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TRACHEAL GASES, RESPIRATORY GAS EXCHANGE, BODY TEMPERATURE AND FLIGHT IN SOME TROPICAL CICADAS

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SUMMARY

Fidicina mannifera Fab. (mass 3 g) can fly at a body temperature of 22 °C, but take-off is usually preceded by an endothermic warm-up that elevates T_{th} to 28 °C or higher. Warm-up is accompanied by slow, almost imperceptible, wing movements, gentle abdominal pumping and an increase in $\dot{V}_{O_2}$ to about 16 times the resting level. During wing-flapping in fixed flight, $\dot{V}_{O_2}$ increases explosively to about 70 times the resting level, and thoracic temperature rises to about 33 °C. Wing-beat frequency increases with T_{th}. Between 25 and 34 °C the mean wing-beat frequency is about 37 Hz. *F. mannifera* does not maintain free flight, or wing flapping in fixed flight, for more than about 100 s. Flight is supported aerobically, and we infer that exhaustion is related to depletion of substrate in the flight muscles.

The volume of the tracheal system of *F. mannifera* is about 45 % of total body volume. At rest, F_{O_2} in the thoracic air sacs remains near 17 % and F_{CO_2}, near 3 %. During non-flapping warm-up, F_{O_2} falls to as low as 1 % and F_{CO_2} rises to as high as 21 %. Thus, gas exchange may limit the rate of warm-up. When wing-flapping commences, F_{O_2} and F_{CO_2} quickly return to near resting levels, presumably as a result of autoventilation.

The interspecific regression of $\dot{V}_{O_2}$ on mass for three species of cicadas at 23–24 °C has a slope of 0·89 and a 1-g intercept of 0·63 ml h^{-1}.

INTRODUCTION

Fidicina mannifera, a large (~3 g) cicada that occurs in the lowland tropics of central America, is able to take off and fly with a body temperature as low as 22 °C. This contrasts sharply with the situation in many beetles and most moths of similar mass, which require thoracic temperatures greater than 30 °C for flight (Heinrich, 1981).

The present study examines the oxygen consumption, body temperature, tracheal gas concentrations and flight characteristics of *F. mannifera*, as well as the energy metabolism of other cicadas at rest. Previously published research on the energetics and body temperatures of cicadas has been directed at the mechanism of sound

Key words: Respiration, temperature, cicadas, tracheal gases.

production (Josephson & Young, 1979) and aspects of behavioural thermoregulation (Heath, Wilkin & Heath, 1972).

MATERIALS AND METHODS

Our studies were carried out during July, 1982 at the Barro Colorado Island Station of the Smithsonian Tropical Research Institute in the Republic of Panama.

Animals

Cicadas were captured at night at lights, or during the day on the trunks and branches of trees, particularly *Zanthoxylum panamense* on which they commonly fed. The cicadas were weighed to the nearest mg and housed individually in ventilated plastic boxes which contained moistened paper and were kept in an air-conditioned room. Physiological measurements were made within 24 h of capture. Species identifications were confirmed by Dr Thomas E. Moore of the Museum of Zoology, University of Michigan, Ann Arbor where the specimens are deposited.

Temperature

Experiments were carried out at 23·0–24·5 °C either in an air-conditioned room or a refrigerated incubator in which ambient temperature (T_a) could be controlled to within half a degree and which was equipped with a window, and a reach-through port.

All temperatures were measured with copper-constantan thermocouples connected to Bailey Bat thermometers. Thoracic temperature was measured with a 40 gauge thermocouple inserted dorsolaterally into the flight muscles to a depth of about 2 mm. The thermocouple was secured to the cuticle with beeswax. A shortened insect pin was inserted transversely through the heavy cuticle on the dorsal part of the caudal end of the thorax and secured with beeswax. A pipe cleaner was looped around the pin and served as a handle for positioning and lifting the cicada and for securing the thermocouple leads (Fig. 1).

Oxygen consumption

Rates of oxygen consumption ($\dot{V}_{O_2}$) were measured with an Applied Electrochemistry S3-A Oxygen Analyzer. Measurements during fixed flapping and non-flapping warm-up were made in a flow-through system. Measurements of inactive cicadas were made in a closed system. In both systems the air was dried and the CO_2 removed before it was introduced into the oxygen sensor. Rates of air flow were measured with a flow meter calibrated against a Brooks mass flow meter.

Flow-through system

The cicada was placed in a cylindrical Lucite respirometer chamber equipped with input and output manifolds to ensure adequate air mixing. The thermocouple and the pipe cleaner that were attached to the cicada were passed through a small hole in the respirometer lid. Air was drawn successively through respirometer chamber, drying train (Drierite), CO_2 absorbent (NaOH pellets), sensor, flowmeter and pump. Flo

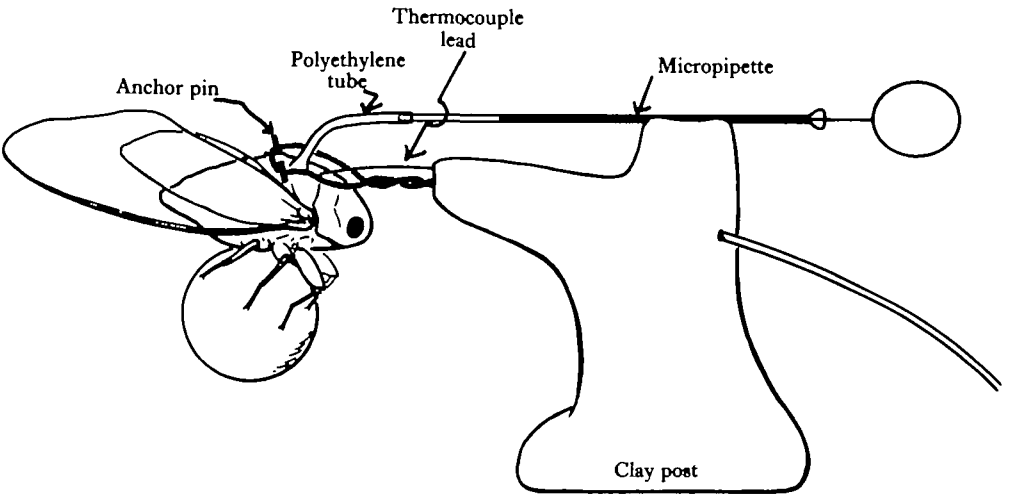

Fig. 1. Experimental preparation for sampling of tracheal gas (see Methods).

was controlled at 73 $cm^3 min^{-1}$ by a needle valve. Tygon tubing was used throughout. The system was calibrated before each run. An AIM-65 microcomputer (Rockwell) controlled a multichannel switching and analogue-to-digital conversion system, recorded the outputs of the sensors and converted these voltages to temperature and to instantaneous rates of oxygen consumption.

Instantaneous $\dot{V}_{O_2}$ was calculated as described in Bartholomew, Vleck & Vleck (1981) using the wash-out curve of the system (effective volume, 1210 cm^3) as a baseline, and making measurements at intervals of 20 or 60 s. The system was functionally the same as the mask systems used for large vertebrates and oxygen consumption was calculated by substituting F_{EEQ} (see Bartholomew *et al.* 1981) for F_{EO_2} in the following formula and correcting to STP:

$$\dot{V}_{O_2} = V(F_{IO_2} - F_{EO_2})/(1 - F_{IO_2}), \quad (1)$$

where V is the flow of dry, CO_2-free air in $cm^3 min^{-1}$, F_{IO_2} is the fractional concentration of oxygen in the incurrent air and F_{EO_2} is the concentration of oxygen in the excurrent air. Under the conditions employed, the flow-through system measured instantaneous rates of oxygen consumption to within 0·05 $cm^3 min^{-1}$, which is about 2 % of the $\dot{V}_{O_2}$ during fixed flapping.

Closed system

For determining the $\dot{V}_{O_2}$ of inactive cicadas, we used syringes as respirometer chambers. The syringes ranged in size from 60 to 400 cm^3 and were equipped with inlet and outlet valves. The cicada was put in a syringe of appropriate size and outdoor air was pumped through it at the rate of 150 $cm^3 min^{-1}$ for 30–60 min during which time the cicada usually settled down and became motionless. The syringe was then adjusted to an appropriate volume (40–200 cm^3 depending on the size of the cicada). The ports were closed, and a stop-watch was started. Measurements lasted for 15–30 min and the insect was watched continuously. If it became active the experiment was ended by opening the inlet and outlet and flushing out the syringe with fresh

air. After the cicada had remained motionless for about 10 min the syringe was again closed and a new period of measurement was begun. At the end of the experiment the syringe was placed in a Razel infusion pump and the air in it was delivered to the oxygen sensor through a Tygon tube containing desiccant and CO_2-absorbent. $\dot{V}_{O_2}$ was calculated from the formula below and converted to STP:

$$\dot{V}_{O_2} = V_{tot} - (V_c + V_{H_2O})\,(F_{IO_2} - F_{EO_2})/(1 - F_{EO_2})t, \qquad (2)$$

where t is time in minutes; F_{IO_2} and F_{EO_2} are as in equation (1); V_{tot} is the volume of air in the syringe at the beginning of the experiment; V_{H_2O} is the volume of water vapour in that air; and V_c is the volume of the cicada excluding its tracheae and air sacs. V_c is equal to the mass of the animal divided by the density of its tissues (assumed to be $1{\cdot}08\,g\,cm^{-3}$).

Tracheal gases

Tracheal gases were sampled through a polyethylene tube 1 cm long (o.d. = 1 mm; i.d. = 0·5 mm) which was inserted into the dorsal air sac through a hole drilled in the cuticle. The tube was sealed to the cuticle with beeswax to ensure an airtight connection. The cicada was attached, as previously described, to a pipe cleaner, one end of which was embedded in a post of plasticine clay (Fig. 1). The cicada was orientated horizontally and given a foam rubber ball to hold so that it could make normal walking movements. A mercury-filled micropipette (Scholander & Evans, 1947) was inserted into the polyethylene tube. The plunger of the pipette was depressed, filling the polyethylene tube with a column of mercury that was continuous with that in the pipette. To obtain a gas sample the plunger was slowly withdrawn, pulling all of the mercury back into the pipette and also drawing 3–5 μl of air from the air sac into the tip of the pipette. A drop of water, slightly acidified with HCl, was placed on the junction of the pipette and the tube. When the pipette was withdrawn from the tube a small quantity of the acidified water entered the tip, preventing exchange between room air and the gas sample. The sample was then stored behind mercury in a glass tube, one end of which was sealed. The pipette was reinserted into the polyethylene tube and the sampling process was repeated as desired. The concentrations of CO_2 and O_2 in the samples were determined as described in Scholander & Evans (1947) except that we used the reagents described by Scholander (1947). A series of 25 determinations of room air gave mean values of 20·88 % ± S.D. 0·09 for O_2 and 0·03 % ± S.D. 0·09 for CO_2.

Tracheal volume, air sac volume and mass of flight muscles

Each cicada was weighed to the nearest mg. The volume of the abdominal air sac was measured by making a small slit in the ventral wall of the abdomen, carefully filling the air sac with water and then reweighing the animal. The cicada was then put in a 60 cm^3 plastic syringe that was equipped with a valve and filled with water to which a detergent had been added. The air in the syringe was ejected, the valve was closed, and a vacuum pulled by hand to draw air out of the tracheae and the air sacs. This air was ejected from the syringe. The process was repeated until no more air could be obtained. The water-filled cicada was then blotted dry and weighed. The increase in the mass was used as a measure of the volume of the respiratory system

The flight muscles were dissected out of the thorax, blotted, and then weighed to the nearest mg.

Wing-loading

The left wings were removed and arranged on translucent paper in the spread position typical of flight, with front and hind wings interlocked. The outline of the wings was traced on opaque paper and cut out. The area of the cut-out was measured with a model L1-3000 Licor portable area meter and multiplied by two.

Wing-beat frequency

Cicadas with thermocouples implanted in the thorax were suspended above a microphone by a pipe cleaner secured to the thorax as previously described. By jiggling the cicada and directing a stream of air at it from a blower it was induced to flap its wings until exhausted while the sound of the wing beats was recorded with a tape recorder. The thoracic temperature was recorded verbally on the tape at intervals. Wing-beat frequency was determined from the recordings with a Kay Sonagraph.

RESULTS

Resting $\dot{V}_{O_2}$ and mass

The relationship between body mass and daytime resting $\dot{V}_{O_2}$ was investigated using three species of cicadas (*Carineta viridicata* Distant, *Zammara smaragdula* Walker and *Fidicina mannifera*) ranging in mass from 0·2 to 3·0 g. Body temperatures did not differ from ambient (23–24·5 °C). The equation for the linear regression of log $\dot{V}_{O_2}$ (Y) on log mass (X) is $Y = 0{\cdot}633X^{0{\cdot}89}$ ($r^2 = 0{\cdot}89$). The slope does not differ significantly from those of beetles and moths measured under similar conditions but the intercept is higher (see Discussion). *Z. smaragdula* and *F. mannifera* feed and call during daylight. Consequently, the values of $\dot{V}_{O_2}$ represent resting metabolism during a time of day when they were normally active.

Morphometrics

F. mannifera is the largest of the cicadas on Barro Colorado Island. The males and females do not differ in mass, wing area or wing-loading (Table 1). Wing-loading increases with body mass in *F. mannifera* ($Y = 0{\cdot}104 + 0{\cdot}056X$; $r^2 = 0{\cdot}77$). A similar relationship exists interspecifically (Fig. 2).

Table 1. *Wing-loading in* Fidicina mannifera

	Mean	S.D.
Mass (g)	2·84	0·36
Wing area (cm^2)	21·51	1·42
Wing loading ($g\,cm^{-2}$)	0·132	0·011
($N\,m^{-2}$)	12·945	1·079

$N = 17$.

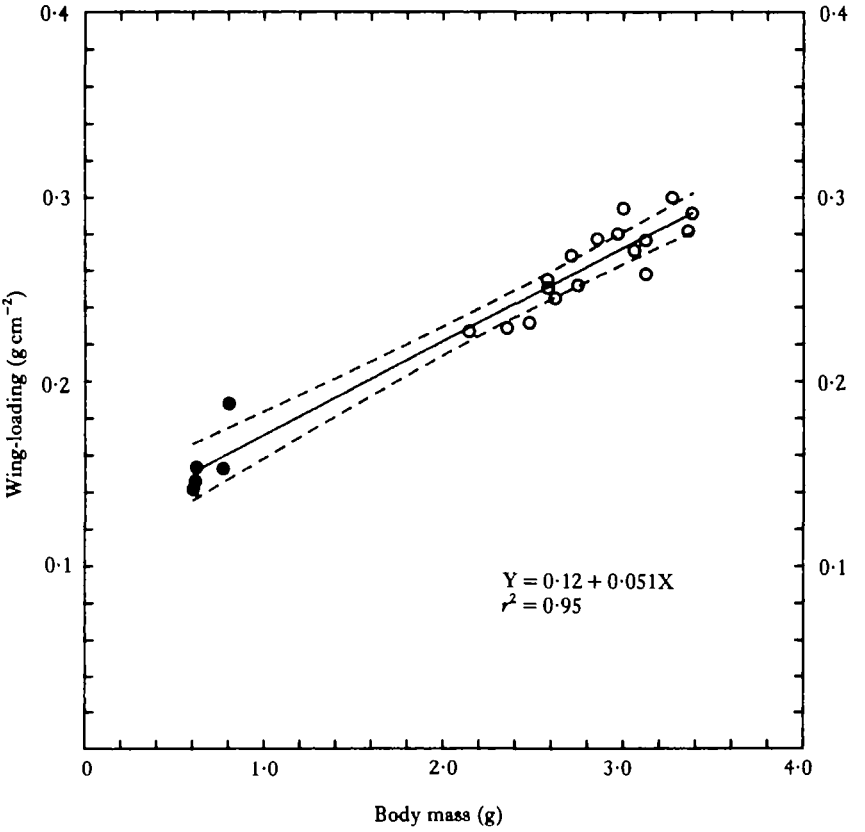

Fig. 2. Wing-loading as a function of body mass in *Fidicina mannifera* (open circles) and *Zammara smaragdula* (shaded circles). Dashed lines enclose the 95 % confidence interval of the regression. To convert g cm^{-2} to N m^{-2} multiply by 98·07.

Table 2. *Volume of tracheal system and mass of flight muscles in male and female* Fidicina mannifera

	Male $N = 4$		Female $N = 5$		
	Mean	S.D.	Mean	S.D.	*P*
Mass (g)	2·68	0·49	2·65	0·15	> 0·1
Flight muscle (g)	0·93	0·11	0·95	0·09	> 0·05
Abdominal air sac (ml)	1·08	0·28	1·12	0·21	> 0·05
Tracheal volume excluding abdominal air sac (ml)	1·25	0·11	0·75	0·22	< 0·01
Total volume of tracheal system (ml)	1·84	0·20	2·37	0·26	< 0·01

P is from Student's *t* = test comparing males and females.

The flight muscles of *F. mannifera* constitute about 35 % of the total mass. The volume of the tracheal system is large, comprising about 41 % of the total body volume in females and 48 % in males. The abdominal air sac accounts for about half the volume of the tracheal system. Tracheal volume is significantly greater in females than in males (Table 2).

$\dot{V}_{O_2}$ *and* T_{th} *during non-flapping warm-up*

All of the *F. mannifera* we observed in the field, and at 22–24·5 °C in the laboratory, were capable of immediate flight when startled. However, in the laboratory, spontaneous take-offs (those in which the insect was not startled into immediate flight) were always preceded by non-flapping warm-up, which was accompanied by barely visible wing movements of low frequency (1–2 s^{-1}). It was usually possible to induce warm-up in the restrained cicadas by brief, gentle prodding. Non-flapping warm-up was sometimes, but not always, followed by an attempt to fly. Mean T_{th} immediately before spontaneous take-off was 29·3 °C (S.D., 2·5; range, 25·4–33·0; $N = 12$). Some individuals that did not attempt to fly after warm-up maintained elevated T_{th} for 20 min or longer (Fig. 3).

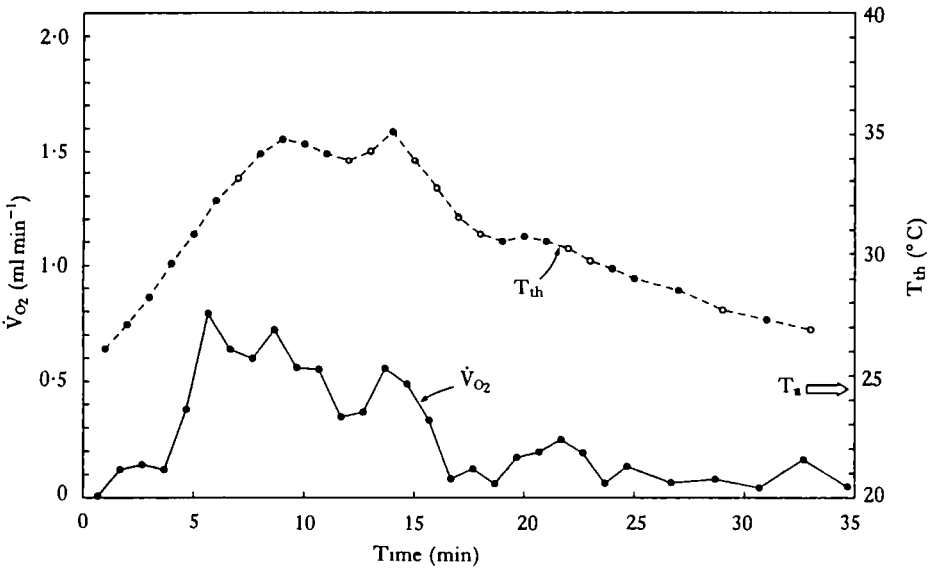

Fig. 3. Thoracic temperature (T_{th}) and $\dot{V}_{O_2}$ during non-flapping warm-up in a specimen of *Fidicina mannifera*; male, 2·76 g. T_a, ambient temperature.

Table 3. *Peak* $\dot{V}_{O_2}$, *peak* T_{th} *and total* V_{O_2} *during bouts of non-flapping warm-up* ($N = 6$) *and during bouts of fixed flapping to exhaustion* ($N = 11$) *in* Fidicina mannifera

	Fixed flapping		Warm-up	
	Mean	S.D.	Mean	S.D.
Mean mass (g)	2·838	0·451	2·628	0·067
Duration (s)	79	10·9	737*	368·2
Peak T_{th} (°C)	32·7	1·98	30·4	3·57
Peak $\dot{V}_{O_2}$ (ml min^{-1})	1·837	0·373	0·470	0·068
Total V_{O_2} (ml)†	2·52	0·584	3·238	2·144

* Period during which $\dot{V}_{O_2}$ exceeded the resting level.

† Total oxygen consumed during and subsequent to the period of flapping or warm-up until $\dot{V}_{O_2}$ returned to the resting level.

T_a = 24–25 °C.

Like the elevation in T_{th}, the increase in $\dot{V}_{O_2}$ during non-flapping warm-up was variable. Peak values of $\dot{V}_{O_2}$ (mean of the two highest readings during each warm-up) were about 16 times the resting rate at the same ambient temperature (Table 3).

$\dot{V}_{O_2}$ and T_{th} during fixed flapping

F. mannifera apparently never makes prolonged flights. The flights we observed were usually no longer than a few tens of metres from one tree to another. We were never able to force them to remain airborne in enclosed areas for more than 100 s. They readily attempted to fly while restrained (see Fig. 1) but would not flap continuously for more than 90 s.

We measured instantaneous $\dot{V}_{O_2}$ and thoracic temperature during fixed flapping to exhaustion 11 times on five female and four male *F. mannifera* (Table 3). Both $\dot{V}_{O_2}$ and T_{th} rose rapidly as soon as wing-flapping began. T_{th} continued to increase after $\dot{V}_{O_2}$ had peaked and started to decrease. Neither reached equilibrium during the period of flapping. As soon as flapping stopped, $\dot{V}_{O_2}$ fell precipitously and T_{th} declined slowly and exponentially (Fig. 4).

The relationship between $\dot{V}_{O_2}$ and T_{th} differs during fixed flapping and post-flight cooling (Fig. 5). The factorial metabolic scope of a 2·84 g *F. mannifera*, calculated as the mean peak $\dot{V}_{O_2}$ during flapping (Table 3) divided by the mean resting $\dot{V}_{O_2}$ (calculated from mean mass and the relation between $\dot{V}_{O_2}$ and mass), is 69.

Effect of anoxia on flapping

By analogy with vertebrates, the rapidity of exhaustion in *F. mannifera*, suggested that flight might be supported anaerobically. We tested this possibility by exposing cicadas to pure nitrogen in a flow-through chamber and then attempting to induce flapping. The animals showed no overt response when the chamber was flushed with

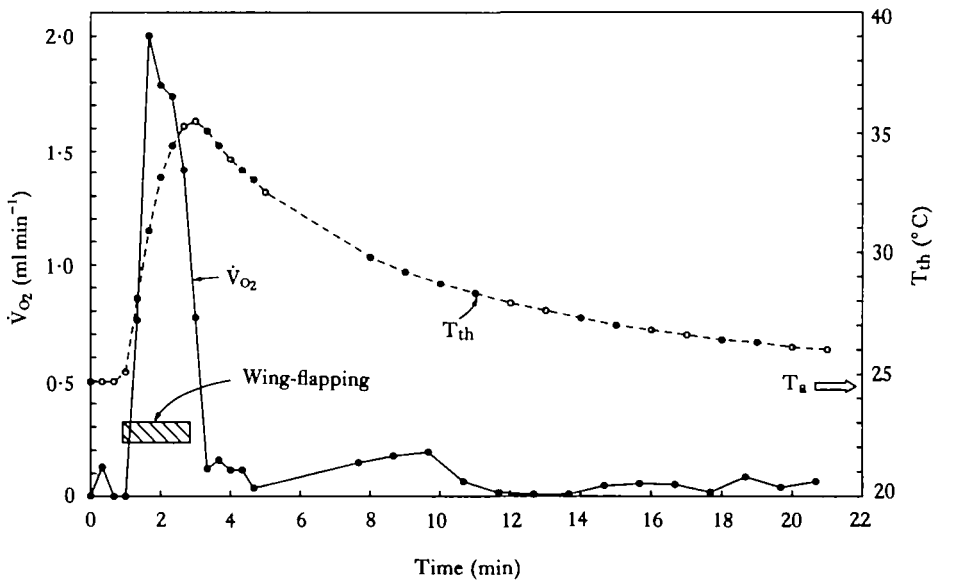

Fig. 4. Thoracic temperature (T_{th}) and $\dot{V}_{O_2}$ during tethered flapping (attempted flight) in *Fidicina mannifera*. The specimen weighed 2·33 g; T_a, ambient temperature.

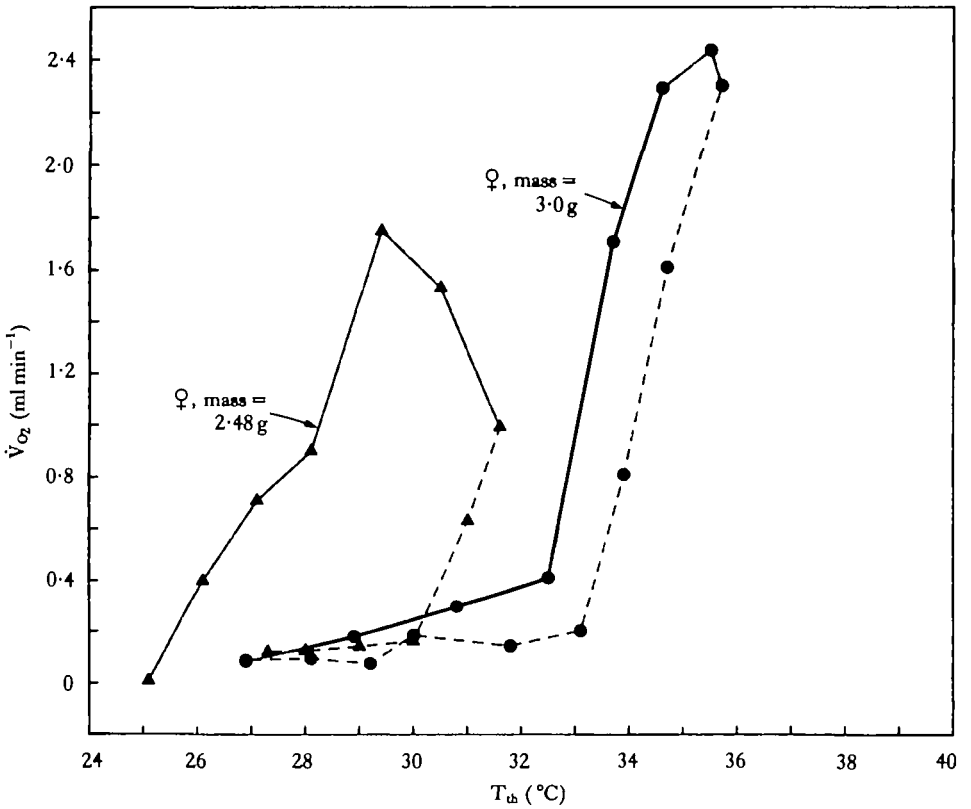

Fig. 5. Relation of mass-specific $\dot{V}_{O_2}$ and T_{th} during tethered flapping. Dotted lines indicate period of post-flight cooling.

nitrogen and remained completely immobile when we attempted to induce flapping. When returned to a normal atmosphere, the cicadas could flap vigorously within less than 1 min.

Minimum temperature for flight

We cooled *F. mannifera* in the temperature-controlled chamber while monitoring T_{th} with an implanted thermocouple. When the desired T_{th} was reached, the thermocouple leads were cut and the cicada was tossed into the air to a height of about 2 m. Even when T_{th} was as low as 16 °C, the cicadas attempted to fly. Cicadas which could not maintain altitude for a distance of 4 to 5 m were judged incapable of effective flight. The cut-off temperature for effective flight was quite sharp. In 15 trials on four cicadas, no successful flights occurred when T_{th} was below 21 °C. When T_{th} was 22 °C or higher the cicadas always flew effectively.

Tracheal gases and activity

When *F. mannifera* were motionless or walking, F_{O_2} in the thoracic air sacs remained near 17 % and F_{CO_2} remained near 3 %. During non-flapping warm-up F_{O_2} fell to as low as 1 % and F_{CO_2} rose to as high as 21 %. When wing-flapping began, both F_{O_2} and F_{CO_2} quickly returned toward the resting levels, and reached about 16 %

and 5%, respectively (Table 4). Immediately after wing-flapping ended, F_{O_2} decreased somewhat and F_{CO_2} increased; both then slowly returned toward resting levels over a period of about 20 min. Changes in F_{O_2} and F_{CO_2} were inverse and roughly symmetrical. However, F_{O_2} changed more rapidly than F_{CO_2} during the first part of warm-up and immediately after flapping (Fig. 6).

Abdominal pumping

Telescoping movement of the abdomen at 15–36 cycles min^{-1} was characteristic of non-flapping warm-up. This pumping also occurred intermittently during and immediately after flapping, but was not necessary for flight. Two unrestrained specimens flew strongly with the abdomen immobilized with wax to prevent pumping and with the abdominal spiracles sealed. Moreover, sealing either the first or third pair of thoracic spiracles in addition to sealing the abdominal spiracles did not prevent flight. When only the second pair of thoracic spiracles was left open, the cicadas could only flap weakly.

Wing-beat frequency

Wing-beat frequency (f) was positively correlated with T_{th} between 25 and 34 °C ($f = 19{\cdot}47+0{\cdot}58T_{th}$; $r^2 = 0{\cdot}36$). However, under the conditions of measurement, high

Table 4. *Tracheal gas concentrations and thoracic temperatures during different types of activity in* Fidicina mannifera

		Fractional concentration of gases (%)		T_{th} at time of sampling (°C)
		CO_2	O_2	
Motionless	Mean	2·88	17·18	25·2
	S.D.	0·86	1·53	0·8
	Min–max	1·45–4·51	13·10–19·55	23·7–26·6
	N	24	24	23
Walking	Mean	2·56	17·55	25·5
	S.D.	0·66	0·95	0·45
	Min–max	1·56–3·49	16·19–19·19	24·9–26·2
	N	7	7	7
Non-flapping warm-up	Mean	13·26	6·04	28·8
	S.D.	4·51	4·60	2·0
	Min–max	3·61–20·97	0·76–17·11	25·7–33·3
	N	18	18	18
Tethered flapping	Mean	4·63	16·16	30·8
	S.D.	0·98	1·22	2·8
	Min–max	3·39–7·08	12·7–17·65	26·9–35·0
	N	14	14	11
Post-tethered flapping	Mean	7·04	12·30	31·1
	S.D.	2·27	3·33	1·8
	Min–max	3·85–12·65	6·68–17·12	27·7–35·2
	N	20	20	19

Samples include both males and females.

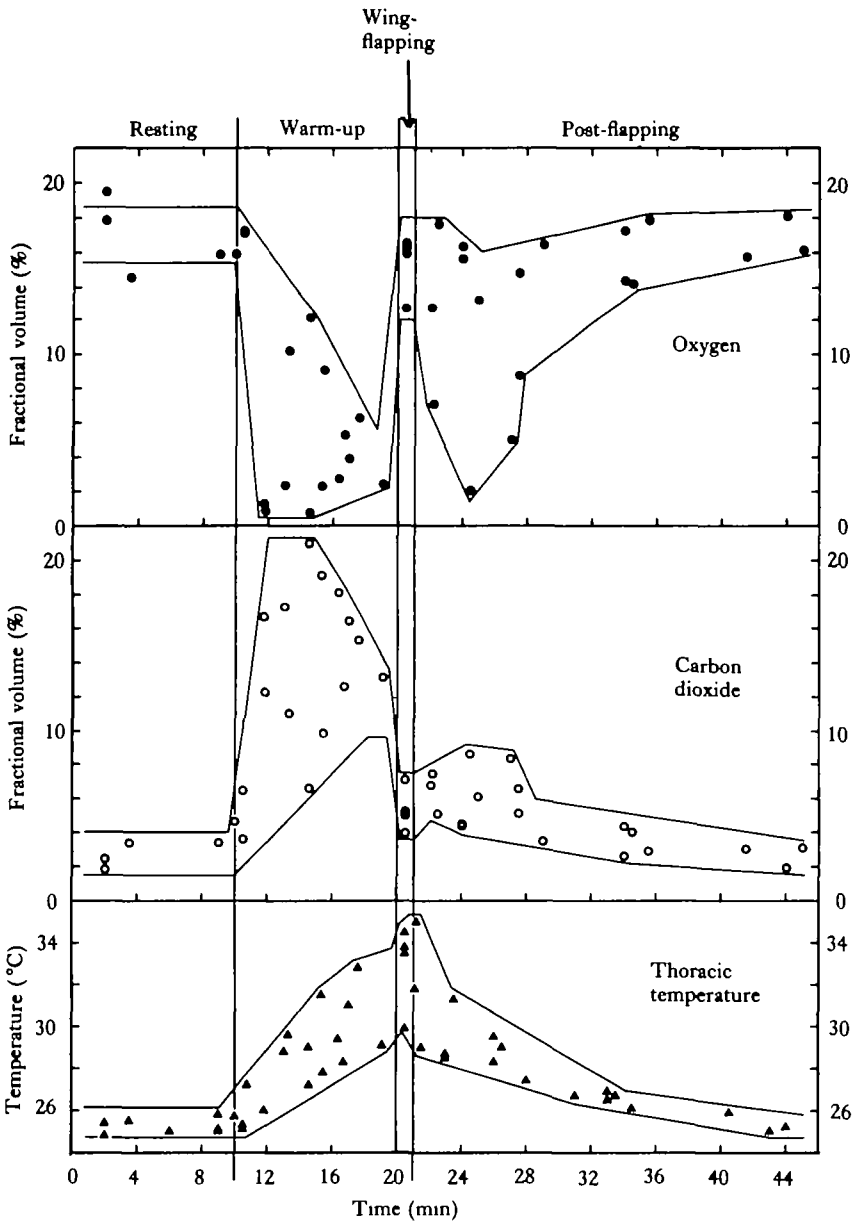

Fig. 6. Changes in tracheal gas concentrations and thoracic temperature during rest, non-flapping warm-up and tethered flapping in *Fidicina mannifera*. The duration of non-flapping warm-up has been normalized to 10 min to synchronize the data from the six individuals whose measurements are included. The envelopes enclose the approximate range of values in relation to time.

T_{th} occurred only towards the end of flapping as the animals approached exhaustion. Thus, the relationship between frequency and temperature may have been partially offset by fatigue. Mean wing-beat frequency between 25 and 34 °C was 36·6 Hz (S.D., ▮8; $N = 55$ on seven specimens).

DISCUSSION

Resting $\dot{V}_{O_2}$

The slope of the regression of log resting $\dot{V}_{O_2}$ on log mass in cicadas is similar to the slopes reported for other orders of insects. However, at a temperature of 22–24 °C the one gram intercept for cicadas (0·633 ml h^{-1}) is substantially higher than that for either beetles (0·23 ml h^{-1}) or heterothermic moths (0·402 ml h^{-1}) (Bartholomew & Casey, 1977, 1978). By analogy with vertebrates, the relatively elevated $\dot{V}_{O_2}$ of the cicadas may be related to the fact that their $\dot{V}_{O_2}$ was measured during an active phase of their daily cycle, while that of the moths and many of the beetles was measured during their inactive phase.

Wing-loading

As in beetles (Bartholomew & Heinrich, 1978) and moths (Bartholomew & Casey, 1978; Casey & Joos, 1983), wing-loading in cicadas increases with increasing body mass (Fig. 2). The wing-loading for *F. mannifera* is higher than for sphingids but lower than for beetles of similar size. Unlike beetles and sphingids of similar size, *F. mannifera* is not conspicuously endothermic, need not warm up prior to flight, and cannot remain airborne for long periods.

Warm-up and tethered flapping

Pre-flight warm-up has not previously been reported in cicadas. *F. mannifera* can warm itself by endothermy but need not do so in order to fly, as long as its body temperature exceeds 22 °C. Its ability to fly at T_{th} as low as 22 °C, together with its diurnal habits and lowland tropical distribution means that it can usually take off without pre-flight warm-up. Nevertheless, in the laboratory *F. mannifera* always warmed up prior to spontaneous take-off. The dependence of wing-beat frequency on body temperature in *F. mannifera* is slight, but it is within the range reported for insects of other orders (May, 1981). A warm-up from 22 to 30 °C would increase wing-beat frequency by about 15 %, which might be selectively advantageous if it resulted in increased flight speed or manoeuvrability. However, the functional significance of endogenous warm-up in *F. mannifera* remains problematic.

The peak $\dot{V}_{O_2}$ during warm-up in a 2·63 g *F. mannifera* (Table 3) is only 11·6 % that of a sphinx moth of similar mass (Bartholomew *et al.* 1981). This difference may be related to relatively limited autoventilatory gas exchange during warm-up in cicadas (see below). Warm-up in cicadas is not accompanied by substantial wing movements, whereas sphinx moths vibrate the wings and thorax vigorously and at high frequency during warm-up and presumably are strongly autoventilated.

Cicadas exhaust quickly during flight, probably due to depletion of muscle stores of substrate for oxidative metabolism in the flight muscles. Exhaustion is evidently not due to any insufficiency in the rate of oxygen delivery. During flapping, F_{O_2} in the thoracic air sacs is high and relatively uniform (Table 4, Fig. 6). Post-flapping oxygen debt (Figs 4, 5) is negligible in comparison with post-flight oxygen debt in sphingid and saturniid moths (Bartholomew *et al.* 1981).

The rapidity of exhaustion during flight indicates that fuel reserves in the flight

muscles are small and that the rate of delivery of substrate to the muscles is low, relative to the rate of utilization during flight. In contrast, cicadas do not become exhausted during warm-up, although the total volume of oxygen consumed during a bout of warm-up exceeds that during a bout of flapping (Table 3). Warm-up is metabolically less intense, but more prolonged, than flapping. After warm-up the animals were capable of flights of normal duration. Thus, substrate was not depleted during warm-up and must have been delivered at least as fast as it was being used.

We did not measure the cost of free flight in cicadas. In the sphinx moth, *Manduca*, $\dot{V}_{O_2}$ during fixed flapping is less than half that during free flight (Heinrich, 1971). However, in *F. mannifera*, it appears unlikely that such a large difference exists between $\dot{V}_{O_2}$ during fixed flapping and free flight. The observed $\dot{V}_{O_2}$ of flapping cicadas in this study is about 70 % of that predicted for a free-flying sphingid of similar size. Moreover, the cicadas exhausted equally rapidly during fixed flapping and free flight, suggesting that $\dot{V}_{O_2}$ under the two conditions may be similar. However, measurements of $\dot{V}_{O_2}$ during free-flapping flight are needed.

Tracheal gases and autoventilation

In many large, flying insects the high demand for gas exchange during flight is met primarily by 'autoventilation' of the thorax; that is, by ventilation directly due to the thoracic movements associated with wing-flapping (Weis-Fogh, 1967). The importance of autoventilation in the gas exchange of *F. mannifera* can be assessed by comparing the overall conductance for oxygen between the thoracic air sacs and the outside air during rest, warm-up and wing-flapping. The exchange of oxygen between the dorsal thoracic air sacs and the air outside the insect can be described as follows:

$$\dot{V}_{O_2} = G_{O_2} \times \Delta P_{O_2}, \tag{3}$$

where $\dot{V}_{O_2}$ is the rate of oxygen consumption (ml min^{-1}), and ΔP_{O_2} is the difference in partial pressure of oxygen between the air sacs and the outside air. G_{O_2}, the overall conductance for oxygen (ml min^{-1} $Torr^{-1}$) between the air sacs and the outside air, describes both diffusive and convective transport. For present purposes we assume that all oxygen consumption takes place in the thorax.

We have calculated G_{O_2} for *F. mannifera* using the resting $\dot{V}_{O_2}$, mean peak $\dot{V}_{O_2}$ during warm-up and during fixed flapping (Table 3), and the thoracic F_{O_2} (Table 4). G_{O_2} is about 0·007 ml min^{-1} $Torr^{-1}$ in resting individuals and increases to about 0·032 ml min^{-1} $Torr^{-1}$ during warm-up. During fixed flapping G_{O_2} increases by about 0·391 ml min^{-1} $Torr^{-1}$, or about 50 times the resting value.

The moderate increase of G_{O_2} during warm-up relative to rest is presumably due to opening of the spiracles and possibly to ventilation by abdominal pumping. High F_{CO_2} and low F_{O_2} in the tracheal system during warm-up presumably induce maximal opening of the spiracles so that resistance to diffusion is minimized (cf. Burkett & Schneiderman, 1974). The larger increase in G_{O_2} during wing-flapping is attributable to autoventilation. If all of the difference in G_{O_2} between warm-up and flapping is due to autoventilation, then autoventilation accounts for about 92 % of gas exchange during wing-flapping. Abdominal pumping often continues during and after flapping, but it is not critical for flight.

Ventilation and locomotor movements can be coupled in birds and mammals as well

as in insects (Bramble & Carrier, 1983; Butler & Woakes, 1980; Weis-Fogh, 1967). In vertebrates, the mechanism and functional significance of this coupling have not been clearly demonstrated. However, in locusts and dragonflies, direct measurements have shown that the movements of the thorax during flapping flight ventilate the thorax at a rate sufficient to sustain flight without the support of any other ventilatory mechanism (Weis-Fogh, 1967). This also appears to be the case in *F. mannifera*.

The concentrations of O_2 and CO_2 in the thoracic air sacs of *F. mannifera* at rest and during fixed flapping are similar to values recorded by Weis-Fogh (1967) under similar conditions in the locust *Schistocerca*. For example, during tethered flapping in *Schistocerca*, F_{O_2} was 13·4% and F_{CO_2} was 5·7%. We are not aware of any previously published data on tracheal gas tensions in an insect during an episode of endothermy. The low F_{O_2} and high F_{CO_2} in *F. mannifera* during warm-up indicate that, in the absence of autoventilation, gas exchange imposes a ceiling on metabolic rate. Therefore, gas exchange may limit the rate of non-flapping warm-up. The rapid restoration of F_{O_2} and F_{CO_2} to near resting levels as soon as wing-flapping commenced, indicates that in *F. mannifera* autoventilation closely matches oxygen supply with demand during flight.

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