data on indivi-

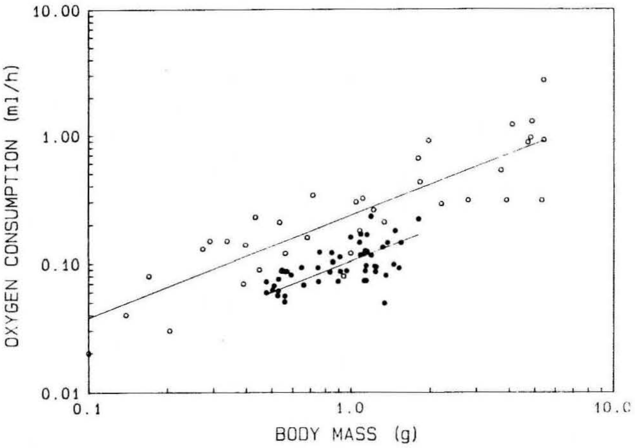

Fig. 3. The regression of $\dot{V}_{O_2}$ on mass of beetles at rest at $T_a = 22–25$ °C during the inactive period of the daily cycle. Each point shows a single individual. Filled circles, 4 species of tenebrionids from the Namib Desert (see also Table 1). Open circles, beetles from the lowland tropical forest in Panama (data from Bartholomew and Casey 1977). The coefficient of determination (r^2) is for the summed variance about both regression lines (see text for details)

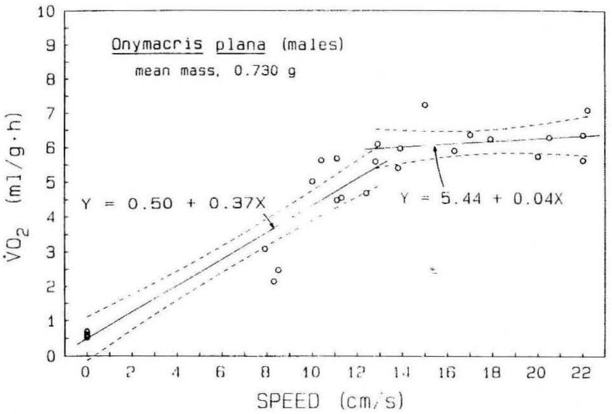

Fig. 4. The relation of oxygen consumption to running speed in *O. plana*. $T_a = 35$ °C. Each point represents the mean value of 5 to 21 consecutive measurements made at 15 s intervals on a single beetle. $N = 16$ individuals. The dashed lines inclose the 95% confidence intervals for the least squares linear regressions fitted to the data for speeds of 0 through 12.9 cm/s and 12.8 through 22.2 cm/s

duals from many species of several families from the lowland tropical forest of Panama (Bartholomew and Casey 1977).

The slopes of the regressions of the log transformed values of $\dot{V}_{O_2}$ on mass for the two groups are not significantly different. We therefore calculated the intercepts of the two groups in terms of their common slope (0.796). For the Namib tenebrionids the allometric equation for the regression of log ml O_2/h on log mass (g) is $Y = 0.105\ M^{0.796}$, and for the Panama beetles it is $Y = 0.238\ M^{0.796}$. The two intercepts differ significantly ($P < 0.001$, ANCOVA). The resting oxygen consumption of the tenebrionids from the Namib Desert is only 38% that of beetles of similar mass from the lowland tropical forests of Panama.

$\dot{V}_{O_2}$ *while running*

Most of the beetles tested would not consistently run in synchrony with the speed of the treadmill. However, we were able to obtain a number of periods of measurement, particularly for *O. plana*, in which the beetles ran synchronously for intervals of 2 to 2.5 min and during which instantaneous $\dot{V}_{O_2}$ measured every 15 s was reasonably uniform. The mean of all the values recorded during intervals of steady running in synchrony with the treadmill were used to estimate rates of energy expenditure. Although the rapidity of limb movements, and probably stride length, varied with running speed, we detected no changes in gait, except possibly in *O. plana* at the highest speeds tested.

Onymacris plana. Only males were measured. *O. plana* are sprinters. In the sand dunes where they normally occur they frequently run 20 or more meters at speeds near 100 cm/s, but we never saw them run continuously for more than a minute (Nicolson et al. 1984). On the treadmill they would not run at speeds less than 7 to 8 cm/s. Because of their pattern of locomotor activity, we were unable to obtain measurements from them during prolonged steady state locomotion. $\dot{V}_{O_2}$ increased with running speeds up to 22 cm/s which was the highest speed at which we could obtain reliable data (Fig. 4). At higher belt speeds the beetles bounced and tumbled and were unable to stay on their feet probably because of the air turbulence generated in the limited confines of the working chamber by the rapid movement of the belt. There was a sharp decline in the rate of increase of $\dot{V}_{O_2}$ at about 13 cm/s. Above 13 cm/s $\dot{V}_{O_2}$ was almost independent of running speed. The slope of the regression at speeds greater than 12.8 cm/s ($Y = 5.44 + 0.04X$) does not differ significantly from zero. The value for mass specific $\dot{V}_{O_2}$ at 100 cm/s, extrapolated from the regression equation (Fig. 4, right), is 9.44 $cm^3/g \cdot h$. This value is within the range of maximum $\dot{V}_{O_2}$'s (6.54–10.63 cm^3) that we measured for individuals of this species on the treadmill (see Metabolic scope).

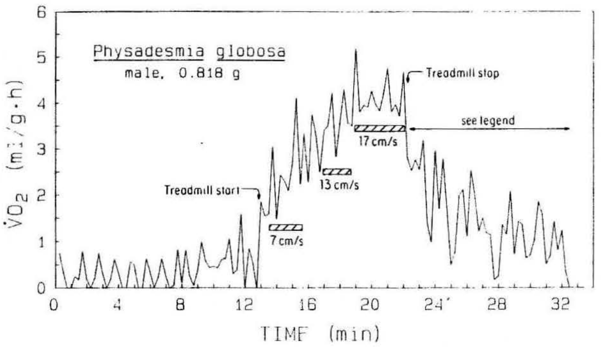

Fig. 5. Instantaneous rates of oxygen consumption before, during, and after treadmill running in an individual *Physadesmia globosa*. $T_a = 35$ °C. Cross-hatched rectangles show running speeds. After the treadmill stopped the beetle remained motionless except for occasionally shifting position by a few cm

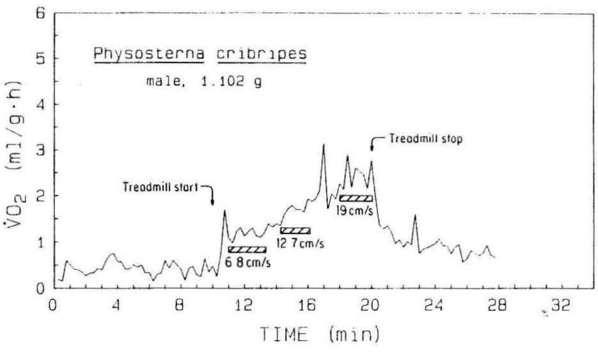

Fig. 6. Instantaneous rates of oxygen consumption before, during, and after treadmill running in an individual *Physosterna cribripes*. Cross-hatched rectangles show running speeds. After the treadmill stopped the beetle remained motionless. $T_a = 35$ °C

Physadesmia globosa. Most individuals tested would not run on the treadmill when it was moving, or ran in such poor synchrony with it that the data were not usable. After many attempts we obtained limited data from 15 to 25 min runs by 9 males (mean mass, 0.626 g) at speeds from 6 to 18.6 cm/s. We used the mean values of instantaneous $\dot{V}_{O_2}$ from periods of steady running lasting from 1 to 3 min. These data suggest that $\dot{V}_{O_2}$ increased slightly with speed, but the slope of the linear regression, ml O_2/g·h = 1.89 + 0.0756 × cm/s, does not differ significantly from zero. However, out of the 12 beetles tested, one individual ran consistently and steadily at each of three different speeds. Its $\dot{V}_{O_2}$ increased with velocity from a mean of 2.7 cm^3/g·h at 7.0 cm/s, to a mean of 4.02 cm^3/g·h at 13.0 cm/s, to a mean of 4.62 at 17 cm/s (Fig. 5). The least squares regression of these three values yields a slope of 0.194 (significantly different from zero; $P < 0.01$, two tailed *t*-test) and an intercept of 1.38 ($r^2 = 0.99$).

It is noteworthy that the $\dot{V}_{O_2}$ of *P. globosa* at all velocities is substantially less than that of *O. plana*. This despite the fact that under natural conditions *P. globosa* is the more sedentary species and runs only about one quarter as fast as *O. plana*.

Physosterna cribripes. Despite repeated efforts with 10 beetles of this species, we were able to get only one individual, a 0.82 g male, to run in synchrony with the speed of the treadmill. This animal did so at three different speeds (Fig. 6). Its $\dot{V}_{O_2}$ increased linearly with running speed, ml O_2/g·h = 0.5697 + (0.1163 × cm/s), $r^2 = 0.99$. The slope differed significantly from zero ($P < 0.01$, two-tailed *t*-test).

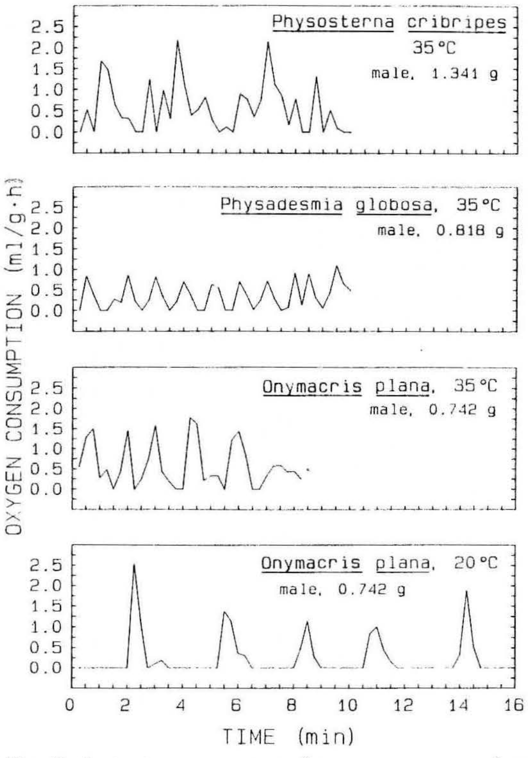

Fig. 7. Instantaneous rates of oxygen consumption showing intermittent ventilation in three species of tenebrionids

Intermittent ventilation

The $\dot{V}_{O_2}$ was cyclical in *O. plana, P. cribripes,* and *P. globosa*. *E. arenicola* was not examined. The oscillations in $\dot{V}_{O_2}$ were most obvious when the animals were motionless (Fig. 7). Although oscillations in oxygen uptake were apparent in all three species, the precise pattern varied with species and ambient temperature. In a male *O. plana* at a T_b

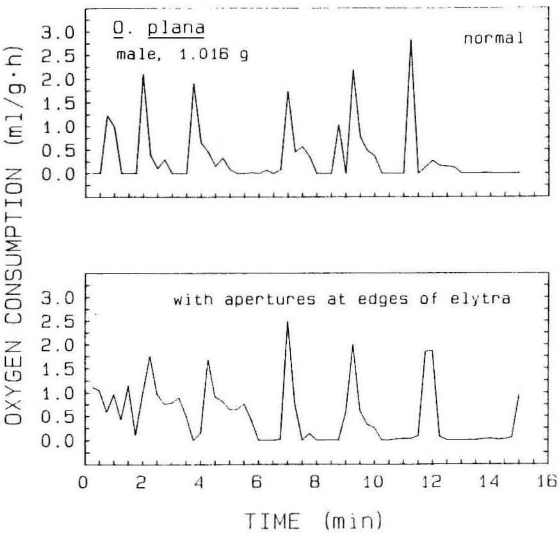

Fig. 8. The independence of intermittent ventilation of the integrity of the elytral cavity in *O. plana*. $T_a=35$ °C. See text for details

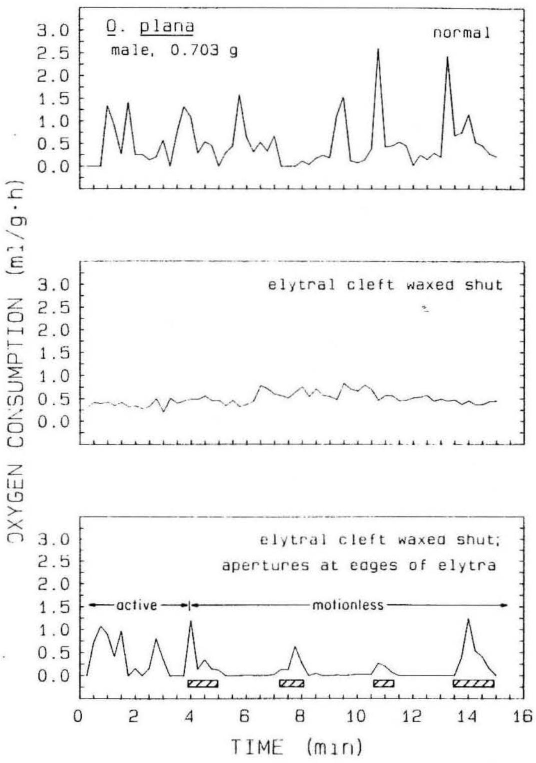

Fig. 9. The effects on the ventilatory pattern of artificially sealing and subsequently opening the elytral cavity of an individual *O. plana*. Cross-hatched bars in lower figure represent periods of abdominal pumping. $T_a=20$ °C

of 20 °C the periods of apnea lasted from 2 to 3 min, but in the same individual at a T_b of 30 °C they rarely lasted for more than 15 s (Fig. 7).

The tenebrionids used in the present study have completely fused elytra that are also continuous with the abdominal sternites which are inflexibly fused to each other. Thus, posterior to the prothorax, the body is completely enclosed in a rigid and continuous capsule of cuticle. The elytral chamber, into which the abdominal spiracles open, is vented to the exterior by an elytral cleft that can be opened and closed by limited movements of the last two abdominal segments.

We initially assumed that the cyclical uptake of oxygen was caused by the periodic openings of the elytral cleft, a movement that is readily observable. However, a series of experiments showed that although the periodic openings and closings of the elytral cleft were synchronized with the peaks in oxygen uptake, these movements were not the primary controls of the cycles in $\dot{V}_{O_2}$.

We made a pair of permanent apertures in the elytra of a male *O. plana* by cutting strips of cuticle measuring about 1 × 3 mm from the lateral surface of each elytron. The oscillatory pattern of oxygen uptake was maintained irrespective of whether the elytra were intact or artificially fenestrated (Fig. 8).

When the elytral cleft of an intact beetle was sealed shut with beeswax and resin, the oscillations in oxygen uptake completely disappeared (Fig. 9, middle). When fenestrae were subsequently cut in the elytra of the same beetle, the oscillatory pattern of oxygen uptake was immediately reestablished (Fig. 9, lower). Using the computerized system for instantaneous measurement of $\dot{V}_{O_2}$ and simultaneous recording of behavioral information, we found that the recurring peaks of oxygen uptake corresponded with the pumping movements of the abdomen which were easily visible through the elytral fenestrae (hatched bars, Fig. 9, lower).

Abdominal pumping in *O. plana* occurred as sets of rhythmic pulsations interspersed with periods of quiescence. One male with windows cut in each elytron was tethered in place so that we could count its rate of abdominal pumping. At a temperature of 22 °C it pumped at a rate of 1.2 contractions per second. We did not examine the mechanics of periodic respiration in *Physosterna* and *Physadesmia*. We assume that they are similar to those of *O. plana*.

Although the oscillatory pattern of oxygen uptake was most obvious in motionless tenebrionids, it was also apparent while they were moving about (see for example, Fig. 9, lower). A strongly fluctuating pattern in $\dot{V}_{O_2}$ was present even during high speed running (Figs. 5 and 6); however the cycles were irregular. It is not possible to characterize precisely the rhythmicity of ventilation in running beetles. Suffice it to say that at rest and during modest activity respiratory pumping was discontinuous in the three species. The periods of eupnea were more closely spaced and the length of both eupnea and apnea were shorter in these tenebrionids than have been reported for other adult insects (see Discussion).

Metabolic scope

Analysis of factorial aerobic metabolic scope for activity in tenebrionids is complicated by the variability of their body temperatures and the fact that at rest they have a diurnal cycle in rate of oxygen consumption. During daytime at 35 °C factorial scope in the three species was near 10. If the nighttime value of $\dot{V}_{O_2}$ at 24 °C is used as a base, which is ecologically reasonable, factorial scope in *O. plana* is 64, which is about twice as great as in *P. globosa* or *P. cribripes* (Table 1).

Discussion

Comparison with other pedestrian insects

The only insects for which data on the energy cost of terrestrial locomotion have been obtained are three species of ants (Jensen and Holm-Jensen 1980; Nielsen et al. 1982) and a cockroach, *Gromphadorhina portentosa* (Herreid 1981). This insect runs much less rapidly than do the Namib tenebrionids. The tenebrionids would not run on the treadmill at less than 6 cm/s, which is almost twice as fast as the most rapid locomotion (0.12 km/h or 3.3 cm/s) for which data on $\dot{V}_{O_2}$ are available for the cockroach. However, from the regressions of $\dot{V}_{O_2}$ on velocity, the calculated values of $\dot{V}_{O_2}$ for the tenebrionids, when corrected to 25 °C using a Q_{10} of 2, are substantially less than those for the cockroach (Table 2). These low values of $\dot{V}_{O_2}$ are consistent with the ability of these tenebrionids to run at extremely high velocities.

We found no significant endothermic elevation of body temperature during running in any of the species studied. Nevertheless, they can substantially elevate body temperature by behavioral thermoregulation. If one compares resting metabolism of *O. plana* at night at 24 °C with its maximum $\dot{V}_{O_2}$ when running at 35 °C the aerobic factorial scope of *O. plana* is more than 60. This is an extremely high value for a terrestrial animal, but is less than half that found in a number of flying insects (Bartholomew 1981).

Terrestrial vertebrate ectotherms sustain intense activity anaerobically. This does not appear to be true for the tenebrionids that we studied. Nevertheless, as in the case of *Gromphadorhina*, after a bout of sustained running, elevated levels of $\dot{V}_{O_2}$ persisted for several minutes (Figs. 5 and 6).

Table 2. The energy cost of running 3.3 cm/s in a cockroach and three tenebrionids

	Mass (g)	T_a (°C)	$\dot{V}_{O_2}$ (ml/gh)	$\dot{V}_{O_2}$ at 25 °C	Source
Gromphadorhina portentosa	5.2	25	1.0	1.0	Herreid et al. 1981a, b
Onymacris plana	0.73	35	1.93	0.97	Present study
Physadesmia globosa	0.626	35	1.72	0.86	Present study
Physosterna cribripes	1.1	35	0.95	0.48	Present study

[a] $\dot{V}_{O_2}$ corrected for temperature assuming $Q_{10}=2$

Oxygen consumption at rest

$\dot{V}_{O_2}$ at the low point in the daily cycle of activity in four species of tenebrionids from the Namib desert was less than 40% that of beetles of similar mass from the tropical forests of lowland Panama. This low rate of energy expenditure should be adaptively advantageous to the Namib beetles because they live in an environment of extremely low productivity where the food supply is both unpredictable and patchy (Seely 1978).

High speed running in O. plana

On the sand dunes where it lives, *O. plana* ($T_b=37$–39 °C) can run without stopping for as far as 30 meters at speeds in excess of a 100 cm/s (Nicolson et al. 1984). This is equivalent to at least 50 body lengths per second. When the beetle is running rapidly it appears to float along like a low flying bumble bee. The height of the body above the ground remains constant and it does not pitch or yaw.

If, as our data indicate, $\dot{V}_{O_2}$ is virtually independent of speed above 13 cm/s, there must be a qualitative change in its pattern of locomotion at this speed – something analogous to the change in gait in mammals. We have no satisfactory data on the nature of the change, but it could involve aerodynamic lift. The body of *O. plana*, particularly in males, resembles a highly cambered delta wing (Fig. 2). We hypothesize that at about 13 cm/s the body of *O. plana* may become effective as

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an airfoil and generate aerodynamic lift. This lift should support part of the beetle's weight and reduce the need for the legs to support the body and allow them to convert more of their work to thrust.

Intermittent ventilation

The sensitivity of our system of measuring instantaneous rates of oxygen consumption at closely spaced intervals allowed a clear demonstration of intermittent respiration in *O. plana, P. globosa,* and *P. cribripes*. The periodicity of this discontinuous respiratory pattern was most apparent when the beetles were motionless at 20 °C (Fig. 7). Nevertheless, even when they were running rapidly with a body temperature of 35 °C, a discontinuous pattern could still be discerned. In the latter situation, however, oxygen consumption did not return to zero. It is also clear from Fig. 7 that the durations of the periods of apnea diminished with increased ambient temperature.

In *O. plana* the primary cause of intermittent respiration was the periodic opening and closing of the abdominal spiracles, accompanied by contractions of the abdominal musculature. The effect of the periodic opening and closing of the elytral cleft, however, superimposed an additional control on the function of the abdominal spiracles and the abdominal pumping.

Qualitatively similar respiratory patterns have been reported in carabid beetles (Punt et al. 1957) and in a scarab beetle during episodes of sustained endothermy at low ambient temperatures, but not when at rest (Morgan and Bartholomew 1982). Intermittent ventilation has also been reported in insects of other orders (see Miller 1981, for a review of insect ventilation).

The intermittent respiration of the Namib tenebrionids and the long periods of apnea when they are at rest, coupled with the fact that the abdominal spiracles open into the subelytral cavity, may, as in the model first proposed by Buck (1958), minimize water loss in the extremely arid environment in which they live.

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