PHILOSOPHICAL TRANSACTIONS OF THE ROYAL SOCIETY B BIOLOGICAL SCIENCES

Pressure Cycles and the Water Economy of Insects

Sarah A. Corbet

Phil. Trans. R. Soc. Lond. B 1988 **318**, 377-407
doi: 10.1098/rstb.1988.0016

Phil. Trans. R. Soc. Lond. B **318**, 377–407 (1988) [377]
Printed in Great Britain

PRESSURE CYCLES AND THE WATER ECONOMY OF INSECTS

By SARAH A. CORBET
Department of Applied Biology, University of Cambridge, Pembroke Street,
Cambridge CB2 3DX, U.K.

(*Communicated by S. H. P. Maddrell, F.R.S. – Received* 27 *August* 1986 – *Revised* 16 *April* 1987)

CONTENTS

Water exchange between insects and their environment via the vapour phase includes influx and efflux components. The pressure cycle theory postulates that insects (and some other arthropods) can regulate the relative rates of influx and efflux of water vapour by modulating hydrostatic pressures at a vapour–liquid interface by compressing or expanding a sealed, gas-filled cavity. Some such cavities, like the tracheal system, could be compressed by elevated pressure in all or part of the haemocoele. Others, perhaps including the muscular rectum of flea prepupae, could be compressed by intrinsic muscles. Maddrell (*Adv. Insect Physiol.* **8**, 199 (1971)) suggested a pressure cycle mechanism of this kind to account for rectal uptake of water vapour in *Thermobia* but did not find it compatible with quantitative information then available. Newer evidence conforms better with the proposed mechanism.

Cyclical pressure changes are of widespread occurrence in insects and have sometimes been shown to depend on water status. Evidence is reviewed for the role of the tracheal system as an avenue for net exchange of water between the insect and its environment.

Because water and respiratory gases share common pathways, most published findings fail to distinguish between the conventional view that the tracheal system has evolved as a site for distribution and exchange of respiratory gases and that any water exchange occurring in it is generally incidental and nonadaptive, and the theory proposed here. The pressure cycle theory offers a supplementary explanation not incompatible with evidence so far available. The relative importance of water economy and respiratory exchange in the functioning of compressible cavities such as the tracheal system remains to be explored.

Some further implications of the pressure cycle theory are discussed. Consideration is given to the possible involvement of vapour-phase transport in the internal redistribution of water within the body. It is suggested that some insect wings may constitute internal vapour–liquid exchange sites, where water can move from the body fluids to the intratracheal gas. Ambient and body temperature must influence rates of vapour–liquid mass transfer. If elevated body temperature promotes evaporative discharge of the metabolic water burden that has been shown to accumulate during flight in some large insects, their minimum threshold thoracic temperature for sustained flight may relate to the maintenance of water balance. The role of water economy in the early evolution of insect wings is considered. Pressure cycles might help to maintain water balance in surface-breathing insects living in fresh and saline waters, but the turbulence of the surface of the open sea might prevent truly marine forms from using this mechanism.

1. INTRODUCTION

The exchange of water between insect body fluids and the environment involves not only the conservation or uptake of water, but also, occasionally, disposal of excess (see, for example, Bertsch 1984). The vapour phase may sometimes constitute a major pathway for rapid exchange of water between the body fluids of the insect and the environment. This paper explores a possible mechanism that would permit insects to exert short-term control over rates of vapour–liquid mass transfer of water by muscular manipulation of the hydrostatic pressure at a vapour–liquid interface. The proposed mechanism is described primarily in relation to the tracheal system of terrestrial insects, although it may also operate in other cavities.

Little attention has been paid up to now to the possible role of hydrostatic pressure changes in water transfer between insects and their environment, perhaps partly because pressure changes involving the whole haemocoele do not appear in *in vitro* studies of isolated organs. It has not been necessary to postulate water exchange by controlled pressure cycles to explain observations on water balance, because the conventional view, that the general body surface is the site of any water exchange for which no alternative location can be established, is flexible enough to embrace most observed phenomena. Only a few aspects remain unexplained. Nor has it been necessary to postulate involvement in vapour–liquid mass transfer to account for the adaptive features of the tracheal system, because oxygen and water vapour behave similarly and most features of the tracheal system are not incompatible with the conventional view that its primary function is respiratory gas transport and exchange. Again, only a few aspects remain unexplained. The hypothesis proposed here is intended to complement, rather than replace, current theory. As well as suggesting how the observed pressure cycles may operate and supplementing the interpretation of some features compatible with conventional theory, the new hypothesis offers explanations for some hitherto enigmatic phenomena and raises questions for further research.

2. The postulated mechanism

Water is the only component of air that is present as both liquid and vapour at biological temperatures and pressures. Thus water can move across a gas–liquid interface by evaporation or condensation, whereas the other components of air do so by adsorption into, or desorption from, solution in the aqueous liquid. The rate of mass transfer at a gas–liquid interface is accordingly much greater for water than for the other components, because the rate of condensation or evaporation of water is usually limited by resistance in the gas phase whereas the rate of adsorption or desorption of gases is usually limited by resistance in the liquid phase, which is much higher than that in the gas phase (see Davies & Rideal 1963). In certain conditions of temperature and pressure, water can undergo rapid condensation (dew formation) or rapid vaporization ('boiling'). The extent to which these phenomena may occur in insects is considered below.

Water evaporates into subsaturated air at a rate proportional to the saturation deficit, the difference between p_0, the saturated vapour pressure of water at that temperature, and p, the actual vapour pressure of water in the air. An isothermal† increase in total pressure at a vapour–liquid interface will give a proportionate rise in p and so decrease the rate of evaporation (figure 1*a*). Further compression will raise p until $p = p_0$, when the supersaturation ratio p/p_0 will be 1. Water condenses rapidly when the supersaturation ratio exceeds a critical value. This critical ratio may be close to 1 in the presence of hydrophilic nucleation sites but higher in their absence (Davies & Rideal 1963; Hirth & Pound 1963, p. 31). Thus any small increase in pressure retards evaporation, and an increase great enough to exceed the critical supersaturation ratio at that temperature can cause sudden condensation.

An isothermal decrease in the total pressure at a vapour–liquid interface will decrease p. Even a small expansion enhances evaporation (figure 1). To decrease the pressure until the total pressure is equal to or less than p_0, and so to achieve rapid vaporization (or boiling) would require very large volume increases coupled with elevation of p_0 by high body temperature. For example, figure 1 shows that at 20 °C an insect that closed its spiracles on intratracheal air at 50% relative humidity at 1 atm‡ pressure would have to expand its tracheal system by a factor of $1/p_0 = 43.4$ times (p_0 at 20 °C $= 0.023$ atm). (At high body temperature, the expansion required would be less, but still great (§4*b*), and it is not clear whether or not insects could achieve it.) The distinction made by chemical engineers between filmwise and bubblewise evaporation (nucleate boiling) may be relevant here (Bergles *et al.* 1981).

There are significant asymmetries between rates of condensation and of evaporation in

---

† The discussion assumes that the volume changes in the sealed cavity are effectively isothermal, that is, they are slow enough to allow heat transfer to or from the surroundings to prevent significant change of temperature in the cavity. If that were not so, during compression the temperature of the air in the cavity would rise, raising p_0, and in the extreme case of adiabatic volume change, the temperature-related rise in p_0 might be faster than the pressure-related rise in p, so that compression could increase the net evaporation rate instead of decreasing it. Similarly, during adiabatic expansion the decrease of p_0 due to the fall in temperature might be faster than the fall in p due to decreased pressure, so that expansion might promote condensation instead of evaporation. In insects, pressure changes are unlikely to be adiabatic. They occur relatively slowly and in very small cavities surrounded by fluids of high thermal conductance. Departures from the isothermal condition are likely to be small. They may reduce, but are unlikely to reverse, the isothermal effects of pressure changes on evaporation rates described above and illustrated in figure 1.

‡ In this paper I express pressures in atmospheres rather than SI units (1 atm = 101330 N m^{-2}) to simplify calculations based on the relation between pressure and volume changes. Final pressure in atmospheres = 1 × (initial volume)/(final volume) if the cavity is sealed at an initial pressure of 1 atm.

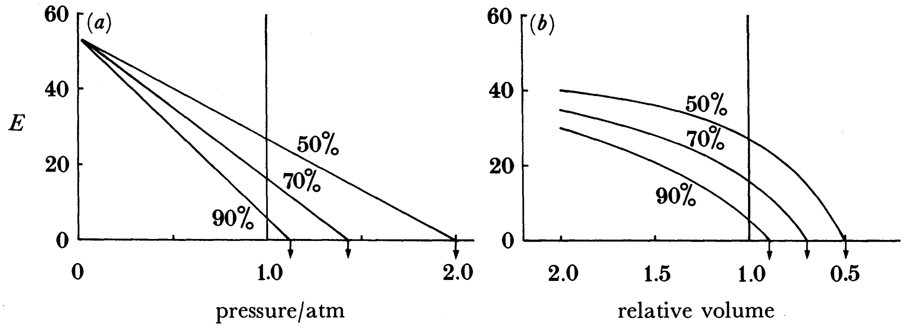

FIGURE 1. Calculated relative rates of net evaporation, E, at an air–water interface in a sealed, compressible cavity in relation to (*a*) total pressure (atm), and (*b*) cavity volume (arbitrary units, set to 1 at 1 atm pressure (vertical line)). In figure 1*a*, oblique lines illustrate changes in relative rate of net evaporation, E, calculated from $E = k(p_0 - p)$ for an arbitrary value of the constant k and values of p_0, the saturated vapour pressure of water, and p, the actual vapour pressure, for an air mass containing a mass of water equivalent to a relative humidity of 50 %, 70 % and 90 % at 20 °C and 1 atm pressure. Isothermal conditions are assumed. Arrows indicate rapid condensation when the supersaturation ratio, p/p_0, exceeds 1. Rapid vaporization would occur where the lines meet (total pressure $= p_0 = 0.023$ atm). Graph (*b*) shows changes in relative rate of net evaporation in relation to the volume of the same cavity (note reversed scale on abscissa) for the same relative humidities at 20 °C and 1 atm pressure.

systems with fluctuating pressures. The relatively small changes in volume required to achieve rapid condensation (figure 1) are probably within the scope of many insects, whereas to achieve rapid vaporization requires very great expansion. Condensation from supersaturated air is much faster than evaporation into subsaturated air. Pressure oscillations with peak pressures giving supersaturation ratios exceeding the critical value would therefore result in net condensation of water. Temperature effects are considered in §4*b*.

I suggest that insects can regulate their water economy by varying the rates of condensation and evaporation at different locations in the body by muscular manipulation of the hydrostatic pressure in a gas-filled cavity. The location within the body would be determined by airflow patterns and by the distribution of hydrophilic nucleation sites. The sites in the body where vapour–liquid mass transfer could be modulated in this way are likely to be hydrophilic areas of the surface freely permeable to water and in contact with the body fluids, and lining a compressible, gas-filled cavity that can be sealed.

Perhaps the most important compressible gas-filled cavity that can be sealed is the tracheal system. The tracheae are lined with cuticle that is unwettable, having a high contact angle for water, and they are considered to be relatively impermeable to water (Beament 1964). But the finest terminations (down to about 50 nm diameter) of the tracheoles investing the mitochrondria in the flight muscles have permeable walls, as indicated by localized leakage of an injected myrcene–kerosene mixture from the tracheoles into the mitochondria (Wigglesworth & Lee 1982). Within the tracheal system, it is these finest tracheolar terminations in the flight muscles (perhaps unlike those in less active tissues such as the epidermis of *Rhodnius* (Wigglesworth & Lee 1982)) that have walls permeable enough to permit rapid water movement. Thus one critical interface for vapour–liquid mass transfer might be the liquid surface in the finest tracheolar terminations, a hydrophilic nucleation site in the generally unwettable tracheal system. Other possible nucleation sites include regions where a hydrofuge water-permeable grid of cuticle supports a meniscus of the gas–liquid interface. Porous, rigid, unwettable grids of cuticle line the foregut and hindgut, and support interfaces with the medium in aquatic insects (§4*c*).

The form of the tracheae, flexible tubes with spiral or annular thickenings, readily permits change in volume (Wigglesworth 1972). Tracheal closing mechanisms are present at, or just inside, the spiracles in nearly all insects except some soft-bodied larvae (see §5) (Wigglesworth 1972; Hassan 1944; Tonapi 1958). (According to Hassan (1944), the Apterygota that he examined lacked closing mechanisms, but Noble-Nesbitt (1969) later found them in *Thermobia*.) Because the tracheal walls are deformable, the hydrostatic pressure in the tracheal lumen must approximately equal that in the surrounding haemocoele when the spiracles are closed. Gas is more compressible than liquid, and elevated haemolymph pressures will compress the gas in the tracheal system. Reduced haemolymph pressures will allow it to expand. Muscles capable of compressing or expanding the abdomen are widespread among insects (Wigglesworth 1972) and have been described in detail in, for instance, the honeybee *Apis mellifera* (Snodgrass 1956) and *Schistocerca* (Miller 1974). In some species re-expansion depends on elasticity of the abdominal cuticle, sometimes enhanced by resilin (Miller 1974). The tracheae themselves show elasticity (Miller 1974). In some insects, haemolymph pressures are modulated independently in different body regions by changes in the nature and direction of the heartbeat (Wasserthal 1981, 1982*b*).

By increasing the pressure in the abdomen (by abdominal contraction or by haemolymph transfer) with closed spiracles and so compressing the tracheal gas, an insect might slow down evaporation. If it exceeded the critical supersaturation ratio, it could promote condensation of water vapour, probably at the surface in the tracheoles, whence the water could enter the body fluids, particularly through very permeable regions of the tracheolar intima (Wigglesworth & Lee 1982). One or a series of brief tracheal compressions, raising the pressure beyond the supersaturation point, before exhalation could condense some of the water from the gas to be exhaled and so retard tracheal water loss. Multiple compressions in such a condensation cycle could promote condensation by repeatedly bringing fresh, humid air in contact with the nucleation sites. Alternatively, the high hydrostatic pressure that promotes condensation could be generated in a gas bubble within a muscular sac such as the pharynx or the rectum by contraction of its walls when it is sealed by closed valves. Water could be taken up from a subsaturated atmosphere by repeatedly inhaling and compressing. I argue in §3*a* that condensation cycles effective enough to result in net uptake of water are more likely to occur in small muscular sacs than in the tracheal system.

By lowering the intratracheal pressure by expanding the gas space with closed spiracles, an insect could promote net evaporation of water into the intratracheal gas, which it could then exhale. The moist air occupying the tracheal system at the end of exhalation could then be replaced with drier ambient air before the next expansion. By repeating this evaporation cycle an insect could promote water loss.

The two types of pressure cycle would both involve alternate expansion and contraction of the gas-filled cavity (and both would presumably involve inflow of air at some phase of the cycle), but condensation cycles and evaporation cycles would differ in the phase of the cycle in which the valves (spiracles) were closed. In condensation cycles the spiracles would be closed during contraction, which might take place in several steps, producing pulses of intratracheal pressure high enough to exceed the critical supersaturation ratio. The spiracles would be open, at least for much of the time, during expansion, so that subatmospheric excursions of intratracheal pressure would be brief or absent. In evaporation cycles, on the other hand, the spiracles would be open during contraction; the intratracheal pressure would never exceed the critical supersaturation ratio and would exceed 1 atm only rarely or briefly. The spiracles would be closed, at least for much of the time, during expansion, so that subatmospheric intratracheal pressures would be sustained. Because rapid condensation above the dewpoint can be achieved, whereas rapid vaporization below the boiling point may be unusual or impossible, condensation cycles would sometimes include rapid pressure oscillations, whereas evaporation cycles would be relatively slow.

Depending on its water status and the ambient conditions, a given species might show either type of cycle, or intermediates differing in the duration of the low-pressure period and in the intensity and frequency of high-pressure periods. Both types might occur at the same time in different parts of the same insect. An insect with a local water excess in, say, the thorax during flight might coordinate airflow with differential pressure changes in different body regions perhaps achieved by pumping haemolymph from one tagma to another, and so transfer water via the tracheal system from thorax to abdomen (§4*a*). Pressure cycles may not be easy to characterize, and may not be obvious externally at all, especially where they depend on the transfer of haemolymph from one region to another, as demonstrated by Wasserthal (1981, 1982*b*), without change in the total volume of the thorax or abdomen.

Mechanisms involving pressure cycles in vapour–liquid mass transfer of water have been proposed before. Maddrell (1971) suggested that rectal uptake of water vapour in *Thermobia* might depend on repeated cycles of compression, but calculations based on data from Noble-Nesbitt (1969) led him to conclude that this mechanism would require improbably high pulsation frequencies to account for observed uptake rates. Recalculation based on Noble-Nesbitt's (1978) more recent data on *Thermobia* (§3*a*) gives results more consonant with Maddrell's suggestion, and I now propose that a mechanism of this kind operates, not only in the rectal system of *Thermobia*, which is reconsidered below, but also, more generally, in the tracheal system and other cavities of insects, in which myogenic pressure cycles promote controlled uptake or loss of water vapour.

Hydrostatic pressure gradients could also be responsible for the movement of water across a membrane with the liquid phase on both sides. Lees (1946*b*) proposed, and Kaufman *et al.* (1982) confirmed, that expansion of the coxal gland of the tick *Ornithodoros moubata* by extrinsic muscles against haemolymph pressure created a hydrostatic gradient that would suck fluid into the sac against an osmotic gradient, producing hypotonic urine, and a similar mechanism was proposed for ultrafiltration of haemolymph by the pulsating frontal bodies of the desert cockroach *Arenivaga* (O'Donnell 1982). The role of hydrostatic pressure differentials in the excretory systems of animals other than insects is widely accepted. Because sacs in insects are more often supplied with intrinsic muscles that compress them than with extrinsic muscles that expand them, one might expect production of hypertonic solutions by compression to be widespread. Systems in which this might be expected include the mouths of ixodid ticks (Rudolph & Knülle 1978) and Psocoptera and Mallophaga (Rudolph & Knülle 1982), in all of which regular pulsations are associated with the production of a hypertonic solution that participates in hygroscopic uptake of water vapour from the air.

This paper concentrates on vapour–liquid mass transfer and considers published studies of ventilation movements and other pulsations in relation to water economy to see whether the findings are compatible with the hypothesis that myogenic pressure cycles participate in the controlled uptake or loss of water via the tracheal system or another cavity. Capillary effects may prove to be relevant when more is known about the system, but the mechanism postulated here does not depend on them.

3. Is the theory compatible with published findings?

(a) *Can myogenic pressure cycles account quantitatively for observed rates of water transfer?*

If pressure cycles make a major contribution to uptake or loss of water, existing measurements of cavity volume, volume change and cycle frequency in relation to net transfer rate at a given humidity should be quantitatively compatible with the mechanism. For no species are all the relevant data established with certainty, but the calculations can be done for some species if estimates are made for missing values. Some quantitative corollaries of the proposed mechanism are examined.

If the firebrat *Thermobia domestica* is desiccated and then returned to moist air, it takes up water from subsaturated air via the rectum (Noble-Nesbitt 1970, 1975, 1978). Its rate of water vapour uptake at 21 °C increases steeply with relative humidity from a threshold at about 45 % relative humidity (Beament *et al.* 1964). Uptake rate increases with relative humidity over a similar range at other temperatures (Noble-Nesbitt 1969). The largest mean uptake rate found by Noble-Nesbitt (1969) was 6.7 mg per 24 h (equal to 4.65 μg min^{-1}), at 37 °C and 83 % relative humidity (r) (i.e. $r = 0.83$). The absolute humidity of saturated air, a_0, at that temperature is 43.9 g m^{-3}, and the absolute humidity at the ambient relative humidity, given by ra_0, is 36.4 g m^{-3}. Maddrell (1971) proposed that water vapour might be taken up by a mechanism involving repeated compressions of the rectum. He assumed that the (expanded) volume of air, v, in the rectal system was halved at each cycle (i.e. the compression ratio, c, compressed volume/expanded volume = 0.5). The mass of water contained in the inhaled rectal gas is given by vra_0, and the mass of water required to saturate the air after compression by cva_0. The mass of water, W_G, available to condense at each cycle is therefore given by

$$W_G = vra_0 - cva_0 = a_0 v(r-c). \tag{1}$$

When *Thermobia* is taking up water, it shows regular pulsations associated with closure of the anal valves, at an estimated frequency of up to 5 cycles s^{-1} (Noble-Nesbitt 1978). Maddrell (1971) made a conservative estimate of 100 nl for the expanded rectal volume. He assumed a temperature of 20 °C ($a_0 = 17.3$ g m^{-3}) and relative humidity of 100 %, and a compression ratio of 0.5, and calculated that vapour uptake at the observed rate by compression cycles would require a cycle frequency of about 80 s^{-1}, which he considered to be improbably high.

Maddrell's estimate of rectal volume did not include the anal sacs described by Noirot & Noirot-Timothée (1971 *b*). From serial sections, dissections and measurements of the abdomen (Noble-Nesbitt 1978 and personal communication), Noble-Nesbitt (1978) estimated the maximum volume of the rectal system in an insect of mass 30 mg as about 250 nl. He calculated that at a temperature of 20 °C ($a_0 = 17.3$ g m^{-3}) and a relative humidity of 100 % ($ra_0 = 17.3$ g m^{-3}), water vapour uptake at the observed rate by a compression mechanism would require a cycle frequency of about 30 s^{-1}. Calculation using the observed temperature of 37 °C ($a_0 = 43.9$ g m^{-3}) and humidity of 83 %, a compression ratio of 0.45 (see below), and the estimated rectal system volume of 250 nl (Noble-Nesbitt 1978) indicates that the observed maximum uptake rate would require a cycle frequency of 18.6 cycles s^{-1} for the pressure cycle mechanism that Maddrell (1971) proposed, if condensation is confined to the rectal system.

The observed rectal pulsations, at a maximum frequency of 5 s^{-1}, are much slower than this.

Thus if all estimates used in the equation are correct, water uptake is not accounted for solely by a pressure cycle mechanism involving compressions of the whole rectal system at the frequency of the observed pulsations.

Further evidence against condensation cycles involving the whole rectal system comes from monitoring of whole-body volume during uptake. Such cycles would be expected to involve whole-body volume changes equivalent to about half the volume of the rectal system, but Noble-Nesbitt (1978) was unable to detect cyclical volume changes of this magnitude when he enclosed *Thermobia* in a rigid capsule closed by a capillary sealed by an indicator droplet of kerosene, even though the system did respond to small volume changes, and the pulsations, sometimes as slow as 1 s^{-1}, would have been slow enough to register for at least part of the time (J. Noble-Nesbitt, personal communication). Regular small volume changes that did occur were interpreted as heartbeat (J. Noble-Nesbitt, personal communication).

If water uptake is not accompanied by large changes in total volume occupied by the animal, any pressure cycle mechanism might involve compensating pulsations of two internal air-filled compartments, rather than gross compression of a single compartment. The rectum might constitute one of these air-filled compartments; it has a muscular wall and a sphincter at its junctions with the ileum (Noirot & Noirot-Timothée 1971 *a*) and with the rectal sacs (Noirot & Noirot-Timothée, 1971 *b*), and could therefore compress gas. The thin-walled rectal sacs would represent the compensating cavity. If this were the case, then rectal compressions would not necessarily be visible from outside the body, and their frequency might be different from, and perhaps much higher than, that of the larger-scale pulsations and anal valve openings whose frequency does not exceed 5 s^{-1}, and which may be involved in tidal replenishment of air (Noble-Nesbitt 1973). Because the rectum is muscular, it is likely to be this cavity whose contractions power the system, and because its volume is probably smaller than that of the anal sacs, the pressure in it during contraction will exceed that in the anal sacs caused by its re-expansion. If the rectum, whose volume was estimated by Maddrell (1971) as 100 nl, were the only region in which the critical supersaturation ratio could be exceeded, a cycle frequency of 46 s^{-1} would be required to achieve uptake at the observed rate at 37 °C and 83% relative humidity by a pressure cycle mechanism.

Thus in the *Thermobia* rectum, water vapour uptake from subsaturated air may involve pressure pulses achieved by high-frequency pulsations of a small internal air-filled cavity, the rectum. Compensating volume changes in another air-filled compartment, represented here perhaps by the anal sacs, would reduce the energetic cost of contraction by obviating the need to distort the whole abdomen to compensate for rectal volume change in every cycle. In other insects using rectal pulsations in water vapour uptake (perhaps flea prepupae and *Tenebrio* larvae), the compliant compensating cavity may be the tracheal system. This hypothesis does not offer a functional interpretation for the elaborate fine structure of the rectal sacs of *Thermobia* (Noirot & Noirot-Timothée 1971 *b*).

With (1) in the form

$$W_G = a_0 v(r - c),$$

it can be seen that a threshold of zero uptake will be reached when r, the relative humidity, equals c, the ratio of compressed volume to expanded volume. This conforms with the striking, but hitherto unexplained, observation (Beament 1964; Edney 1977; Wharton 1985) that the threshold for water vapour uptake for a given arthropod species or stage generally lies at a more or less constant relative humidity independently of temperature; hence the concept of Critical Equilibrium Humidity (CEH) or Critical Equilibrium Activity (CEA) (Wharton & Devine 1968; Edney 1977). Maddrell (1971) used a value of $c = 0.5$, close to the observed CEA of 0.45 for *Thermobia*.

Equation (1) shows that at a given temperature, uptake rate will increase linearly with relative humidity. Knülle (1967) found this to be so for larvae of the flea *Xenopsylla cheopis*, and so did Machin (1978) for *Tenebrio* larvae. In both groups a pressure-cycle mechanism may operate: the rectum is air-filled, and pulsations are known to occur in fleas (Rudolph & Knülle 1982) and ventilation is postulated in *Tenebrio* larvae, which take up water faster than it can be supplied to the rectum by diffusion alone (Machin *et al.* 1982).

In evaporation cycles, the maximum potential mass of water available to be lost per cycle, W_L, would be the difference between that contained in the expanded cavity at saturation, va_0, and that contained in the compressed cavity when mixing has brought the contained air to ambient humidity, $cvra_0$, and is given by

$$W_L = a_0 v(1-rc). \tag{2}$$

Equation (2) permits W_L to be estimated for the cicada *Fidicina mannifera* from data of Bartholomew & Barnhart (1984). During flight the mean peak thoracic temperature was 32.7 °C (equivalent $a_0 = 35.6 \text{ g m}^{-3}$). The mean tracheal volume of females, v, was $2.37 \times 10^{-6} \text{ m}^3$. Of this, $1.12 \times 10^{-6} \text{ m}^3$ is accounted for by the abdominal air sacs. The compression ratio, c, is therefore probably about 0.5, or less if other regions of the tracheal system are compressible. At an ambient humidity of, say, $r = 0.8$, $W_L = 35.6 \times 2.37 \times 10^{-6} \times [1-(0.8 \times 0.5)] = 50.6 \times 10^{-6}$ g water per cycle, or 1.82 mg min^{-1} at the observed maximum frequency of 36 cycles min^{-1}.

During flight, the mean peak rate of oxygen uptake was $1.837 \text{ ml min}^{-1}$, equivalent to production of metabolic water of 1.23 mg min^{-1} assuming carbohydrate as the substrate (Edney 1977, table 31). Evidently, this cicada could discharge metabolic water by evaporation cycles as fast as it is produced during flight if it ventilated at the maximal rate and if evaporation were complete in each cycle. But ventilation is intermittent during flight, and evaporation may not be complete at such high cycle frequencies. It may be because of an accumulating metabolic water burden that this cicada can fly for only 100 s at a time, and continues to ventilate after settling.

Equations (1) and (2) imply that increasing v, the expanded volume of the cavity, would increase rates of uptake or loss in given ambient conditions. For condensation cycles, which depend on pressures above atmospheric, the maximum tension that muscles can exert is likely to set the lower threshold for the compression ratio, and the muscle tension, T, required to achieve a given pressure, P, in a sphere is inversely related to the radius, r, ($P = 2T/r$) (Alexander 1983). The compression ratio, c, reflected in the CEA, is rarely less than 0.5 (Edney 1977). Thus small values of c can only be achieved in small cavities, and net water vapour uptake by condensation cycles with a small CEA is likely to involve small muscular internal sacs, rather than compression of the whole abdomen. The muscular rectum may represent that cavity in flea prepupae and *Tenebrio* larvae (see Rudolph & Knülle 1982), and in *Thermobia*.

In evaporation cycles, a pressure change of a given magnitude is associated with a larger volume change (figure 1), and c is more likely to be limited by v. Very large air sacs are characteristic of large species with high power requirements and a potential need to discharge a metabolic water burden by evaporation cycles. It will be interesting to see whether the large v in these forms permits very small values of c. Large abdominal air sacs are a feature of aculeate Hymenoptera (which pump by visible contractions of the abdomen) and calpyterate flies (in at least some of which tracheal ventilation is achieved by pumping haemolymph to and fro between thorax and abdomen (Wasserthal 1982*b*). It is probably because of their large air sacs that calypterate flies typically float in water traps, when other flies sink (R. H. L. Disney, personal communication 1986). Desert tenebrionid beetles have a subelytral cavity closed by a caudal valve. This cavity has been shown to play a part in water exchange (Cooper 1983; Nicolson *et al.* 1984), and up-and-down movements of the elytra might enable it to function as a bellows, giving a large v and a small compression ratio. Fusion of the elytra, hitherto a puzzling feature of these beetles (Slobodchikoff & Wismann 1981), would enable the cavity to support the necessary pressure differentials. Extensions of the body, such as the head and mandibles of stag beetles *Lucanus cervus* (Wigglesworth 1982), may also contribute to increased v if they contain air sacs that can be compressed by distortion or by haemolymph pressure. The possibility that such extensions included the thoracic lobes from which wings later evolved is considered in §5.

The expanded cavity volume may vary according to the insect's physiological state. The expanded volume of the tracheal system can be decreased if the air sacs are displaced by developing eggs, as in *Lucilia* (Evans 1935), or by a large meal of a fluid such as blood or nectar. A 200 mg bumblebee can drink up to 400 mg of nectar (Bertsch 1984) and *Rhodnius* may take about ten times its mass of blood (Buxton 1930). In such cases, gravid females or newly fed individuals may be expected to show lower rates of uptake or loss per cycle than conspecifics. The water elimination that follows a large meal takes place largely in the liquid phase in bees (Bertsch 1984) and in *Rhodnius* (Wigglesworth 1972), and in ticks, which lose the ability to take up water vapour when engorged (Lees 1946*b*). Surprisingly, the rate at which desiccated *Thermobia* take up water vapour from humid air is constant 'almost until full recovery' (Noble-Nesbitt 1969). The relation between degree of hydration and uptake per cycle remains unexplored in *Thermobia*. Conversely, decreased haemolymph volumes resulting from desiccation would increase the expanded cavity volume and so might increase rates of uptake or loss per cycle. Thus Okasha (1971) showed that in *Thermobia* the final mass of water (and therefore body volume) attained by hydrated insects hardly varied with the duration of starvation, even though the dry mass/wet mass ratio was much smaller in insects starved for a long time because of solute loss. This result would be predicted on the basis of (1) if rate of uptake depends on expanded volume and this in turn depends on the proportion of the body occupied by fluid. Similarly, in some forms the mass of water in the body at equilibrium, m_∞, rises with ambient relative humidity (Wharton 1985). Equation (1) predicts that the value of v at which W_G balances transpiratory loss rate will fall as r rises. Because m is inversely related to v, m_∞ will rise with r. This would be so for forms whose pressure cycles involve the whole haemocoele, and in which, therefore, v depends on the water content of the haemolymph, but not necessarily for forms whose pressure cycles involve pulsations of a muscular internal sac, in which v need not depend on water content. It is so for flea larvae, but in the prepupal stage m_∞ becomes independent of r (Wharton 1985). Perhaps this changeover coincides with the rectal emptying that permits the rectum to become a major site of water uptake (Rudolph & Knülle 1982).

In the moulting cycle, as the insect grows in its inextensible cuticle, the proportion of the body volume occupied by tissues and fluid will increase from a small value just after one moult to a large value just before the next, giving a corresponding decrease in v, and perhaps an increase in c. Equations (1) and (2) predict that newly moulted insects would show unusually high rates of uptake or loss (as Williams (1971) found for water vapour uptake by the mallophagan *Goniodes colchici*), whereas insects approaching their next moult would show low transfer rates (as Okasha 1971) found for water vapour uptake in *Thermobia*).

(*b*) *Do cyclical pressure changes occur?*

If effective water uptake from low humidities by condensation cycles involves pulsation of small internal muscular cavities (§3*a*), perhaps with compensatory volume change in another compartment, little will be visible from outside the insect. Regular pulsations have been described in the tracheal system of adult fleas (Wigglesworth 1935; Herford 1938) and the rectum of flea larvae (Rudolph & Knülle 1982).

Even where changes of volume are visible externally, changes of internal pressure cannot be inferred from volume changes without knowledge of the pattern of closure of valves. Indirect evidence for intratracheal pressure changes comes from visual observation of the hedgehog flea, *Archaeopsylla erinaceae erinaceae*, described by Herford (1938), in which it was possible to see movements of the tracheae and the tracheolar meniscus. The tracheae collapse slowly, shortening and, in wider regions that are oval in cross section, flattening. The main spiracles close at the beginning of the collapse period and all are closed by the end of it. Movements of the fluid in the tracheoles can be seen if the flea is in pure oxygen; during collapse, the fluid extends along the tracheoles. This slow collapse is followed by rapid inflation when the main spiracles open, the tracheae lengthen and resume their round or oval cross section, and the tracheolar fluid retreats towards the fine terminations of the tracheoles. This cycle is repeated at intervals of 5–80 s. Herford (1938) did not directly demonstrate associated changes in intratracheal pressure, or identify the tracheal pulsations with body contractions which, he said, 'may act synchronously with the tracheal rhythm but independently from it'. He interpreted tracheal collapse as resulting from respiratory oxygen depletion lowering intratracheal pressure, but the volume changes he illustrates seem greater than can be accounted for in this way. (Even if the flea used up all the oxygen in its tracheal system in the 5–80 s period of spiracular closure, the volume should decrease by only about 20%.) More probably, volume decrease and tracheolar fluid migration during spiracular closure result from compression of the tracheal gas by elevated intra-abdominal pressure. Herford's (1938) description may represent condensation cycles.

Evaporation cycles are more likely to involve visible volume changes of the whole body. Visible pulsations involving the tracheal system and described as ventilation movements (Miller 1981) are widespread among insects. They are seen as distortions of the abdomen in, for instance, *Periplaneta* and pupae of *Hyalophora* (Kestler 1985), hornets *Vespa crabro*, *Schistocerca* (Weis-Fogh 1967), *Locusta* (Loveridge 1968), dragonflies (Miller 1964), and the honeybee *Apis mellifera* (Bailey 1954). Some of the insects that exhibit these conspicuous abdominal pulsations, particularly after flight, are well-defended forms such as hornets (Weis-Fogh 1967), and honeybees (Snodgrass 1956) and their mimics (*Eristalis tenax*; S.A.C., personal observation). For more vulnerable, cryptic insects, pulsations visible to predators might be disadvantageous. In large asilid flies the tergites remain still and pulsations can be seen only from below, and in *Calliphora* the tracheal volume changes that result from haemolymph transfer do not produce effects visible externally (Wasserthal 1982*b*). In the giant silkmoth, *Attacus atlas*, recording reveals ventilation cycles with a period of several minutes (Wasserthal 1981). Cycles may go unnoticed if they are as slow as that, or if changes in tracheal volume result from the pumping of haemolymph to and fro between thorax and abdomen without evident changes in abdominal volume, as in *Calliphora* (Wasserthal 1982*b*).

Refined techniques have revealed hitherto unresolved details of the temporal patterns of intratracheal pressure cycles in *Hyalophora* pupae and in *Periplaneta* (Kestler 1985). Kestler (1985) identified two distinct patterns of ventilation, which he termed CFV (spiracles 'constrict', spiracles 'flutter', 'ventilate') and CFO ('constrict', 'flutter', 'open'). The CFV type occurred in dehydrated cockroaches and conforms with the pattern predicted above for condensation cycles in that it contains multiple hyperbaric pulses. Kestler's figures 6.13 and 6.15 illustrate changes in intratracheal pressure during CFV ventilation. There was a steady fall in pressure with the spiracles shut (the constriction phase), followed by a rapid rise to just below atmospheric pressure when the spiracles fluttered and air was, presumably, sucked in. The flutter phase was followed by the ventilation phase, a series of rapid and transient pressure fluctuations, perhaps representing a sequence of compressions with closed spiracles.

Periods of subatmospheric intratracheal pressure would enhance transfer from the liquid to the vapour phase of both carbon dioxide and water. Brief hyperbaric pulses exceeding the critical supersaturation ratio for water and producing condensation would enhance transfer from the vapour phase to the liquid phase for water more than for carbon dioxide. Thus a low-pressure period followed by brief high-pressure pulses might be expected to reclaim water preferentially.

Kestler (1985) measured intratracheal pressures of up to a few hundred pascals (that is, up to only about 0.005 atm) above or below atmospheric. This unexpectedly small value is considered further below.

The CFO ventilation type that Kestler (1985, figures 6.12 and 6.14) found in hydrated cockroaches and in *Hyalophora* pupae differed from the CFV type described above in that it lacked the sequence of compressions following the flutter period, and it would therefore not function as condensation cycling to conserve water. It is not clear whether or not it represents evaporation cycling. After a long period with slightly subatmospheric pressure and fluttering spiracles, the spiracles opened, restoring atmospheric pressure. The spiracles then closed (constriction phase), and the pressure fell. Water evaporating during the subatmospheric pressure of the flutter phase might be discharged during the subsequent open period if the animal then contracted with open spiracles. Surprisingly, the pressure fall during the constriction phase was said to be accompanied by a volume decrease. If so, it cannot have been due to abdominal expansion, but it may have been due to depletion of respiratory gases.

Cyclic carbon dioxide release in pupae of *Hyalophora* is generally seen as an adaptation that conserves water. That water loss at a given relative humidity would be increased if the spiracles were held open has been predicted by Buck (1958) on the basis of theoretical calculations that disregarded mass flow, but has not been established experimentally (Edney 1977, p. 78). Kanwisher (1966) showed that water loss just balanced metabolic water production at high relative humidity, and the finding of Kafatos (1968) that these pupae accumulate in the labial glands a large volume of isosmotic fluid, which is discharged at or soon after adult emergence, is consistent with the hypothesis that in some conditions maintenance of water balance might require discharge of metabolic water, rather than water conservation. It may be worth exploring the possibility that cyclical carbon dioxide release in *Hyalophora* pupae is associated with evaporation cycles.

Wasserthal (1980, 1981, 1982*a*,*b*) inferred cyclical changes in intratracheal pressure associated with the pumping of haemolymph between thorax and abdomen in the lepidopterans *Papilio machaon* and *Attacus atlas*, the beetles *Goliathus* and *Oryctes*, and the fly *Calliphora*. Using delicate techniques of contact thermography in combination with observation of abdomen length and spiracle closure, he has described patterns of ventilation movement and spiracular behaviour coordinated with haemolymph flow between thorax and abdomen resulting from periodic reversals of the heartbeat. Resting individuals of the giant silkmoth *Attacus atlas* showed a ventilation cycle in the abdomen that included a 'flutter' phase and a 'ventilation' phase of 'volleylike' contractions, but no 'constriction' phase of sustained spiracular closure (Wasserthal 1981). These cycles may, therefore, represent condensation cycles with a period of several minutes. When moths were disturbed, and perhaps therefore gained extra metabolic water making condensation cycles unnecessary, they omitted the 'ventilation' phase.

After post-ecdysial diuresis in the giant silkmoth, the absence of inflation of the thoracic pleural membrane indicated persistent subatmospheric pressure in the thorax (Wasserthal 1982*a*). In the abdomen, on the other hand, pulses of excess pressure were a normal component of the ventilation cycle. The abdomen contracted with open spiracles while the heart pumped haemolymph forward into the thorax. The ventral plate constituted a one-way valve, allowing backward but not forward flow. Thus when the flow of haemolymph into the thorax could no longer be accommodated by further expiration and tracheal compression, haemolymph flowed ventrally into the abdomen. The heartbeat now reversed and pumped haemolymph from thorax to abdomen, allowing the thoracic tracheae to reinflate. In the abdomen, the spiracles appeared to be fluttering at this stage and it is not clear whether intratracheal pressure excesses were achieved. Then followed a sequence of brief 'volleylike' contractions in the abdomen, and spiracular closure in each segment coordinated with its contraction may have resulted in a sequence of high-pressure pulses in the abdomen. The valve at the waist prevented their transmission to the thorax, in which they were not detectable.

Wasserthal (1982*a*) also described pressure cycles in the wings in the giant silkmoth *Attacus*. Within the rigid veins the tracheae are bathed in haemolymph and the pressure deficit caused by the pulsatile organ pumping haemolymph out of the wings is antagonized by the elastic contraction of the tracheae sucking haemolymph back into the wings. Elastic contraction of the wing tracheae is not longitudinal, but radial (as can be measured on figure 12 in Wasserthal (1982*b*)), presumably powered by the unusual microspiralling of the taenidia themselves in an axis transverse to the long axis of the trachea; each taenidial coil consists of a spiralled filament. Scanning electron micrographs of taenidia from individuals frozen at different stages of the cycle showed a change from about 23 windings per 100 μm in the contracted state to about 14 windings per 100 μm in the expanded state. If there were no inflow of air and no longitudinal expansion of the tracheae, a change of circumference of this magnitude would reduce the intratracheal pressure from 1 to 0.37 atm. Similar tidal oscillations of pressure and volume were described in the legs of moths and in the ladder-like array of air sacs in the elytra of the beetle *Oryctes nasicornis* (Wasserthal 1982*b*). Wings and legs may therefore supplement the flight muscles as sites for the transfer of water from the thorax to the intratracheal vapour.

Thus cyclical pulsations, involving small muscular internal sacs or changes in total body volume or flow of haemolymph from one tagma to another, or both, and coordinated with spiracular closure, are widespread in insects, and have been shown to be associated with pressure changes in some species.

Few measured values of intratracheal pressure excess are available: 0.005 atm in *Periplaneta* (Kestler 1985) and 0.04 atm in *Dissosteira* (McCutcheon 1940). Because the tracheal system is not rigid, the intratracheal pressure is expected to equal that in the haemocoele. Davey & Treherne (1964) measured a pressure deficit of 0.07 atm in the haemocoele of *Periplaneta*. Some haemocoele pressure excesses measured by various techniques are: 0.12 atm in larvae of *Aeschna nigriflava* (Tanaka & Hisada 1980); 0.59 atm in the leg of the spider *Tegenaria* (Parry & Brown 1959); 0.001 atm in grasshoppers (Watts 1951); and 0.04 atm in *Dissosteira* (McCutcheon 1940). Parry (1983) calculated a pressure excess of 0.05 atm in larvae of the dragonfly *Anax imperator*. In some soft-bodied insect larvae, operation of a hydrostatic skeleton depends on pressure excesses of up to 0.03 atm in the haemocoele (Jones 1978).

In the crop, Davey & Treherne (1964) found a transient peak of 0.12 atm in *Periplaneta*, Bennet-Clark (1963) found that *Rhodnius* could feed against a pressure deficit of at least 0.2 atm, and Pivnick & McNeil (1985) calculated a pressure deficit of 0.5 atm during feeding in the skipper butterfly *Thymelicus lineola*.

Some of the measured pressure differentials may be underestimated. Not all of the techniques used would be capable of registering high-frequency transient peaks such as might be involved in pressure cycles, and the pressure-modulating behaviour of insects is readily disrupted by even slight disturbance (Kestler 1985). Further, because of the way the pressure that can be exerted by circular muscles scales with size, the greatest pressure differentials are to be expected in the smallest cavities, in which pressures are hardest to measure.

However, it is clear that internal pressures compatible with the operation of a pressure cycle mechanism can be achieved; pressure excesses of up to 0.59 atm have been recorded in arthropods, and even small pressure differentials are expected to influence rates of vapour–liquid mass transfer. For instance, intratracheal air at 90% relative humidity when the spiracles are open would reach the threshold for rapid condensation ($p/p_0 > 1$) at an intratracheal pressure of 1.11 atm (a pressure excess of 0.11 atm); air in equilibrium with arthropod body fluids would be at a higher initial relative humidity (about 99.5%) (Edney 1977) and would require a correspondingly smaller pressure excess (0.005 atm) to achieve a supersaturation ratio of 1. Thus even the small excess pressures found by Kestler (1985) in desiccated *Periplaneta* are in the range that would enable the insect to condense a little water from humid intratracheal air before exhalation. Beament (1964) inferred an intratracheal humidity of more than 99% in *Periplaneta*.

(c) *Is the tracheal system a site of transfer of water?*

Pressure cycles could operate in any sealable, gas-filled cavity capable of being compressed and expanded by pressure changes in the surrounding body fluids, by its own muscles, or by elasticity. The tracheal system is one such cavity. The rectum of *Thermobia* is another. Even an air bubble in the pharynx might function this way.

Features of the tracheal system appear to make it a possible site for evaporation cycles, which are likely to be more common in large than in small animals. Because of scale effects, the tracheal system may be expected to be less suitable for condensation cycles, and extreme examples of net uptake from low ambient humidities are more likely to be found in small internal muscular sacs (§3*a*). Any condensation cycles that occur in the tracheal system are expected to involve small reductions in the water content of humid intratracheal air before exhalation, allowing reclamation of water originating elsewhere in the body, rather than net uptake from low ambient humidities.

Some water efflux is inevitable in terrestrial insects because of the gradient in water activity between the insect and its environment (Wharton & Richards 1978). Experiments using tritiated water have shown that the continuing exchange of water between insect and environment involves influx, as well as efflux, of water vapour (Arlian & Vaselica 1979; Arlian & Eckstrand 1975; Cooper 1982, 1983), although the net result is normally a continuous net water loss, without which metabolic water production and solute consumption would presumably cause a progressive increase in the water:solute ratio of a fasting insect. Gravimetric techniques can detect experimentally induced changes in the rate of net gain or loss of water but cannot resolve influx and efflux components (Loveridge 1980). The decreased rate of mass loss that follows blocking of the spiracles (Bursell 1957; Ahearn 1970; Cooper 1983; Ramsay 1935) and the increased rate induced by holding the spiracles open by carbon dioxide treatment (Mellanby 1934) are attributed to changes in the rate of efflux, and these findings are taken to support the notion that the tracheal system is a site of water loss.

Water uptake is not easily studied by gravimetric experiments. Influx is normally masked by efflux, and can be demonstrated gravimetrically only in those rare situations where it predominates, notably in certain dehydrated insects given recent access to water vapour and incapable of restoring their water:solute ratio by vigorous metabolism. The forms listed by Edney (1977) as capable of water vapour uptake are unusual not only in their inability to make metabolic water fast (Edney comments that they are all incapable of flight, although flighted psocids have since been found capable of uptake (Rudolph & Knülle 1982)), but also in the special adaptations that permit unusually rapid water uptake (Knülle 1967). These adaptations include accessory sites of water vapour uptake other than the tracheal system, associated with the rectum in *Thermobia*, *Tenebrio* larvae and flea prepupae (Rudolph & Knülle 1982), and the mouth in Psocoptera, Mallophaga and *Arenivaga* (O'Donnell 1982). Although gravimetric experiments have not revealed any species in which the tracheal system is the major site of net uptake, it is not safe to conclude that uptake in the tracheal system is insignificant in less specialized insects.

Some long-standing conclusions require reappraisal because they are based on early interpretations placed on gravimetric experiments before it was fully realized that net changes in mass represent a balance between influx and efflux. An experimental manipulation that affects influx and efflux differentially will have a net effect on water exchange that depends on the relative magnitudes of the effects on influx and efflux. Water loss down a gradient of water activity may take place over the general body surface as well as in the tracheal system and other cavities. Uptake against the water activity gradient, in so far as it depends on a pressure cycle mechanism, would be confined to sealable cavities. Thus, disabling the tracheal pressure cycle mechanism by holding the spiracles open or shut may reduce influx more than efflux. In the rare cases where influx is important or predominant, effects on influx rates might be detectable gravimetrically, but where efflux heavily outweighs influx, as it often does, effects on efflux rate will dominate net gravimetric changes.

Attempts have often been made to influence water exchange via the tracheal system by keeping the spiracles continuously open or closed. The conventional theory that spiracular control acts to conserve water (Kaars 1981) might predict that, whatever the initial water status of the insect, rates of water loss would be increased by preventing spiracular closure, and decreased by blocking the spiracles. The theory presented here predicts that disablement of the coordinated cycle of spiracular behaviour, whether achieved by keeping the spiracles open or by blocking them, would disrupt both influx and efflux of water, so that its net effect on water balance would depend on the current relative magnitude of tracheal influx and efflux. In hydrated insects using evaporation cycles to achieve a net loss of water, the rate of that loss might be decreased by such treatment; in desiccated insects using condensation cycles to retard water loss or achieve a net uptake of water vapour via the tracheal system, loss might be accelerated or net uptake rates decreased.

That net water loss in desiccated animals is accelerated by keeping spiracles open (Mellanby 1934; Cooper 1983; and Browning (1954) for the argasid tick *Ornithodoros moubata*) is compatible with both theories. The ixodid tick *Amblyomma variegatum* showed reduced rates of water vapour uptake in the presence of carbon dioxide, perhaps because the tracheal component of its uptake mechanism was disabled by spiracular opening or by anaesthesia (Rudolph & Knülle 1978).

That blocking spiracles retards water loss by hydrated individuals (Bursell 1957; Ahearn 1970; Cooper 1983; Ramsay 1935) is compatible with both theories. In the ixodid tick *Amblyomma variegatum*, blocking the spiracles slowed water vapour uptake of dehydrated ticks but did not wholly prevent it; evidently hypertonic saliva also contributes to water vapour uptake in this tick (Rudolph & Knülle 1978). But if spiracular closure affects influx (for which the tracheal system may be a major site) more than efflux (much of which may occur over the general body surface), it may enhance net loss. It may be relevant that Treherne & Willmer (1975) found that cockroaches, *Periplaneta americana*, showed reduced spiracle opening associated with *accelerated* water loss when decapitated. (The possibility that condensation cycles in *P. americana* help to reduce net water loss is considered above.) In unfed nymphs of the argasid tick *Ornithodoros moubata*, blocking the spiracles increased the rate of water loss by non-desiccated individuals in dry air (Browning 1954), and decreased the rate of uptake by desiccated individuals in air at humidities above their critical equilibrium activity (Lees 1946*a*; Browning 1954). The results of the experiments on *O. moubata* are compatible with the pressure cycle theory; but because they are hard to explain on conventional theory, they are partly responsible for the long-held view that water exchange is not an important function of the tracheal system (Beament 1964; Lees 1946*a*; Berridge 1970).

Since the tracheal system was proposed as a major site of water exchange by Hazelhoff (1927) and Mellanby (1934), gravimetric experiments have led to its general acceptance as a site of water loss, but for reasons outlined above it has not been accepted as a site of water vapour uptake. The tracheal system lost further credibility as a major site of water vapour uptake when Beament (1964) showed by estimating the dewpoint depression that the relative humidity of the tracheal gas in *Periplaneta* was too high to permit inward diffusion of water vapour from an unsaturated atmosphere. The tracheal system can now be reconsidered as a possible site for influx, as well as efflux, because evidence has accumulated to show that tracheal gas exchange involves mass flow as well as diffusion (see, for example, Kestler 1985), and because the pressure cycle mechanism proposed here would cause fluctuations in dewpoint depression.

This section focuses on the tracheal system because tracheal ventilation is widespread and any mechanism involving it is likely to be operated by a wide range of tracheate arthropods.

But the tracheal system is not the only possible site of water vapour uptake. Atracheate arthropods that take up water vapour must use other sites; some tracheate forms have been shown to use other sites in conjunction with, or instead of, the tracheal system (e.g. *Thermobia* (Noble-Nesbitt 1978) and fleas (Rudolph & Knülle 1982); and rapid net uptake from air of low humidity is particularly likely to involve small muscular internal cavities (§3*a*)).

(*d*) *Do patterns of ventilatory behaviour depend on water status?*

The coordinated movements of ventilation and spiracular closure are usually regarded as adaptations permitting exchange of respiratory gases while minimizing water loss (Wigglesworth 1972; Miller 1981; Kaars 1981; Kestler 1985). According to conventional theory, the water status of an insect should have little effect on its ventilation movements, except perhaps to reduce ventilation (thereby conserving water) in desiccated insects. According to the pressure cycle theory presented here, desiccation (at least in insects unable to counter it by the metabolic water production of vigorous activity such as flight) should enhance condensation cycles (in humid air) or suppress evaporation cycles.

Kestler's (1985) observation that the bursts of pressure pulses seen in desiccated *Periplaneta* were absent in hydrated individuals is compatible with the theory presented here. Perhaps the desiccated cockroaches were showing condensation cycles, which stopped when the water deficit was met.

Krasfur (1971) found that adult mosquitoes, *Aedes triseriatus* and *A. aegypti*, deprived of the opportunity to drink, showed progressive changes in ventilation behaviour as their water reserves became depleted. The thoracic spiracles opened less widely and for less time but more frequently in the desiccated group than in fed controls, and desiccated insects showed more frequent spontaneous activity, which would alter the water balance and which was normally associated with extended spiracular opening (Krasfur *et al.* 1970). Abdominal ventilatory pulsations, which could not be correlated with the movement of the thoracic spiracles, often occurred during, and for up to 30 s after, flight (Krasfur *et al.* 1970). These observations indicate that ventilatory behaviour depends on water status in mosquitoes, but without further information they are not easy to interpret. The abdominal movements associated with flight may represent evaporation cycles, helping to rid the insect of excess metabolic water; or they may be condensation cycles reducing evaporative loss or assisting uptake if in these small insects the effect of flight in accelerating water loss more than compensates for the extra metabolic production (Unwin & Corbet 1984). Gillett (1982) found regular contractions of the abdomen in *Aedes aegypti* and other species. The possible role of air bubbles in the crop is considered in §5. The increased frequency of briefer and narrower spiracular openings observed during desiccation may represent condensation cycles helping to reduce water loss with the exhaled air.

When Miller (1964) manipulated the water status of adult dragonflies (*Ictinogomphus ferox*) by allowing them to drink or keeping them in dry air, he found a clear effect of hydration on the degree of spiracular opening in an atmosphere of 3% oxygen in nitrogen; the spiracles opened more in hydrated insects than in desiccated ones. This finding is compatible with both conventional and pressure cycle theories.

Even the lowest metabolic rate that meets the energetic requirements of maintenance may yield enough metabolic water to increase the water:solute ratio in the body fluids, at least in large insects. In a non-feeding insect this accumulating water burden cannot be balanced by net solute gain, and in the long term is unlikely to be countered by mobilization of reserves. In large and highly waterproof starved, pupal or diapausing insects in which the rate of metabolic gain exceeds the rate of loss by cuticular transpiration, regulation of the water economy may therefore involve disposal of excess water in the vapour phase. The diapausing pupa of *Hyalophora* produces enough metabolic water to balance its water loss, even in a dry atmosphere (Kanwisher 1966), and its ventilation pattern, similar to the CFO type found in hydrated cockroaches (§3*b*) (Kestler 1985), may represent evaporation cycles. According to the theory proposed here, these waterproof resting stages may sometimes exhibit enhanced evaporation cycles or reduced condensation cycles, whereas conventional theory might predict that the lowered oxygen requirement would always lead to reduced ventilation movements.

The elevated rate of metabolic water production during vigorous activity such as flight or struggling should tend to increase the water:solute ratio, and at least in large insects this increase may outweigh the increased convective loss due to body movements. That large insects can accumulate a water burden during flight has been demonstrated by Bertsch (1984) for male bumblebees (*Bombus lucorum*) and by Nicolson & Louw (1982) for the carpenter bee *Xylocopa capitata*. In both studies, measurements of rates of oxygen or carbon dioxide exchange and evaporative water loss showed that metabolic water production exceeded evaporative water loss during flight. The bumblebees discharged part of their water burden by excreting in flight.

According to the pressure cycle theory, large insects accumulating water during vigorous activity may be expected to contribute to the discharge of the water burden by enhancing evaporation or suppressing condensation cycles, and perhaps to continue the modified ventilation pattern for a time after activity until water balance is restored. Conventional theory would expect ventilation to be enhanced to supply respiratory needs during activity, but not after it, unless there was an oxygen debt. That ventilation movements are enhanced during struggling in *Locusta* (Loveridge 1968) and during warm-up in *Vespa crabro* and other aculeate Hymenoptera (Weis-Fogh 1967; Nicolson & Louw 1982) and the beetle *Geotrupes stercorarius* (Krogh & Zeuthen 1941) is compatible with either theory. Possibly these were evaporation cycles. Suppression of condensation cycles during activity when metabolic water production could complement or replace uptake from the air favours the pressure cycle theory. Thus Herford (1938) found that the ventilation movements (possibly condensation cycles, §3*b*) of *Archaeopsylla* were retarded during struggling, and Miller (1981) found that two species of phorid fly ventilated continuously while inactive but not during flight or running. The pressure cycle theory is also supported by reports of effects persisting for a period after struggling or flight in *Archaeopsylla* (Herford 1938), *Aedes* (Krasfur *et al.* 1970), honeybees (Snodgrass 1956), and *Schistocerca* and cicadas, both of which have been shown to accumulate no significant oxygen debt (Weis-Fogh 1967; Bartholomew & Barnhart 1984).

These examples show that the pattern of ventilation behaviour can vary with water status. At very low or high partial pressures of oxygen or carbon dioxide, respiratory requirements may outweigh water status as determinants of ventilation behaviour, but under less extreme conditions the nature and rate of ventilation might be markedly affected by changes in the water status of the insect or in the relative humidity of the air such as might incidentally accompany a change of gas supply. Studies in which changes in spiracular or tracheal rhythm have followed changes in gas supply (see, for example, Herford 1938) seldom specify constant relative humidity. Herford's (1938) finding that pure oxygen reliably re-established the tracheal rhythm (probably condensation cycles) inhibited after struggling might result from a different relative humidity in the high-oxygen treatment, but is hard to explain on the conventional theory.

4. Some further implications

(a) *The tracheal system as an avenue for internal redistribution of water within the body*

Redistribution of water vapour within the tracheal system would allow water removed from sites with a local excess (such as the flight muscles) to supply sites of local deficit elsewhere in the body (as in the abdomen) without diluting the haemolymph on the way. An insect might control rates of net gain or loss in different regions by manipulating the relative intensity and duration of the evaporation and condensation phases of the pressure cycle (and perhaps also the distribution of body temperature, §4*b*). Ventilation during or after flight in large insects commonly involves directional airflow (Miller 1974; Weis-Fogh 1967; Bailey 1954), usually from the thorax (where metabolic water would be produced) towards the abdomen (where it may be taken up). McCutcheon's (1940) observation that inflation and compression of air sacs was not synchronous throughout the body during ventilation in the grasshopper *Dissosteira carolina* gives further evidence for the intratracheal airflow that would be a prerequisite for water vapour transport. Regional differences in the pressure régime would require the regions to be separated by a barrier capable of supporting a pressure difference. Examples of such barriers include pressure-proof valves between thorax and abdomen in the lepidopterans *Papilio machaon* (Wasserthal 1980) and *Attacus atlas* (Wasserthal 1981, 1982*a*), the fly *Calliphora* (Wasserthal 1982*b*), the beetle *Oryctes nasicornis* (Wasserthal 1982*b*) and the bumblebee *Bombus vosnesenkii* (Heinrich 1976); and the neck (Wasserthal 1982*b*) that could perhaps protect the contents of the head from the fluctuating water balance in the thorax.

In the resting silkmoth, Wasserthal's (1981, 1982*a*) description of events is compatible with the hypothesis that water is transferred via the intratracheal vapour phase, with the thorax as a water source and the abdomen as a pump which sometimes abstracts water from the stream of tracheal gas before exhaling it. The pressure cycles described in the abdomen resemble the condensation cycles postulated here.

Transfer of water into the tracheal transport system would be favoured by rich tracheation at the source. The major source of metabolic water during flight or running will be the thoracic muscles, whose rich tracheation has been described in many insect species (see, for example, Wigglesworth & Lee 1982). From Wasserthal's (1982*a*, *b*) account of cyclical pressure changes in the wing tracheae (§3*b*) it appears that the vapour–liquid interface in the tracheoles of the wings may also function as a site for evaporative transfer of water from the haemolymph originating in the thorax to the tracheal vapour phase, at least in *Attacus* and *Oryctes*. If wing tracheoles are important sites for evaporative discharge of water into the tracheal system, the wing tracheation might be expected to be richly branched in insects needing rapid elimination of metabolic water during flight, namely those with a massive thorax and a large metabolic rate such as might be associated with a high wing loading or a high wingbeat frequency or both. Surveying 55 species of Lepidoptera, each from a different subfamily, Kirk (1983) noted that wing tracheation was generally either extensive or sparse, but rarely intermediate. Its distribution among species did not strictly follow phylogenetic groupings. He showed that extensive wing tracheation was not significantly correlated with a wing length greater than

15 mm ($p = 0.64$) or with whether the species was a moth or a butterfly ($p = 0.18$). Kirk (personal communication 1986) has now re-examined the 55 species in his original survey, and finds that extensive tracheation is correlated with an index of wing loading {[(thoracic width)^2 × body length]/(wing length) × (wing width)} ($p = 0.002$; two-tailed Mann–Whitney U test).

Another possible source of water to be evaporated into the tracheal system and transported therein is the rectum. Water taken up from fluid or air in the rectum might evaporate into the tracheoles investing the rectal wall and could then be redistributed in the tracheal system. Its uptake would be promoted by high pressure within the rectal lumen, and its evaporation would be promoted by low pressure in the adjacent tracheal system. In *Periplaneta*, in which Wall & Oschman (1970) show tracheoles penetrating deep into the rectal epithelium, the high rectal pressure could be achieved by contraction of the muscular rectal wall. The low intratracheal pressure could be achieved at the same or a different phase of the cycle by expanding the abdomen (or preventing its contraction) with closed spiracles. In *Thermobia*, low intratracheal pressure would coincide with high pressure pulses in the rectal system if the anal and tracheal valves were closed.

Dust entering the tracheal system and acting as a nucleation site might disrupt the precise localization of condensation. Hassan (1944), in his study of dipteran spiracles, found dust-excluding filters in insects inhabiting dry places and in actively flying forms, but not in slow-moving insects confined to moist places, like most of the Nematocera he investigated. Thus filters were found in those species in which a water deficit or burden is likely to be countered by condensation cycles. The condensation that Beament (1964) observed on the hydrofuge walls of large tracheae under experimental conditions may have been due to contaminants acting as nucleation sites or to very high supersaturation ratios.

(*b*) *Pressure cycles and body temperature*

In studies of small-scale patterns of microclimatic change in space and time it is usually found that relative humidity and temperature vary in such a way that the absolute humidity remains more or less constant, unless water is being supplied to the air by, for instance, transpiring leaves. It is not usual to find that relative humidity stays constant while the absolute humidity varies, as might happen, for instance, in air in contact with an aqueous solution of constant water activity.

Figure 2*a* shows how W_G, the maximum potential gain of water per cycle calculated according to (1), would vary with temperature. The continuous lines show how W_G would vary for three different compression ratios ($c = 0.4$, $c = 0.6$ and $c = 0.8$) as the temperature rises at a constant ambient absolute humidity of 13.8 g m^{-3}, equivalent to 80% relative humidity at 20 °C. When the air is saturated ($a_0 < 13.8$ g m^{-3}), W_G rises with temperature, but at higher temperatures ($a_0 > 13.8$ g m^{-3}), W_G falls with temperature.

The dashed lines in figure 2*a* show that if the relative humidity of the ambient air is held constant at 80%, W_G rises with temperature. $W_G = 0$ when $r = c$, and the lines for a compression ratio of 0.8 lie on the line $W_G = 0$ when $r \leqslant 0.8$. These lines show why maximum uptake rates in *Thermobia* require high ambient temperatures as well as high relative humidities.

These considerations apply if body temperature, T_B, and ambient temperature, T_A, are equal. If $T_B > T_A$, when air at ambient relative humidity is inhaled it will warm up with a concomitant fall in r. Uptake will be slowed if $T_B > T_A$. Insects using condensation cycles to counteract a water deficit are therefore likely to select sites and postures that minimize radiative warming, and will avoid endothermic heating.

W_G is the gain per cycle. Temperature-related changes in cycle frequency may contribute to temperature-dependent changes in the rate of uptake per unit time.

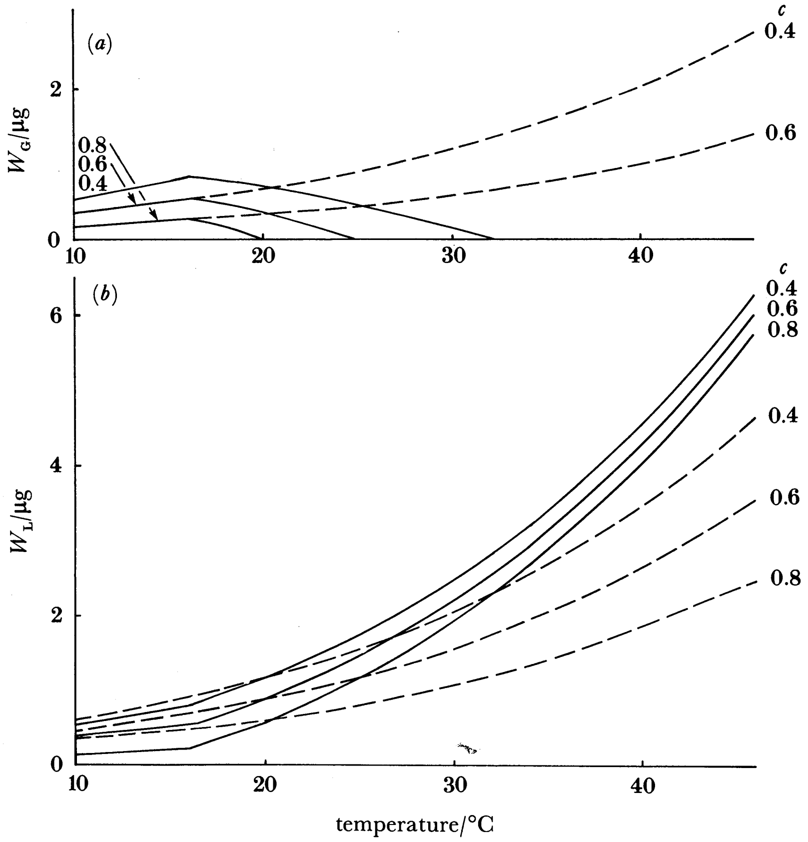

FIGURE 2. Effects of temperature on (a) W_G, the maximum potential mass of water gained per condensation cycle, calculated from (1) [$W_G = a_0 v(r-c)$], and (b) W_L, the maximum potential mass of water lost per cycle, calculated from (2) [$W_L = a_0 v(1-rc)$] (see text), for three different values of the compression ratio, c (compressed cavity volume/expanded cavity volume), assuming an expanded volume, v, of 100×10^{-9} m^3. Continuous lines: absolute humidity, a_0, constant at 13.8 g m^{-3}, equivalent to a relative humidity, r, of 0.8 at 20 °C (giving saturated air below 17 °C). Broken lines: relative humidity constant at $r = 0.8$. In saturated air $r = 1$ and equation (1) = equation (2) so that $W_G = W_L = a_0 v(1-c)$.

Figure 2b shows how W_L, the maximum potential rate of loss of water per cycle, calculated according to (2), would vary with temperature. The continuous lines show how W_L would vary for compression ratios of 0.4, 0.6 and 0.8 as the temperature rises for a constant ambient absolute humidity of 13.8 g m^{-3} equivalent to 80% relative humidity at 20 °C. While the air is saturated, W_L rises slowly with temperature, but at higher temperatures where the air is unsaturated W_L rises more steeply with temperature with the rise in a_0 and the fall in the relative humidity of the ambient air occupying the cavity before expansion. These effects depend on T_B rather than T_A, and can be achieved at low ambient temperatures by raising T_B. Insects using evaporation cycles to discharge a water burden may therefore be expected to favour a high T_B, whether achieved by conduction (selecting microhabitats of high T_A), radiation (basking) or endothermy.

The dashed lines in figure 2*b* show that if the relative humidity of the ambient air is held constant at 80%, W_L rises less steeply with temperature; the absolute humidity of the ambient air occupying the cavity before expansion now rises with temperature. Evidently, high rates of water loss per cycle can be achieved at high ambient relative humidity if T_B is high.

Here, too, temperature-related changes in cycle frequency may contribute to temperature-dependent changes in rates of loss per unit time. The influence of temperature on evaporation cycle frequency may be mediated by effects on evaporation rate dictating the effective duration of a cycle, as well as by more direct effects on behaviour. Evaporation into subsaturated air is much slower than condensation from supersaturated vapour. At $T_B = 45$ °C, $p_0 = 0.095$ atm, so that an expansion of 10.5 times would be required to achieve the rapid vaporization that occurs when the total pressure equals p_0. It will be interesting to see whether any species have large enough compression ratios to achieve this during evaporation cycles at high T_B.

Heat and water are both produced in metabolizing tissues, and both may accumulate harmfully if not rapidly dissipated. Because the cuticular barrier that confers impermeability to molecules such as water does not prevent heat transfer, a higher proportion of heat loss than water loss probably takes place through the cuticle. Phenomena that retard or accelerate loss from the surface (such as insulation or airflow during flight, respectively) are likely to have a greater proportionate effect on the rate of loss of heat than of water. Conversely, changes in the rate of tracheal ventilation may have relatively more effect on the rate of transfer of water than of heat. Rates of loss of both heat and water depend on body size. Rates of production of heat and water depend on metabolic rate which increases in proportion to a higher power of body mass, M, in insects (about 1) than in mammals (about $\frac{2}{3}$) (Keister & Buck 1974). If rates of loss via the surface increase more nearly in proportion to surface area ($M^{\frac{2}{3}}$), then during vigorous activity, the problem of metabolic water accumulation (like that of heat accumulation) (Heinrich 1981) will be more serious in large insects than in small ones.

A rise in temperature would ease the water burden if the rate of metabolic water production were to rise more slowly with temperature than does the potential rate of evaporative elimination. The Q_{10} for the metabolic rate for insects is often lower (typically about 1) in the temperature range normally experienced by the animals than it is at lower temperatures (where it is typically about 2) (Hoffmann 1985). According to figure 2*b*, the maximum potential rate of elimination of water per evaporation cycle shows temperature dependence equivalent to a Q_{10} well above 1 (2.0 at 25–35 °C), even if no account is taken of the possible increase in cycle frequency with temperature. In the temperature range where the 'Q_{10}' for W_L exceeds the Q_{10} for respiratory rate and therefore for metabolic water production, the maximum metabolic rate at which water balance can be sustained would rise with body temperature, and there would be a critical threshold body temperature corresponding with the critical threshold metabolic rate for flight. Such a critical threshold body temperature for sustained flight has been identified in many large insects, and has been interpreted in terms of the temperature-dependence of muscle action (Heinrich 1981). I now suggest that the temperature-dependence of the water-eliminating mechanism may also be relevant. The high thoracic temperature needed for sustained flight in some insects with high power requirements may represent the minimum threshold at which water can be eliminated as fast as it is produced. In some cases thermoregulation may be seen as a step towards water regulation, rather than as an adaptive feature in its own right.

Above the critical temperature, I suggest that an insect might eliminate water as fast as it is produced, by modulating the frequency, intensity and nature of pressure cycles. Below the critical temperature, sustained flight would be impossible, leading to progressive accumulation of a metabolic water burden as Nicolson & Louw (1982) found for *Xylocopa* and Bertsch (1984) found for *Bombus* (§3*d*)). Brief flights would create a transient water burden which might be dispelled by vigorous pumping immediately after settling. Wasps (*Vespula germanica*), forced to fly continuously, suffered swelling and disruption of the flight muscle mitochrondria (Wigglesworth 1982).

Heinrich & Mommsen (1985) found that the flight of winter noctuid moths with a high wing loading and high wingbeat frequency required a thoracic temperature greater than 30 °C, whereas small geometrids with lower wing loading and a lower wingbeat frequency could sustain flight with thoracic temperatures close to ambient down to below 0 °C. These authors suggested that it was the unusually low metabolic cost of flight that permitted the small species to fly at such low thoracic temperatures. They did not find the physiological differences that would be expected if the thoracic temperature is related to the temperature-dependence of muscle action, but their findings are consistent with the suggestion put forward here. If the high thoracic temperature functions to enhance evaporative elimination of the metabolic water burden, its distribution (like that of extensive wing tracheation in Lepidoptera) may be expected to correlate with surface: volume ratio and some index of metabolic water production such as wing loading or wingbeat frequency.

If sustained flight is impossible for large insects at low temperatures because metabolic water is produced in the thorax faster than it can be eliminated, preflight warm-up will be necessary to permit water balance to be sustained. Some insects achieve this by basking, warming the thorax (and the wings, in which evaporation cycles may take place, as in butterflies (Wasserthal 1975, 1980)) and so increasing the heat content presumably without increasing the water content. This can work for insects with large dark wings, and a large enough body not to cool down during flight (Unwin & Corbet 1984), but it restricts flight to sunny times and places.

Endothermic warm-up frees insects from the dependence of flight on insolation, but will itself contribute to a metabolic water burden. The study of Heinrich & Mommsen (1985) on winter-flying moths reveals a mechanism that appears to permit the thorax to accumulate heat without accumulating water. The moths warm up slowly at first, progressively increasing the metabolic rate as the thoracic temperature increases, so perhaps keeping metabolic water production in step with evaporative elimination, until eventually the thorax is hot enough to dispel the water produced by a metabolic rate high enough to support flight. Adaptations that reduce costs in time and energy during warm-up may be expected to involve a compromise between reducing the rate of heat dissipation (e.g. by thermal insulation) and reducing the rate of water accumulation (e.g. by ventilation). Features that would help to reduce the rate of accumulation of water include vigorous ventilation during endothermic warm-up, which has been recorded in some insects (Weis-Fogh 1967; Bartholomew & Barnhart 1984; Krogh & Zeuthen 1941); and use of a respiratory substrate that yields little water per unit of energy, such as fat. Migrant insects of several orders use lipids as metabolic substrates for sustained flight and some of these use carbohydrate for short flights (Kammer & Heinrich 1978). Perhaps the equivocal ecological distinction between migration and trivial flight (Kennedy 1975) reflects the difference between prolonged, often lipid-fuelled flight in which water balance is sustained, and short flights which are fuelled by carbohydrate which may come directly from the gut rather than the fat body, and in which progressive disturbance of the water balance limits flight duration, necessitating frequent settling and recovery (see Jutsum & Goldsworthy 1976).

Features that would help to minimize heat loss but have relatively little effect on water loss rate include thick insulation (Church 1960) and minimization of radiative loss (or maximization of gain) by posture or habitat choice. By keeping its wings still, the warming-up insect avoids the air movement which, during flight, must increase convective heat loss without having so much effect on water loss.

The relative balance between rates of loss of heat and of water must depend on body size. The bigger the insect, the higher the temperature required for water loss to balance gain, and the higher the minimum thoracic temperature for flight actually observed (Casey & Joos 1983). The maximum size of insects will presumably be reached when the minimum temperature for flight nears the maximum physiologically tolerable body temperature. In moths, beetles and dragonflies (Heinrich 1981) the flight threshold temperature increases with mass up to a plateau value. Above that, further mass increase is presumably accompanied by reduction of mass-specific metabolic rate (and therefore of water production rate) perhaps by a decrease in wingloading or wingbeat frequency. Associated with this would be a decrease in aerobatic manoevrability (Casey & Joos 1983). Insects with a low power requirement for flight can reach a larger size before unphysiological body temperatures are required to achieve water balance. The large Palaeozoic insects (Wootton 1976) may have been clumsy fliers, although their pigmented wings (Douglas 1981) may have helped evaporation cycles by absorbing radiation.

The mass of water lost per evaporation cycle depends on the volume and compression ratio of the gas-filled cavity (equation (2)). A running insect limited to short sprints by accumulation of metabolic water might therefore find adaptive advantage in increasing the compressible tracheal volume in the thorax, perhaps by trachea-filled lobes. If these could be warmed by radiation their effectiveness would be much increased, and they might therefore be flat and dark. In some modern forms evaporation cycles can be achieved by modulation of the direction and nature of the heartbeat, but in less sharply tagmatized forms, pressure changes require muscular distortion of the body wall. These volume changes are achieved by telescoping in insects with a cylindrical abdomen, but by dorsoventral contraction (often antagonized by elastic recoil) (Miller 1974) resulting in regular up-and-down movements in flattened structures such as the abdomen of hoverflies. Thus the dark, flat flaps on the thorax would be subject to regular muscular pulsations or flapping. Kingsolver & Koehl (1985) present experimental evidence in support of their hypothesis that wings could have evolved from thoracic lobes with a primarily thermoregulatory function. They suggest that the moveable articulation essential for the evolution of flapping flight arose as a means of positioning the wings for thermoregulation. I now suggest that both the absorption of radiation and the ability to flap originally functioned to enhance water regulation by pressure cycles. Evolving as instruments for transferring metabolic water from the haemolymph to the tracheal system, the thoracic lobes may eventually have given rise to wings. The function of these structures as sites for evaporative exchange would be enhanced by the rich venation characteristic of primitive insect groups (Kingsolver & Koehl 1985). This role of the wings may be less important in insects whose pressure cycles depend on haemolymph transfer between tagmata. In the groups now known for their reduced venation – Diptera and Hymenoptera – the active forms have short, stout bodies and distinct waists.

The Hymenoptera and Diptera are characterized by asynchronous flight muscles, high wingbeat frequencies and the manoeuvrable flight and ability for sustained hovering that are the concomitants of high power input (Casey & Joos 1983). Perhaps it is an ability to dispose of metabolic water fast that sets these apart from other insects. With their reduced wing venation and distinct waists, perhaps the active forms depend on haemolymph transfer for their pressure cycles. Some members of these orders are very small. 'Large insects are limited in their ability to fly at high air temperatures by their physiological capacities to dissipate heat' (Heinrich 1981) and at low body temperatures, perhaps, by their capacities to dissipate metabolic water. Small insects can dissipate heat and water relatively faster and can therefore fly at higher irradiance (Willmer 1983) and at lower thoracic temperatures (Heinrich & Mommsen 1985).

It will always be difficult to know whether the constraints that pattern flight activity in space and time depend on heat balance or water economy, because heat and water are both generated by muscular activity and lost to the environment at a rate that depends on surface/volume ratio.

(*c*) *Aquatic insects*

Freshwater insects must continuously counter a water burden arising from inward leakage. A major part of their regulation of water economy is achieved by drinking the medium and excreting hypotonic urine (Stobbart & Shaw 1974). Elimination of water via the Malpighian tubules and gut must be accompanied by solute loss. This is compensated to some extent by inward secretion of ions at specific sites such as the anal papillae of mosquito larvae (Stobbart & Shaw 1974). Pressure cycles might significantly complement the action of the Malpighian tubules and gut in water elimination because they could permit water discharge without solute loss, and because, in pupae, drinking and urine discharge cannot contribute to water regulation. Some freshwater holometabolans pupate on land (aquatic Megaloptera (Elliott 1977; *Eristalis* (Gilbert 1986)) or retain spiracular connection with the atmosphere (most mosquitoes) or with the air in plants (*Mansonia richiardii* (Marshall 1938)). Among the few that do not are pupae with spiracular gills (Hinton 1968).

An aquatic insect whose tracheal system communicates with the atmosphere might transfer water from the tissues into the vapour phase in the tracheal system by using evaporation cycles, and by puffing out humid air it could eliminate water without losing solutes. This system could be used by insects with a large compressible volume v represented by large air sacs or a large compressible cavity outside the body.

In the rat-tailed larva of the hoverfly *Eristalis* the tracheal system contains large air sacs which can be isolated by internal valves (Alsterberg 1934), and communicates with the air via spiracles at the tip of the siphon. The larva shows regular volume cycles lasting about 15 s or more and consisting of a slow volume increase (accompanied by inspiration and a decrease in density to below that of water) equivalent to up to about half the expanded volume of the tracheal system, followed by rapid contraction with expiration (presumably discharge of humid air with open spiracles) (Krogh 1943; Alsterberg 1934). A larva denied access to the atmosphere increased in volume and after 0.5–2.0 h floated to the surface where it ventilated for a time before sinking again and repeating the cycle. These findings suggest that *Eristalis* larvae use evaporation cycles to eliminate water. If these and other soft-bodied freshwater larvae whose tracheal systems communicate with the atmosphere use evaporation cycles in this way, they must somehow be able to re-expand the air sacs, producing subatmospheric pressures. Water could be lost by evaporation according to (2), even into saturated air.

Adult water beetles, corixids and *Notonecta* carry air under the elytra when submerged, and cycles of tracheal compression and dilation can be seen in the water beetle *Cybister* when it comes to the surface (Brocher 1912, cited in Wigglesworth 1972). It is not clear whether these represent evaporation cycles. As in desert tenebrionids, the subelytral air space might increase the compressible volume if it could be compressed by movements of the elytra.

The extent to which elevation of body temperature may enhance internal evaporation rates in freshwater insects remains unknown.

Whereas freshwater insects must counter inward osmosis by continuous elimination of excess water, insects in hypertonic media such as the sea must counter a water deficit due to outward osmotic leakage. This is done by drinking the medium and excreting hypertonic urine in larvae of saltwater mosquitoes and ephydrids (Phillips & Bradley 1977). I have suggested (§3*a*) for terrestrial insects that the tracheal system may be a site more appropriate for evaporation cycles than for condensation cycles which, to operate at small values of CEA, would be more effective in a small muscular internal sac. For the large values of CEA (and therefore *c*) that concern marine insects, the tracheal system might be an adequate cavity. Seawater is in equilibrium with a relative humidity of about 98% (Edney 1977). If the tracheal system had access to the atmosphere, insects living in hyperosmotic media might condense water from the atmosphere by using condensation cycles. It would be interesting to know whether this mechanism is used by pupae and possibly also larvae of ephydrids and mosquitoes, and by dipteran larvae living in petrol (see Thorpe 1930). I know of no marine insects capable of taking up water from subsaturated air via the rectum.

If condensation cycles depend on sustained access to the atmosphere, they are unlikely to be important in the sea. The true marine habitat is necessarily rough, because the maintenance of its salinity depends on mixing with the open sea. Like the rough open water of lakes, the open sea lacks insect larvae that rely on an undisturbed spiracular connection with the atmosphere at the surface. These forms are generally confined to habitats that permit spiracular contact with the atmosphere either because they are protected from mixing with the open sea (and are therefore likely to have a salinity different from that of seawater, as in hypersaline lagoons or rockpools), or because their littoral habitat is periodically emersed.

If it is not possible to maintain water balance in such hypertonic media without the aid of vapour–liquid pressure cycles, the poverty of the marine insect fauna may be related to the unavailability of pressure cycles in the open sea.

5. Discussion

Pressure changes in a gas-filled cavity may depend on the mechanical properties of the body wall or on the mechanical properties of the wall of the cavity itself. If condensation cycles participate in the most active water vapour uptake systems, they probably involve pulsations of an internal sac containing air and with muscular or elastic walls. The muscular and richly tracheated rectum (Sharif 1937) of flea larvae and prepupae contains air and pulsates

(Rudolph & Knülle 1982) and may represent the site of condensation cycles. It would be interesting to know if the rectum is involved in pressure cycles in the cryptonephridial complex of the larvae of beetles and caterpillars. In *Periplaneta*, in which tracheoles are intimately associated with the cells of the rectal pad (Wall & Oschman 1970), juxtaposition of the tracheoles and the rectal wall might permit water condensing there from the air in the rectum to enter the tracheal transport system. The pharynx of *Periplaneta* normally contains air (Bell & Ayodi 1981) and as a muscular sac may also participate in pressure cycles. The ventral diverticulum ('crop') of the mosquito *Aedes aegypti* is commonly inflated with air to occupy much of the abdomen (Christophers 1960), and because of the abdominal pulsations recorded by Krasfur *et al.* (1970) and Gillett (1982) this too may be a site for pressure cycles.

Evaporation cycles are more likely to involve a large compliant cavity such as the tracheal system. In adult and other insects in which the cuticle is rigid enough to support pressure cycles, changes of internal pressure may involve distortions of the whole body. Volume changes are achieved by telescoping, as in bees, in which case re-extension by intersegmental muscles could generate subatmospheric pressures, or by dorsoventral contraction in a flattened abdomen, as in hoverflies, in which case re-extension is aided by the elastic recovery of the cuticle (Miller 1974).

In insects in which the cuticle is rigid and the haemocoele is subdivided into pressure-proof compartments, pressure cycles can involve the transfer of haemolymph from one compartment to another instead of (*Calliphora*) or as well as (*Attacus*) distortions of the abdomen. Pressure cycles of this type have been described in some higher flies, Lepidoptera and beetles.

However appropriate the morphology of the insect may be, pressure cycles may be precluded at certain times, as when ecdysis interferes with the tracheal pathway between the body fluids and the environment; or when the volume of the compressible cavity has been reduced by growth of an instar within the cuticle, by maturation of eggs or by the ingestion of a very large meal. On the other hand, pressure cycles might be increased in effectiveness if the compressible volume is increased by the extension of the cuticle that accompanies ecdysis or by the decrease in haemolymph volume that accompanies dehydration.

Thus mechanical constraints set limits to the types of pressure cycle available to insects of particular morphological types or physiological states. Ecological demands must help to determine which cycles come to be used. A means of elevating the water: solute ratio by uptake of water vapour from the environment would be particularly advantageous in forms where the alternatives of metabolic water production by flight, or of drinking are not available. Condensation cycles are therefore expected in flightless insects that do not feed (pupae, unless these are very large or highly waterproof or both), or that go for long periods without feeding (blood-suckers and some predators), or that take food in which the water: solute ratio is very low (flea larvae, stored-product insects) and in desert species where uptake from humid air at night may be critical (desert tenebrionids) (Louw *et al.* 1986). Evaporation cycles are to be expected in pupae in which a water burden arises because of a low surface: volume ratio (*Hyalophora*) or aquatic habitat (*Simulium*).

A means of lowering the water: solute ratio by discharge of water in the vapour phase would be particularly advantageous where discharge must be continuous rather than intermittent, as in large insects during flight or pre-flight warm-up, or in insects living submerged in freshwater.

Some of the distinctive features of pterygote insects may be linked with their hypothetical ability to regulate water economy by pressure cycles: an extensive tracheal system with valves; an open haemocoele with tagmatization; and the morphological and physiological machinery to support the intense metabolic activity of flight. Thus pressure cycles may have brought evolutionary opportunities; but they do not seem able to overcome the hurdles that limit the success of insects in the sea or set upper limits to insect body size.

Some of the implications and predictions of the pressure cycle theory are also compatible with conventional theory. Respiration involves the transfer of oxygen, carbon dioxide, water and heat, all of which show similarities of behaviour and sometimes share common pathways. Many of the features discussed in this paper have been interpreted elsewhere purely in terms of maintenance of oxygen supply or heat balance. Without denying that role, I draw attention to the additional possibility that some features may function also in maintaining water balance. Perhaps the tracheal system functions not only in the supply of respiratory gases, but also as a water-handling system.

I thank the following people for discussing with me parts or all of this paper at various stages and giving comments, suggestions, ideas, explanations and encouragement that have contributed greatly to it: Professor Sir James Beament, F.R.S.; Professor P. S. Corbet; Dr F. S. Gilbert; Dr S. H. P. Maddrell, F.R.S.; Professor J. L. Monteith, F.R.S.; and Mr D. M. Unwin. I am grateful to Dr J. Noble-Nesbitt and Dr W. D. J. Kirk, both of whom kindly allowed me to include their unpublished results.

REFERENCES

Ahearn, G. A. 1970 The control of water loss in desert tenebrionid beetles. *J. exp. Biol.* **53**, 573–595.

Alexander, R. M. 1983 *Animal mechanics.* Oxford: Blackwell Scientific Publications.

Alsterberg, G. 1934 Beiträge zur Kenntnis der Anatomie und Biologie der limnophilen Syrphidenlarven. *Biol. Zbl.* **54**, 1–20.

Arlian, L. G. & Eckstrand, I. A. 1975 Water balance in *Drosophila pseudoobscura*, and its ecological implications. *Ann. ent. Soc. Amer.* **68**, 827–832.

Arlian, L. G. & Vaselica, M. M. 1979 Water balance in insects and mites. *Comp. Biochem. Physiol.* **64**A, 191–200.

Bailey, L. 1954 The respiratory currents in the tracheal system of the adult honey-bee. *J. exp. Biol.* **31**, 589–593.

Bartholomew, G. A. & Barnhart, M. C. 1984 Tracheal gases, respiratory gas exchange, body temperature and flight in some tropical cicadas. *J. exp. Biol.* **111**, 131–144.

Beament, J. W. L. 1964 The active transport and passive movement of water in insects. *Adv. Insect Physiol.* **2**, 67–129.

Beament, J. W. L., Noble-Nesbitt, J. & Watson, J. A. L. 1964 The waterproofing mechanism of arthropods. III. Cuticular permeability in the firebrat, *Thermobia domestica* (Packard). *J. exp. Biol.* **41**, 323–330.

Bell, W. J. & Ayodi, K. G. 1981 *The American cockroach.* London: Chapman & Hall.

Bennet-Clark, H. C. 1963 Negative pressures produced in the pharyngeal pump of the blood-sucking bug, *Rhodnius prolixus. J. exp. Biol.* **40**, 223–229.

Bergles, A. E., Collier, J. G., Delhaye, J. M., Hewitt, G. F. & Mayinger, F. 1981 *Two-phase flow and heat transfer in the power and process industries.* Washington: Hemisphere Publishing Corporation, McGraw-Hill Book Company.

Berridge, M. J. 1970 Osmoregulation in terrestrial arthropods. In *Chemical ecology V* (ed. M. Florkin & B. T. Scheer), pp. 287–319. New York: Academic Press.

Bertsch, A. 1984 Foraging in male bumblebees (*Bombus lucorum L.*); maximising energy or minimizing water load? *Oecologia* **62**, 325–336.

Brocher, F. 1912 Recherches sur la respiration des insectes aquatiques. Le cybister. *Annls Biol. lacustre* **5**, 218–219.

Browning, T. O. 1954 Water balance in the tick *Ornithodoros moubata* Murray, with particular reference to the influence of carbon dioxide on the uptake and loss of water. *J. exp. Biol.* **31**, 331–340.

Buck, J. 1958 Possible mechanism and rationale of cyclic CO_2 retention by insects. *Proc. Xth Int. Congr. Ent.* **2**, 339–342.

Bursell, E. 1957 Spiracular control of water loss in the tsetse fly. *Proc. R. ent. Soc. Lond.* A **32**, 21–29.

Buxton, P. A. 1930 The biology of a blood-sucking bug, *Rhodnius prolixus*. *Trans. R. ent. Soc. Lond.* **78**, 227–236.

Casey, T. M. & Joos, B. A. 1983 Morphometrics, conductance, thoracic temperature, and flight energetics of noctuid and geometrid moths. *Physiol. Zool.* **56**, 160–173.

Christophers, S. R. 1960 *Aedes aegypti (L.), the yellow fever mosquito*. Cambridge University Press.

Church, N. S. 1960 Heat loss and the body temperatures of flying insects. II. Heat conduction within the body. *J. exp. Biol.* **37**, 186–212.

Cooper, P. D. 1982 Water balance and osmoregulation in a free-ranging tenebrionid beetle, *Onymacris unguicularis*, of the Namib desert. *J. Insect Physiol.* **28**, 737–742.

Cooper, P. D. 1983 Components of evaporative water loss in the desert tenebrionid beetles *Eleodes armata* and *Cryptoglossa verrucosa*. *Physiol. Zool* **56**, 47–55.

Davey, K. G. & Treherne, J. E. 1964 Studies on crop function in the cockroach (*Periplaneta americana* L.). III. Pressure changes during feeding and crop emptying. *J. exp. Biol.* **41**, 513–524.

Davies, J. T. & Rideal, E. K. 1963 *Interfacial phenomena*. New York: Academic Press.

Douglas, M. M. 1981 Thermoregulatory significance of thoracic lobes in the evolution of insect wings. *Science, Wash.* **211**, 84–86.

Edney, E. B. 1977 *Water balance in land arthropods*. Berlin: Springer-Verlag.

Elliott, J. M. 1977 A key to British freshwater Megaloptera and Neuroptera. *Freshwat. Biol. Ass. Sci. Publ.* no. 35.

Evans, A. C. 1935 Some notes on the biology and physiology of the sheep blowfly *Lucilia sericata*, Meig. *Bull. ent. Res.* **26**, 115–122.

Gilbert, F. S. 1986 *Hoverflies*. Cambridge University Press.

Gillett, J. D. 1982 Circulatory and ventilatory movements of the abdomen in mosquitoes. *Proc. R. Soc. Lond.* B **215**, 127–134.

Hassan, A. A. G. 1944 The structure and mechanism of the spiracular regulatory apparatus in adult Diptera and certain other groups of insects. *Trans. R. ent. Soc. Lond.* **94**, 103–153.

Hazelhoff, E. H. 1927 Die Regulierung der Atmung bei Insekten und Spinnen. *Z. vergl. Physiol.* **5**, 179–190.

Heinrich, B. 1976 Heat exchange in relation to blood flow between thorax and abdomen in bumblebees. *J. exp. Biol.* **64**, 561–585.

Heinrich, B. 1981 Temperature regulation during locomotion in insects. In *Locomotion and energetics in arthropods* (ed. C. F. Herreid & C. R. Fourtner), pp. 391–417, New York: Plenum Press.

Heinrich, B. & Mommsen, T. P. 1985 Flight of winter moths near 0° C. *Science, Wash.* **228**, 177–179.

Herford, G. M. 1938 Tracheal pulsation in the flea. *J. exp. Biol.* **15**, 327–338.

Hinton, H. E. 1968 Spiracular gills. *Adv. Insect Physiol.* **5**, 65–161.

Hirth, J. P. & Pound, G. M. 1963 *Condensation and evaporation*. Oxford: Pergamon Press.

Hoffmann, K. H. 1985 Metabolic and enzyme adaptation to temperature. In *Environmental physiology and biochemistry of insects* (ed. K. H. Hoffmann), pp. 1–32. Berlin: Springer-Verlag.

Jones, H. D. 1978 Fluid skeletons in aquatic and terrestrial animals. In *Comparative physiology: water, ions and fluid mechanics* (ed. K. Schmidt-Nielsen, L. Bolis & S. H. P. Maddrell), pp. 267–281. Cambridge University Press.

Jutsum, A. R. & Goldsworthy, G. J. 1976 Fuels for flight in *Locusta*. *J. Insect Physiol.* **22**, 243–249.

Kaars, C. 1981 Insects – spiracle control. In *Locomotion and energetics in arthropods* (ed. C. F. Herreid and C. R. Fourtner), pp. 337–366. New York: Plenum Press.

Kafatos, F. C. 1968 The labial gland: a salt secreting organ of saturniid moths. *J. exp. Biol.* **48**, 435–453.

Kammer, A. & Heinrich, B. 1978 Insect flight metabolism. *Adv. Insect Physiol.* **13**, 133–228.

Kanwisher, J. W. 1966 Tracheal gas dynamics in pupae of the cecropia silkworm. *Biol. Bull. mar. biol. Lab., Woods Hole* **130**, 96–105.

Kaufman, S. E., Kaufman, W. R. & Phillips, J. E. 1982 Mechanism and characteristics of coxal fluid excretion in the argasid tick *Ornithodorus moubata*. *J. exp. Biol.* **98**, 343–352.

Keister, M. & Buck, J. 1974 Respiration: some exogenous and endogenous effects on rate of respiration. In *The physiology of Insecta VI* (ed. M. Rockstein), pp. 470–509. New York: Academic Press.

Kennedy, J. S. 1975 Insect dispersal. In *Insects, science and society* (ed. D. Pimentel), pp. 103–119. New York: Academic Press.

Kestler, P. 1985 Respiration and respiratory water loss. In *Environmental physiology and biochemistry of insects* (ed. K. H. Hoffmann), pp. 137–183. Berlin: Springer-Verlag.

Kingsolver, J. G. & Koehl, M. A. R. 1985 Aerodynamics, thermoregulation, and the evolution of insect wings: differential scaling and evolutionary change. *Evolution* **39**, 488–504.

Kirk, W. D. J. 1983 The tracheation of the wings of adult Lepidoptera. *J. Zool.* **199**, 385–393.

Knülle, W. 1967 Physiological properties and biological implications of the water vapour sorption mechanism in larvae of the oriental rat flea, *Xenopsylla cheopis* (Roths.) *J. Insect Physiol.* **13**, 333–357.

Krasfur, E. S. 1971 Influence of age and water balance on spiracular behavior in *Aedes* mosquitoes. *Ann. ent. Soc. Amer.* **64**, 97–102.

Krasfur, E. S., Willman, J. R., Graham, C. L. & Williams, R. E. 1970 Observations on spiracular behavior in *Aedes* mosquitoes. *Ann. ent. Soc. Amer.* **63**, 684–691.

Krogh, A. 1943 Some experiments on the osmoregulation and respiration of *Eristalis* larvae. *Saertr. Ent. Medd.* **23**, 49–65.

Krogh, A. & Zeuthen, E. 1941 The mechanism of flight preparation in some insects. *J. exp. Biol.* **18**, 1–10.

Lees, A. D. 1946*a* The water balance in *Ixodes ricinus* L. and certain other species of ticks. *Parasitology* **37**, 1–20.

Lees, A. D. 1946*b* Chloride regulation and the function of the coxal glands in ticks. *Parasitology* **37**, 172–184.

Louw, G. N., Nicolson, S. W. & Seely, M. K. 1986 Respiration beneath desert sand: carbon dioxide diffusion and respiratory patterns in a tenebrionid beetle. *J. exp. Biol.* **120**, 443–447.

Loveridge, J. P. 1968 The control of water loss in *Locusta migratoria migratorioides* R. & F. II. Water loss through the spiracles. *J. exp. Biol.* **49**, 15–29.

Loveridge, J. P. 1980 Cuticular water relations techniques. In *Cuticle techniques in arthropods* (ed. T. A. Miller), pp. 301–366. New York: Springer-Verlag.

McCutcheon, F. H. 1940 The respiratory mechanism in the grasshopper. *Ann. ent. Soc. Amer.* **33**, 35–55.

Machin, J. 1978 Water uptake by *Tenebrio*: a new approach to studying the phenomenon. In *Comparative physiology; water, ions and fluid mechanics* (ed. K. Schmidt-Nielsen, L. Bolis & S. H. P. Maddrell), pp. 67–77. Cambridge University Press.

Machin, J., O'Donnell, M. J. & Coutchie, P. A. 1982 Mechanisms of water vapour absorption in insects. *J. exp. Zool.* **222**, 309–320.

Maddrell, S. H. P. 1971 The mechanisms of insect excretory systems. *Adv. Insect. Physiol.* **8**, 199–331.

Marshall, J. F. 1938 *The British mosquitoes*. London: British Museum.

Mellanby, K. 1934 The site of loss of water from insects. *Proc. R. Soc. Lond.* B **116**, 139–149.

Miller, P. L. 1964 Factors altering spiracle control in adult dragonflies: water balance. *J. exp. Biol.* **41**, 331–343.

Miller, P. L. 1974 Respiration – aerial gas transport. In *The physiology of Insecta VI*, 2nd edn (ed. M. Rockstein), pp. 346–402. New York: Academic Press.

Miller, P. L. 1981 Ventilation in active and inactive insects. In *Locomotion and energetics in arthropods* (ed. C. F. Herreid & C. R. Fourtner), pp. 367–390. New York: Plenum Press.

Nicolson, S. W. & Louw, G. N. 1982 Simultaneous measurement of evaporative water loss, oxygen consumption, and thoracic temperature during flight in a carpenter bee. *J. exp. Zool.* **222**, 287–296.

Nicolson, S. W., Louw, G. N. & Edney, E. B. 1984 Use of a ventilated capsule and tritiated water to measure evaporative water losses in a tenebrionid beetle. *J. exp. Biol.* **108**, 477–481.

Noble-Nesbitt, J. 1969 Water balance in the firebrat, *Thermobia domestica* (Packard). Exchanges of water with the atmosphere. *J. exp. Biol.* **50**, 745–769.

Noble-Nesbitt, J. 1970 Water balance in the firbrat, *Thermobia domestica* (Packard). The site of uptake of water from the atmosphere. *J. exp. Biol.* **52**, 193–200.

Noble-Nesbitt, J. 1975 Reversible arrest of uptake of water from subsaturated atmospheres by the firebrat, *Thermobia domestica* (Packard). *J. exp. Biol.* **62**, 657–669.

Noble-Nesbitt, J. 1977 Active transport of water vapour. In *Transport of ions and water in animals* (ed. B. L. Gupta, R. B. Morton, J. L. Oschman & B. J. Wall), pp. 571–597. London: Academic Press.

Noble-Nesbitt, J. 1978 Absorption of water vapour by *Thermobia domestica* and other insects. In *Comparative physiology: water, ions and fluid mechanics* (ed. K. Schmidt-Nielsen, L. Bolis & S. H. P. Maddrell), pp. 53–66. Cambridge University Press.

Noirot, C. & Noirot-Timothée, C. 1971*a* Ultrastructure du proctodeum chez le Thysanoure *Lepismatodes inquilinus* Newman (= *Thermobia domestica* Packard) I. La région antérieure (iléon et rectum). *J. Ultrastruct. Res.* **37**, 119–137.

Noirot, C. & Noirot-Timothée, C. 1971*b* Ultrastructure du proctodeum chez le Thysanoure *Lepismodes inquilinus* (= *Thermobia domestica* Packard) II. Le sac anal. *J. Ultrastruct. Res.* **37**, 335–350.

O'Donnell, M. J. 1982 Water vapour absorption by the desert burrowing cockroach, *Arenivaga investigata*: evidence against a solute dependent mechanism. *J. exp. Biol.* **96**, 251–262.

Okasha, A. Y. K. 1971 Water relations in an insect, *Thermobia domestica* I. Water uptake from subsaturated atmospheres as a means of volume regulation. *J. exp. Biol.* **55**, 435–448.

Parry, D. A. 1983 Labial extension in the dragonfly larva *Anax imperator*. *J. exp. Biol.* **107**, 495–499.

Parry, D. A. & Brown, R. H. J. 1959 The hydraulic mechanism of the spider leg. *J. exp. Biol.* **36**, 423–433.

Phillips, J. E. & Bradley, T. J. 1977 Osmotic and ionic regulation in saline-water mosquito larvae. In *Transport of ions and water in animals* (ed. B. L. Gupta, R. B. Moreton, J. L. Oschman & B. J. Wall), pp. 709–734. London: Academic Press.

Pivnick, K. A. & McNeil, J. N. 1985 Effects of nectar concentration on butterfly feeding: measured feeding rates for *Thymelicus lineola* (Lepidoptera: Hesperiidae) and a general feeding model for adult Lepidoptera. *Oecologia* **66**, 226–237.

Ramsay, J. A. 1935 The evaporation of water from the cockroach. *J. exp. Biol.* **12**, 373–383.

Rudolph, D. & Knülle, W. 1978 Uptake of water vapour from the air: process, site and mechanism in ticks. In *Comparative physiology: water, ions and fluid mechanics* (ed. K. Schmidt-Nielsen, L. Bolis & S. H. P. Maddrell), pp. 97–113. Cambridge University Press.

Rudolph, D. & Knülle, W. 1982 Novel uptake systems for atmospheric water vapour among insects. *J. exp. Zool.* **222**, 321–333.

Sharif, M. 1937 On the internal anatomy of the larva of the rat-flea *Nosopsyllus fasciatus* (Bosc). *Phil. Trans. R. Soc. Lond.* B **227**, 465–538.

Slobodchikoff, C. N. & Wismann, K. 1981 A function of the subelytral chamber of tenebrionid beetles. *J. exp. Biol.* **90**, 109–114.

Snodgrass, R. E. 1956 *Anatomy of the honey bee.* London: Constable & Co.

Stobbart, R. H. & Shaw, J. 1974 Salt and water balance; excretion. In *The physiology of Insecta V* (ed. M. Rockstein), pp. 362–446. New York: Academic Press.

Tanaka, Y. & Hisada, M. 1980 The hydraulic mechanism of the predatory strike in dragonfly larvae. *J. exp. Biol.* **88**, 1–19.

Thorpe, W. H. 1930 The biology of the petroleum fly (*Psilopa petrolii* Coq.). *Trans. R. ent. soc. Lond.* **78**, 331–343.

Tonapi, G. T. 1956 A comparative study of spiracular structure and mechanisms in some Hymenoptera. *Trans. R. ent. Soc. Lond.* **110**, 489–520.

Treherne, J. E. & Willmer, P. G. 1975 Hormonal control of integumentary water-loss: evidence for a novel neuroendocrine system in an insect (*Periplaneta americana*). *J. exp. Biol.* **63**, 143–159.

Unwin, D. M. & Corbet, S. A. 1984 Wingbeat frequency, temperature and body size in bees and flies. *Ecol. Ent.* **9**, 115–121.

Wall, B. J. & Oschman, J. L. 1970 Water and solute uptake by rectal pads of *Periplaneta americana*. *Am. J. Physiol.* **218**, 1208–1215.

Wasserthal, L. T. 1975 The role of butterfly wings in regulation of body temperature. *J. Insect Physiol.* **21**, 1921–1930.

Wasserthal, L. T. 1980 Oscillating haemolymph 'circulation' in the butterfly *Papilio machaon* L. revealed by contact thermography and photocell measurements. *J. comp. Physiol* B **139**, 145–163.

Wasserthal, L. T. 1981 Oscillating haemolymph 'circulation' and discontinuous tracheal ventilation in the giant silkmoth *Attacus atlas* L. *J. comp. Physiol.* B **145**, 1–15.

Wasserthal, L. T. 1982*a* Antagonism between haemolymph transport and tracheal ventilation in an insect wing (*Attacus atlas* L.). A disproof of the generalized model of insect wing circulation. *J. comp. Physiol.* B **147**, 27–40.

Wasserthal, L. T. 1982*b* Wechselseitige funktionelle und strukturelle Anpassungen von Kreislauf- und Tracheensystem bei adulten Insekten. *Verh. dt. zool. Ges.* **1982**, 105–116.

Watts, D. T. 1951 Intratracheal pressure in insect respiration. *Ann. ent. Soc. Amer.* **44**, 527–538.

Weis-Fogh, T. 1967 Respiration and tracheal ventilation in locusts and other flying insects. *J. exp. Biol.* **47**, 561–587.

Wharton, G. W. 1985 Water balance in insects. In *Comprehensive insect physiology, biochemistry and pharmacology vol. 4* (ed. G. A. Kerkut & L. I. Gilbert), pp. 565–601. Oxford: Pergamon Press.

Wharton, G. W. & Devine, T. L. 1968 Exchange of water between a mite, *Laelaps echidnina*, and the surrounding air under equilibrium conditions. *J. Insect Physiol.* **14**, 1303–1318.

Wharton, G. W. & Richards, A. G. 1978 Water vapour exchange kinetics in insects and acarines. *A. Rev. Ent.* **23**, 309–328.

Wigglesworth, V. B. 1935 The regulation of respiration in the flea, *Xenopsylla cheopis* Roths. (Pulicidae). *Proc. R. Soc. Lond.* B **118**, 397–419.

Wigglesworth, V. B. 1972 *The principles of insect physiology*. London: Chapman & Hall.

Wigglesworth, V. B. 1982 The physiology of insect tracheoles. *Adv. Insect Physiol.* **17**, 85–148.

Wigglesworth, V. B. & Lee, W. M. 1982 The supply of oxygen to the flight muscles of insects: a theory of tracheole physiology. *Tissue Cell* **14**, 501–518.

Williams, R. T. 1971 *In vitro* studies on the environmental biology of *Goniodes colchici* (Denny) (Mallophaga: Ischnocera). III. The effects of temperature and humidity on the uptake of water vapour. *J. exp. Biol.* **55**, 553–568.

Willmer, P. G. 1983 Thermal constraints on activity patterns in nectar-feeding insects. *Ecol. Ent.* **8**, 455–469.

Wootton, R. J. 1976 General discussion. In *Insect flight* (ed. R. C. Rainey) (*Symp. R. ent. Soc. Lond.* **7**, pp. 235–254. Oxford: Blackwell Scientific Publications.