Abstract

The results of a long-established investigation into pupal transpiration are used as a rudimentary data set. These data are then generalised to all temperatures and humidities by invoking the property of multiplicative separability, as well as by converting established relationships in terms of constant humidity at fixed temperature, to alternatives in terms of a calculated, water loss rate. In this way a formulation which is a series of very simple, first order, ordinary differential equations is devised. The model is extended to include a variety of Glossina species using their relative surface areas, their relative pupal and puparial loss rates and their different 4th instar excretions. The resulting computational model calculates total, pupal water loss, consequent mortality and emergence. Remaining fat reserves are a more tenuous result.

The model suggests that, while conventional wisdom is often correct in dismissing variability in transpiration-related pupal mortality as insignificant, the effects of transpiration can be profound under adverse conditions and for some species, in general. The model demonstrates how two gender effects, the more significant one at the drier extremes of tsetse fly habitat, might arise.

Keywords: pupal water loss; transpiration; dehydration; mortality; emergence; tsetse; Glossina morsitans; Westwood; trypanosomiasis; gambiense; rhodesiense; sleeping sickness; diptera; glossinidae.

1 Introduction

Early stage mortality is considered to be, by far, the most significant effect in any model of tsetse population dynamics (HARGROVE [5]) and pupal dehydration appears to represent the
most challenging aspect of modelling it. The implications of pupal dehydration are far greater
than pupal emergence and mortality alone. Water loss continues after eclosion up until the
moment the teneral has its first meal. To give some idea of relative importance, it can be
argued that, while teneral water loss rates are generally 20 times puparial rates and 100 times
pupal rates (comparing Bursell [1] with Bursell [2] data), puparial rates generally prevail
6 times longer and pupal rates 24 times longer than teneral rates. Thus, any teneral that dies
of dehydration could be said to be, at very least, 35% as likely to have died as a result of
pupal water loss. If it is further specified that the teneral was of average age, the figure is
closer to 51%. Water loss during the pupal phase can decide the fate of the teneral. Combined
dehydration and fat loss are thought to culminate in massive teneral mortality. Pupal and teneral
mortality rates are crucial in deciding the viability of any Tsetse population. The ultimate effect
of cumulative water loss on a given cohort is therefore likely to be best assessed in terms of
the proportion which have sufficient reserves to achieve their first feed. The vastly different
dynamics of water loss during the pupal and teneral phases, however, afford pupal water loss
the status of a topic in its own right.

This work is almost exclusively based on the findings of one experimentalist with all the haz-
ards implied. In 1958, the late E. Bursell published the results of his experiments on pupal
water loss. Today, in an age of mainstream computing, that work turns out to be a somewhat
tantalizing, scientific riddle. As one might imagine, Bursell’s results are not of much use in the
form in which they were presented. Most of the work was carried out for steady humidities at
24.7°C. The main challenge to exploiting it for the purposes of a computational model, lies in
generalising the results to all temperatures and humidities. That challenge could be said to be
in three, very specific respects: A function for transpiration, the historical conditioning of sensu
strictu pupal transpiration, then linking water loss to observed pupal emergence. Two further
obstacles arise in the form of, firstly, extending the Glossina morsitans–based model to the rest
of the Glossina genus and, secondly, resolving the dependence of emergence on humidity.

The transpiration data were assigned to one of three categories for the purposes of this work:
Temperature dependent data, humidity dependent data and time dependent data. One observes
a certain amount of corroboration between points on the respective curves. Some of this cor-
roboration is demanded, for example, at intersections, however, other of it comes as a pleasant
surprise. The time dependent data is a case in point. Time dependent transpiration would
appear to be nothing more than an alternation between pupal and puparial rates. The final for-
mulation, hence solution to the problem, is predicated on five major assumptions. In addition
to the assumptions explicitly stated and explored, two others are taken for granted. The first
is that it is assumed that Bursell [1] is comprehensive, to the extent that it encapsulates all
salient aspects of pupal water loss. The second is that there is no transpirational water loss at
dewpoint. The problem is then reduced to a series of first order, ordinary differential equations
for water loss.

Although these equations are extremely simple, they are both numerous and voluminous.
The relevant domains of applicability are also non–trivial. This renders preferred integra-
tion schemes, such as the fourth order accurate Runge–Kutta–Fehlberg (R–K–F–4–5) method
slightly impractical. Since the problem is not intractably large, expedience takes precedence
over taste and the more pedestrian Euler’s method is the preferred integration technique. The re-
resulting problem becomes a computational one, rather than a mathematical one. A least squares fit, Newton’s method and a half-interval search are the only other techniques employed, the mathematics in the model being nothing more than utility.

This model is an experimental model. “Experimental” in the sense that is based on data gleaned mostly from pre–1960s–published graphs and it relies almost exclusively on the work of one experimentalist. It assumes that issues such as inferior quality pupae, differing puparial durations and the shortage of statistically significant data can be rectified at a later stage. Extending a *G. Morsitans*–based model to other species is work that can best be described as exploratory. The results at the end make it an interesting and justifiable exercise, nonetheless.

## 2 Generalising Scant Transpiration Data to a Function of Variable Humidity and Temperature

**Burssel** [1] obtained one set of data points for variable temperature (at 0% r.h.), one for variable humidity (at 24.7 ± 3°C) and another for temporal dependence (at 0% r.h. and 24.7 ± 3°C), during his investigations into pupal water loss. Yet a fourth set of data points can be inferred by reason. One expects no transpirational water loss at dewpoint, regardless of the temperature. Although of some assistance, the challenge, nonetheless, remains: How does one generalise these data to all temperatures and humidities? Fortunately, enough of the aforementioned data exist to suggest that any transpiration function is not only continuous, it is also surprisingly simple and smooth; monotonic, in fact.

**Assumption 1** Transpiration rate is a multiplicatively, separable function of humidity and temperature. Put succinctly, if \( \frac{dk}{dt} \) is the transpiration rate, then there exist two functions \( \phi \) and \( \theta \), dependent exclusively on humidity and temperature respectively, so that

\[
\frac{dk}{dt}(h, T) = \phi(h) \theta(T),
\]

in which \( h \) denotes humidity and \( T \), the temperature.

Just how reasonable is this assumption? Certainly it is consistent with, and replicates, the fourth, inferred set of data points entertained above. The perceived wisdom is that the region of interest is between 16°C and 32°C (due, in part, to other causes of mortality). For the “H” of data which exists across the humidity–temperature domain one reasonably expects rates to be bounded by the wet and dry end data, furthermore, to be close to monotonic. One would also expect any unusual, capricious behaviour, or even failure in the waterproofing, to manifest itself in dry air. The dry–air, temperature–dependent data set is, fortunately, reasonably complete and suggestive of behaviour which is smooth, monotonic and simple (pure exponential, in this case). Thus, in the very likely event that water loss rates are not multiplicatively separable, multiplicative seperability should not be a bad substitute.
Of course, one can never be sure in these matters. Anything is possible. As much as someone who models with data in the ideal format of a grid is ultimately ignorant of the behaviour between grid points, one is faced here with the same possibility of some magic combination of humidity and temperature. One simply doesn’t know; one can only surmise. Engineers make the same assumption under what are sometimes, seemingly, a lot less favourable circumstances. Their justification? It works.

The multiplicative separability assumption fulfills a secondary purpose in that it facilitates the following legerdemain

\[ \frac{dk}{dt}(w, h, T) = \frac{dk}{dt}(w, h, 24.7) \frac{\theta(T)}{\theta(24.7)}, \]

the need for which will become clear further on (\( w \) is a total historical water loss).

### 2.1 The Dependence of Transpiration on Temperature

Two types of transpirational temperature dependence are recognised in keeping with the multiplicative separability assumption. The first is a puparial type and the second is a pupal type. Both are exponential in nature.

#### 2.1.1 For the Puparium

Certainly so far as transpiration rates are concerned, for the puparium it is a case of the worst first. Puparial transpiration rates oscillate wildly over time and a fairly substantial difference in data which should corroborate is documented. An average of the relevant data points from BURSELL [1] Figures 2a, 2b, 3 and 8a (those at 0% r.h. and 24.7\( ^\circ \)C) were accordingly used to adjust an exponential fit to the Figure 8a data upward. The basis for this decision was threefold. Firstly, the Figure 8a data were read from a logarithmic curve with a consequently greater, implied possibility of error. Secondly, the humidity data were more comprehensively presented. Thirdly, the study was overwhelmingly an in-depth study of the effects of humidity, strongly suggestive of an overall greater attention to detail and accuracy pertaining to humidity dependence. The following function was the result,

\[ \theta_{\text{puparium}}(T) = e^{0.110268T - 9.92201} + 0.000354783, \]  

the units of which are \( G. \text{ morsitans} \), initial pupal masses per hour. The asymptotic standard errors\(^1\) in fitting the constants for the exponential power were 6.8% and 3.32% respectively. The sum of squares of residuals\(^1\) was 2.98448 \times 10^{-7}.

\(^1\)It is for consistency with this information that no attempt to guess the number of significant figures has been made.
Figure 1: The fit to the Bursell Figure 8a data were adjusted upward.

Of course, one might just as well have used the aforementioned graphs to argue the case for an upward adjustment of 0.00039619. There are many alternatives, however, a decision had to be made and so ‘modeller’s licence’ was invoked to make the choice which best takes cognizance of the, as yet unused, BURSELL Figure 1 data.

2.1.2 For the Pupa

Relevant data points from BURSELL Figures 5b and 6 (those at 0% r.h. and 24.7°C) were added to the Figure 8b data of the same author. The following fit was obtained,

\[ \theta_{\text{pupa}}(T) = e^{0.161691 T - 12.9591}, \]  

the units of which are \( G. morsitans \), initial pupal masses per hour. The asymptotic standard errors\(^1\) in fitting the above constants were 4.597% and 2.651% respectively. The sum of squares of residuals\(^1\) was 3.62324 \( \times 10^{-8} \).

Note that, strictly speaking, the BURSELL Figure 8a data only pertains to the first day of the puparial duration. This will be of relevance in devising a temporal dependence.
2.2 The Dependence of Transpiration on Humidity

Two basic types of transpirational humidity dependence are recognised in keeping with the multiplicative separability assumption. The first is a puparial type and the second is a pupal type. Both are dimensionless.

2.2.1 For the Puparium

A cursory inspection of BURSELL [1] Figures 2a and 2b leads to the deduction that

\[ \phi_{\text{puparium}}(h) = \frac{100 - h}{100}. \] (4)

The dependence of transpiration on humidity is linear.

Figure 2: The fit to the Bursell Figures 8b, 5 and 6 data.
2.2.2 For the Pupa

Pupal transpiration is not as straightforward. While the above relation may prevail during the initial transition down to pupal rates, one dependent on both total historical water loss and humidity is ultimately required. Historical conditioning, what one might term ‘drought hardening’, alternatively depletion, is a phenomenon which pertains to Tsetse pupae. During the sensu strictu pupal phase, transpiration becomes conditioned by the temperature and humidity which prevailed during the early stages (3rd and 4th instars inclusive). Present transpiration is conditioned by the recent past, in addition to the prevailing humidity and temperature.

Relevant data is that published in Figures 5a, 5b and 6 of BURSELL [1]. While it was, no doubt, acquired with a different purpose to the present one in mind and certainly proves a point, it is, of little use as presented. The problem is that historical humidities are steady, furthermore, the data were obtained at 24.7°C.

**Assumption 2** *The transpiration rate, conditioned by a given historical water loss, is the same as the transpiration rate conditioned by an historically steady humidity, at 24.7°C, which produced an equivalent total water loss.*

In other words, a conversion of the independent variable, historically–steady–humidity–at–24.7°C, to an associated total water loss is inferred. Transpiration can then be re–expressed as a function of historical water loss. An historical conditioning of the pupa which is dependent on historically–non–steady variables is devised in this way. How reasonable is the assumption? Do different histories in temperature and humidity, which produce the same water loss, imply the same historical conditioning? If not, there are additional historical effects that have never been detected.

The BURSELL [1] Figures 5a, 5b and 6 data can be interpreted as transections through a surface which intersect at their ends, once their dependence on humidity has been converted to one of total historical water loss. They suggest a very simple surface, one which appears to be of no higher order than bi–quadratic, by inspection. It was therefore decided to fit a bi–quadratic surface to the historically conditioned transpiration data, that is

\[
\frac{dk}{dt_{\text{pupa}}} (w, h, 24.7) = c_1 + c_2 h + c_3 w + c_4 w h + c_5 h^2 + c_6 w^2,
\]

using the method of least squares, ‘on the fly’ so–to–speak. The results were pleasing in that the surfaces retained their fundamental character, even for fictitious, negatively–large humidities, the importance of which will become apparent further on.
Figure 3: The hourly transpiration rate as a function of humidity and water lost during the first 8/30 of the puparial duration (for *G. morsitans*).

The surface is, nonetheless, a surface of transpiration when, instead, the humidity dependence is sought. The following legerdemain

\[ \phi_{\text{pupa}}(w, h) = \frac{d k}{d t}_{\text{pupa}}(w, h, 24.7) \]

\[ \theta_{\text{pupa}}(24.7) \]  

is based on the multiplicative separability assumption. Thus, the humidity dependence

\[ \phi_{\text{pupa}}(w, h) = \frac{c_1 + c_2 h + c_3 w + c_4 w h + c_5 h^2 + c_6 w^2}{\theta_{\text{pupa}}(24.7)} \]

is obtained.

### 3 The Dependence of Transpiration on Time

Time dependent transpiration would appear to be nothing more than an alternation between pupal and puparial rates. Only the following stages of the puparial duration, \( \tau \), were deemed
Pupal Water Loss in *Glossina*

Worthy of any time–dependent modelling, the vagaries of which were entirely reduced to visually fitting four straight lines to the as–yet–unused BURSELL [1] Figure 1 data.

**The Period \( \frac{4}{30} \tau \) to \( \frac{6}{30} \tau \)**

During this period there is an adjustment from the puparial rate down to the pupal rate so that the total transpiration rate can be approximated as

\[
\frac{dk}{dt} = \frac{dk}{dt_{\text{puparium}}} - \frac{27}{31} \left( \frac{t - \frac{4}{30} \tau}{\frac{4}{30} \tau} \right) \left( \frac{dk}{dt_{\text{puparium}}} - \frac{dk'}{dt_{\text{pupa}}} \right),
\]

in which \( t \) is time,

\[
\frac{dk}{dt_{\text{puparium}}} = \phi_{\text{puparium}}(h)\theta_{\text{puparium}}(T) \quad \text{and} \quad \frac{dk'}{dt_{\text{pupa}}} = \phi_{\text{puparium}}(h)\theta_{\text{pupa}}(T),
\]

\( \frac{dk'}{dt_{\text{pupa}}} \) being a temporary, or transitional transpiration rate; one defined shortly prior to that for which the dependence on historical water loss is known.

**The Period \( \frac{6}{30} \tau \) to \( \frac{8}{30} \tau \)**

This period represents final adjustment down to the pupal rate. The equation

\[
\frac{dk}{dt} = \frac{dk}{dt_{\text{puparium}}} - \frac{27}{31} \left( \frac{dk}{dt_{\text{puparium}}} - \frac{dk'}{dt_{\text{pupa}}} \right) - \frac{3}{31} \left( \frac{t - \frac{6}{30} \tau}{\frac{6}{30} \tau} \right) \left( \frac{dk}{dt_{\text{puparium}}} - \frac{dk'}{dt_{\text{pupa}}} \right)
\]

was used.

**The Period \( \frac{8}{30} \tau \) to \( \frac{25}{30} \tau \)**

Transpiration during this phase is predominantly at the pupal rate. A small component of loss at puparial–rates increases linearly with time. The resulting combination was deemed to be

\[
\frac{dk}{dt} = \frac{dk}{dt_{\text{pupa}}} + \frac{1}{30} \left( \frac{25}{30} \tau - \frac{8}{30} \tau \right) \left( \frac{dk}{dt_{\text{puparium}}} - \frac{dk}{dt_{\text{pupa}}} \right),
\]

in which

\[
\frac{dk}{dt_{\text{pupa}}} = \frac{\frac{dk}{dt}(w, h, 24.7)\theta_{\text{pupa}}(T)}{\theta_{\text{pupa}}(24.7)},
\]

based on equation 5.
The Period $\frac{25}{30} \tau$ to $\frac{29}{30} \tau$

Transpiration begins its return to puparial rates during the pharate adult phase and is modelled by

$$\frac{dk}{dt} = \frac{dk}{dt}_{pupa} + \frac{1}{30} \left( \frac{dk}{dt}_{puparium} - \frac{dk}{dt}_{pupa} \right) + \frac{7}{30} \left( t - \frac{25}{30} \tau \right) \left( \frac{dk}{dt}_{puparium} - \frac{dk}{dt}_{pupa} \right) + \frac{7}{30} \left( t - \frac{25}{30} \tau \right) \left( \frac{dk}{dt}_{puparium} - \frac{dk}{dt}_{pupa} \right)$$

(10)
in this work.

4 Extending the Model to Other Species

It is generally suspected that the *Glossina* genus derives from a common, tropical, rain–forest dwelling ancestor, adjusted to moist, warm climates. One might therefore also suspect that all tsetse species actively pursue a strategy to minimise water loss for the majority of modern habitats and have hydrational mechanisms preventative of desiccation. It is generally accepted that most of the genus is not well adapted to arid environments GLASGOW [4]. The challenge to pupae, indeed the major threat, is dehydration.

**Assumption 3** The hydrational mechanisms and water management strategies of the majority of Tsetse fly species differ only with respect to relative pupal surface area, relative puparial loss rates, relative pupal loss rates, the different amounts excreted during the 4th instar and initial reserves.

Water loss rates for the puparium and pupa, $p_{puparium}$ and $p_{pupa}$, respectively, have been measured for a number of species and are tabulated in BURSELL [1]. Permeability is dependent on pressure and is quoted in units of mg h$^{-1}$cm$^{-2}$(mm Hg)$^{-1}$. No variation with pronounced variation in temperature and humidity is indicated and it is of some comfort that the conversion of the *G. morsitans* model to other species involves relative rates.

Surface area data is likewise available. The same surface area is used for both the puparium and pupa in this work, the justification being that the puparial exuviae render the puparium marginally bigger while the pupal surface is not as regular.

4.1 For the Puparium

A dimensionless, species conversion factor for puparial transpiration rates can be defined as follows

$$\delta_{puparium} = \frac{p_{puparium}}{p_{morsitans puparium}} \times \frac{s_{species}}{s_{morsitans}}$$
Pupal Water Loss in *Glossina* in which \( p_{\text{puparium}} \) is the rate of water loss for the species in question, \( p_{\text{morsitans puparium}} \) is the equivalent water loss for *G. morsitans*, \( s_{\text{species}} \) is the puparial surface area for the species in question and \( s_{\text{morsitans}} \) is the equivalent, *G. morsitans* surface area. This factor enables the puparial transpiration rate for another species to be calculated from *G. morsitans* values. Note that the unit is still in *G. morsitans* initial pupal masses (31mg) per hour. Actual values of \( \delta_{\text{puparium}} \) for ten different species are tabulated in Table 1.

| Group | Species           | \( \delta_{\text{puparium}} \) | \( \delta_{\text{pupa}} \) (for minima) | \( \delta_{\text{pupa}} \) (for maxima) |
|-------|-------------------|-------------------------------|----------------------------------|----------------------------------|
| morsitans | austeni           | 1.60                          | 0.712                            | 0.723                            |
| morsitans |                  | 1                             | 1                                | 1                                |
| pallidipes |                 | 1.50                          | 1.24                             | 1.31                             |
| submorsitans |              | 2.44                          | 0.950                            | –                                |
| swynnertoni |                | 0.830                         | 0.869                            | 0.892                            |
| palpalis | palpalis          | 2.54                          | 1.41                             | 1.36                             |
| tachinoides |                 | 1.26                          | 0.743                            | –                                |
| fusca | brevipalpis       | 10.3                          | 4.57                             | 3.06                             |
| fuscipalpis |              | 8.84                          | 4.45                             | 3.16                             |
| longipennis |             | 3.62                          | 2.45                             | 2.30                             |

Table 1: Species conversion factors for the model calculated from data, ultimately sourced from Buxton and Lewis [3], presented in Burrell [1].

### 4.2 For the Pupa

A dimensionless, species conversion factor for pupal transpiration rates can be defined as follows

\[
\delta_{\text{pupa}} = \frac{p_{\text{pupa}}}{p_{\text{morsitans pupa}}} \times \frac{s_{\text{species}}}{s_{\text{morsitans}}}
\]
in which $p_{\text{pupa}}$ is the rate of water loss for the species in question, $P_{\text{morsitans \ pupa}}$ is the equivalent water loss for *G. morsitans*, $s_{\text{species}}$ is the pupal surface area for the species in question and $s_{\text{morsitans}}$ is the equivalent, *G. morsitans* surface area. This factor enables the puparial transpiration rate for another species to be calculated from *G. morsitans* values. Note that the unit is still in *G. morsitans* initial pupal masses (31mg) per hour. Actual values of $\delta_{\text{pupa}}$ for ten different species are tabulated in Table [1].

On the face of it, Assumption 3 is certainly the most tenuous. How valid is it? Does such a simplistic approach work? Very little data is available for other species, however, 3rd instar, puparial loss rates for both *Glossina brevipalpis* and *Glossina palpalis* are known. Conversion of 3rd instar, *G. Morsitans*—model, transpiration rate values to *G. brevipalpis* and *G. palpalis* values, yielded errors of 6% and 10% respectively. The $\delta_{\text{pupa}}$ for pupal maxima and minima in Table [1] are, furthermore, remarkably similar (for all except *G. brevipalpis* and *Glossina fuscipleuris*). This is very encouraging and suggestive of a similar slope in the transpirational time dependence for the various species. The suggestion for *G. brevipalpis* and *G. fuscipleuris*, however, is that Assumption 3 could possibly be captious.

What are the implications? It means that knowing only the appropriate *G. morsitans* $\phi$ and $\theta$ is adequate. The only questions pertaining to species conversion which remain are whether the temporal interplay between pupal and puparial transpiration rates is the same for the entire puparial duration and whether the historical conditioning is the same; not withstanding some difference in strategy a la the difference in 4th instar excretions\(^1\).

## 5 The Resulting Model for Pupal Water Loss

Taking into account one, further formula (that for puparial duration), results in a model.

### 5.1 The Puparial Duration

The puparial duration in days, $\tau$, is calculated according to the formula

$$\tau = \frac{1 + e^{a+bT \kappa}}{\kappa},$$

in which $\kappa = 0.057 \pm 0.001$, $a = 5.5 \pm 0.2$ and $b = -0.25 \pm 0.01$, for females and $\kappa = 0.053 \pm 0.001$, $a = 5.3 \pm 0.2$ and $b = -0.24 \pm 0.01$, for males (PHelps and BURROWS [2] modified by HARGROVE [6]). The puparial durations of all species, with the exception of *G. brevipalpis*, are thought to lie within 10% of the value predicted by this formula PARKER [8]. *G. brevipalpis* takes a little longer.

Newton’s method is used to solve for a puparial duration based on the daily average, which is, of course, dependent on itself. The same applies for the various fractions of puparial duration.

\(^1\) Although, in that case, the associated water loss is too small to be of any real consequence.
For this reason the notation \( \tau_{30} \) is adopted, where

\[
\tau_{30} \equiv \frac{1}{\tau_{30}} \left[ \left( \tau_{30} - \text{floor}\{\tau_{30}\} \right) \frac{r}{30} \tau(T_{\text{day}} \text{floor}\{\tau_{30}\} + 1) + \sum_{i=1}^{\text{floor}\{\tau_{30}\}} \frac{r}{30} \tau(T_{\text{day} i}) \right],
\]

it being the average \( \tau_{30} \times \tau \) over the time interval \((0, \tau_{30}]\), for a specified \( r \).

### 5.2 The Governing Equations

Collecting together all prior observations and thoughts gives rise to the following series of first order, ordinary differential equations. Note that what would otherwise have been a unit of \( 31 \text{mg h}^{-1} \) can be replaced by a dimensionless

\[
\frac{m_{\text{morsitans}}}{m_{\text{species}}} \text{ initial pupal masses} \times \frac{24 \tau_1}{1 \text{ puparial duration}}
\]

for the usual reasons, where \( m_{\text{morsitans}} \) and \( m_{\text{species}} \) are the initial pupal masses of \( G. \text{morsitans} \) (31mg) and the species in question respectively. In other words, a dimensionless rate unit of initial–pupal–masses per puparial–duration is preferred.

#### The Period 0 to \( \tau_{4.30} \)

The water loss rate for the greater part of the third and fourth instars is at the puparial rate (obtained by the substitution of equation 2 and equation 4 into equation 1). Generalising the resulting expression to all species and writing the equation in dimensionless form results in

\[
\frac{d k}{d t} = (e^{0.110268T - 9.92201} + 0.000354783) \frac{100 - h}{100} \frac{P_{\text{puparium}}}{P_{\text{morsitans} \text{ puparium}}} \frac{s_{\text{species}}}{s_{\text{morsitans}}},
\]

in which \( t' \) is a developmental ‘time’, \( t' = \frac{t}{\tau_1} \).

#### The Period \( \tau_{4.30} \) to \( \tau_{6.30} \)

During this period there is an adjustment from the puparial rate down to the pupal rate dictated by equation 7. Generalising equation 7 to all species and writing the equation in dimensionless form results in the expression

\[
\frac{d k}{d t} = \left[ (e^{0.110268T - 9.92201} + 0.000354783) \left( 1 - \frac{27}{31} \left( \frac{t' - \tau_{4.30}}{\tau_{6.30} - \tau_{4.30}} \right) \right) \right] \frac{P_{\text{puparium}}}{P_{\text{morsitans} \text{ puparium}}} \frac{s_{\text{species}}}{s_{\text{morsitans}}},
\]

in which \( t' \) is a developmental ‘time’, \( t' = \frac{t}{\tau_1} \).
The Period $\tau_{830}^{630}$ to $\tau_{830}^{830}$

During this period there is a final adjustment from the puparial rate down to the pupal rate dictated by equation 8. Generalising equation 8 to all species and writing the equation in dimensionless form results in

$$\frac{dk}{dt} = \left[ (e^{0.110268T-9.92201} + 0.000354783) \left( \frac{4}{31} - \frac{3}{31} \left( \frac{t' - \tau_{830}^{630}}{\tau_{830}^{830} - \tau_{830}^{630}} \right) \right) \frac{P_{\text{puparium}}}{P_{\text{morsitans puparium}}} \right. + e^{0.161691T-12.9591} \left( \frac{27}{31} + \frac{3}{31} \left( \frac{t' - \tau_{830}^{630}}{\tau_{830}^{830} - \tau_{830}^{630}} \right) \right) \frac{P_{\text{pupa}}}{P_{\text{morsitans pupa}}} \right] \frac{100 - h}{100} \frac{s_{\text{species}}}{s_{\text{morsitans}}} \left( \tau_{830}^{830} \right) \left( t' - \tau_{830}^{830} \right), \right. (14)$$

Excretion

If water loss is sufficiently low during the first $\frac{8}{30}$ of the puparial duration, cognizance must be taken of the small amount excreted. In this unlikely scenario the formula

$$k = x_2 + \frac{h_{3\text{rd instar}}}{100} (x_1 - x_2)$$

was implemented, for want of any better wisdom. The total water loss during the 3rd and 4th instars, in the event of dewpoint prevailing for the former, is $x_1$. In the event of 0% relative humidity prevailing for the 3rd instar, the amount is $x_2$. The only 4th instar excretion data known to exist is that for G. morsitans, G. palpalis and G. brevipalpis. This lack of information is a minor obstacle as the excretions are generally small and only relevant for humidities close to dewpoint.

The Period $\tau_{830}^{830}$ to $\tau_{2530}^{830}$

Transpiration during this phase is predominantly at the pupal rate. There is also deemed to be a small component of loss at puparial–rates, which increases linearly with time and which is included for good measure. Generalising equation 9 to all species and writing the equation in dimensionless form results in

$$\frac{dk}{dt} = \left[ e^{0.161691(T-24.7)} \left( c_1 + c_2 h + c_3 w + c_4 w h + c_5 w^2 + c_6 w^2 \right) \left( 1 - \frac{1}{30} \left( \frac{t' - \tau_{830}^{2530}}{\tau_{830}^{2530} - \tau_{830}^{830}} \right) \right) \frac{P_{\text{puparium}}}{P_{\text{morsitans puparium}}} \right. + (e^{0.110268T-9.92201} + 0.000354783) \frac{100 - h}{100} \frac{s_{\text{species}}}{s_{\text{morsitans}}} \left( \tau_{2530}^{830} \right) \left( t' - \tau_{2530}^{830} \right), \right. (15)$$
The Period $\tau_{25}^{30}$ to $\tau_{29}^{30}$

Transpiration begins its return to puparial rates during the pharate adult phase. Generalising equation [10] to all species and writing the equation in dimensionless form results in

$$\frac{dk}{dt} = \left[ e^{0.161691(T-24.7)} \left( c_1 + c_2 h + c_3 w + c_4 wh + c_5 h^2 + c_6 w^2 \right) \left( \frac{29}{30} - \frac{7}{30} \left( \frac{t' - \tau_{25}^{30}}{\tau_{29}^{30} - \tau_{25}^{30}} \right) \right) \right] \times \frac{P_{pup} \morsitans \, pupa - P_{pup} \morsitans \, pupa + (e^{0.110268T-9.92201} + 0.000354783) \frac{100-h}{100} \times \left( \frac{1}{30} + \frac{7}{30} \left( \frac{t' - \tau_{25}^{30}}{\tau_{29}^{30} - \tau_{25}^{30}} \right) \right) \frac{P_{pup} \morsitans \, puparium - P_{pup} \morsitans \, puparium}{s_{species}} \right] \frac{s_{morsitans}}{s_{morsitans}}.$$ (16)

The Period $\tau_{29}^{30}$ to $\tau_1$

There is a return to puparial rates shortly before eclosion and equation [12] once again applies.

5.3 Solving the Equations

The above rate formulae constitute a series of first order, ordinary differential equations. One expects the resulting function to be Lipshitz continuous over each of the developmental sub–stages identified, likely even a contraction. While a fourth–order–accurate Runge–Kutta–Fehlberg method (R–K–F–4–5) would normally be the preferred method of integration, the series of equations is voluminous and the relevant domains of applicability are also non–trivial.

Euler’s method is usually considered distasteful from the point of view of its error. The local error per step, of length $\Delta t$, is $O(\Delta t^2)$. Since the required number of steps is proportional to $\frac{1}{\Delta t}$, the global error is $O(\Delta t)$. This is indeed primitive. The method is, nonetheless, considered robust for the type of first order, ordinary differential equation to be solved. The real strength of Euler’s method lies in its robustness at discontinuities and points of non–differentiability. The maximum, additional error introduced at such points is of the same order as the method’s global error (this is easy to see). The same cannot be said for the higher order methods. The use of one or other of the higher order methods is still not precluded in the problem at hand, since the discontinuities and points at which differentiability breaks down are predictable. Using Euler’s method, however, one has one problem to solve, whereas using one of the higher order methods entails solving six, separate problems; each confined to its own respective domain of Lipshitz continuity, scaling etc..

The handicap of a poor error is easily overcome computationally. That is by using a small step length e.g. $\frac{1}{1000}$th of a puparial duration. Two significant figures are all that is sought.
Since the problem is not intractably large, expedience takes precedence over taste and the more pedestrian Euler’s method is considered the appropriate choice.

6 Pupal Emergence and Mortality

Two challenges arise when it comes to pupal emergence: The first is to establish some kind of credible relationship between the numbers of emergent and humidity. The second is, consequently, how to relate emergence to total water loss.

6.1 What is the Relationship Between Pupal Emergence and Humidity?

What does one make of the very rudimentary data in Figure 4? There are insufficient data points for each species to perform any kind of rigorous hypothesis testing.

Figure 4: Emergence data as presented by BURSELL [1]. All are at 24°C, except Tachinoides (30°C).
Since the number of pupae contributing to each data point is so low, neither the law of large numbers can be invoked, nor therefore, the central limit theorem applied. This does, nonetheless, not necessarily preclude the use of the aforementioned in argument. Large numbers of pupae do exist. When doctrinaire methods fail a little thought can still go a long way.

At the simplest level, one would expect each species to be adapted to some ideal humidity for which emergence is optimal. One also expects the individual pupae of each species to exhibit a certain amount of variation about the mean so far as size, reserves, competency of the integuments and so on, is concerned. Some pupae will be slightly bigger, have slightly bigger reserves and more competent integuments. Yet others will be slightly smaller, have slightly smaller reserves and less competent integuments. To be succinct, one expects emergence to be Gaussian.

**Assumption 4** The relationship between pupal emergence and humidity is a Gaussian curve, or a part thereof.

At one extreme, one has environmentally highly specialised species with low hydrational inertia (e.g. *Glossina austeni*\(^1\) and *G. brevipalpis*\(^1\)), for which one expects variation over a small range in conditions to provide adequate data to fit the Gaussian curve.

At the other extreme, species which exhibit massive hydrational inertia exist, such as *G. longipennis* and *G. swynnertoni*. They provide little, or no clue as to the underlying Gaussian relationship between emergence and humidity. The range of conditions, the domain, is not obviously suggestive of an underlying Gaussian emergence curve. All one sees is a very small, consequently flat—in—appearance, sample of the top of the curve. These species ought to have been investigated in terms of water loss rather than humidity. The curves for other species lie between these extremes.

In the wild, there is a compounding factor in that, not only is emergence based on variation within a given species, it is also based on variation within the environment. A whole range of microclimates exist within breeding sites, some of which are compost, rot holes and soil, to name only a few. Seasonal variation is a further compounding factor.

While the focus of this work is desiccation it is of interest to note that emergence also declines at very high humidities. As to whether drowning or some fungus is the desiderate explanation, it can only be speculated.

A chi squared test is not expected to elucidate any more than visual inspection. Despite the impossibility of any rigorous hypothesis testing the author maintains that the asymptotic standard errors obtained in Table 2 make a compelling argument for Assumption 4.

\(^1\) *G. austeni* has low hydrational inertia by virtue of its small size (which implies a high surface area to volume ratio), *G. brevipalpis* has low hydrational inertia due to inferior waterproofing.
Figure 5: Species with low hydrational inertia (e.g. *G. austeni* and *G. brevipalpis*) are good indicators of the underlying Gaussian relationship between emergence and humidity. (Particular attention is drawn to the data for the Brevipalpis fit in Table 2 on page 19.)

Figure 6: Species with high hydrational inertia (e.g. *Glossina longipennis* and *Glossina swynnertoni*) provide little, or no clue as to the underlying Gaussian relationship between emergence and humidity.
Table 2: The percentage emergence, the asymptotic standard errors and the sum of squares of the residuals for the fit in each species.

| group   | species         | percentage emergence          | percentage asymptotic standard error in | sum of squares of residuals |
|---------|-----------------|-------------------------------|----------------------------------------|-----------------------------|
|         |                 | $E(h) = a e^{-\frac{(h-b)^2}{2c}}$ | $a$         | $b$       | $c$       |                               |
| morsitans | austeni        | $101.663e^{-\frac{(h-73.1591)^2}{2\times30.6468^2}}$ | 3.855 | 2.077 | 6.401 | 41.6495 |
| morsitans |                  | $94.4792e^{-\frac{(h-70.6391)^2}{2\times77.34895^2}}$ | 5.177 | 18.45 | 29.07 | 305.227 |
| pallidipes |                | $86.6257e^{-\frac{(h-71.5636)^2}{2\times54.9713^2}}$ | 2.833 | 6.205 | 9.518 | 48.7588 |
| submorsitans |            | $94.5092e^{-\frac{(h-81.1805)^2}{2\times75.4474^2}}$ | 6.524 | 37.45 | 57.03 | 80.4127 |
| swynnertoni |              | $94.0194e^{-\frac{(h-61.4064)^2}{2\times75.2539^2}}$ | 4.343 | 8.65  | 17.19 | 21.3715 |
| palpalis | palpalis       | $95.8732e^{-\frac{(h-78.8419)^2}{2\times23.4835^2}}$ | 13.89 | 5.412 | 23.94 | 725.514 |
| tachinoides |               | $98.8383e^{-\frac{(h-79.6877)^2}{2\times40.8616^2}}$ | 11.02 | 17.66 | 29.46 | 427.406 |
| fusca    | brevipalpis    | $94.0057e^{-\frac{(h-84.0199)^2}{2\times13.6443^2}}$ | 0.5123 | 0.1352 | 0.907  | 0.268286 |
The Issue of Sub–Standard, Laboratory Pupae

In BURSELL [1] it is somewhat heuristically argued that the laboratory pupae in question were too small and that all emergence curves should therefore be displaced 10% to the left (the right in those graphs). An alternative argument based on puparial transpiration and in which the pupa is approximated as a spheroid, is preferred (on page 30 of the addendum). It entertains replacing the emergence function, $E(h)$, with

$$E \left( \frac{h + 3.57}{\sqrt{\frac{100}{90}}} \right)$$  \hspace{1cm} (17)$$

as an alternative.

\[ G. longipennis \] is the single exception (a straight line had to be fitted to the only two data points).
6.2 Survival to Emergence for Historically–Non–Constant Humidities and Temperatures

Problems similar to those encountered for historical water loss, compound matters when it comes to the survival to eclosion for each species. Historical humidities are steady, furthermore, the data were obtained at a constant 24°C.

**Assumption 5** *The pupal emergence for a given water loss, is the same as the pupal emergence for a steady humidity at 24°C, that produced an equivalent total water loss.*

In other words, it is assumed that emergence can be re–expressed in terms of total water loss. Do different histories in temperature and humidity, which produce the same water loss, imply the same pupal emergence, or is the amount of water present at some particular stage more relevant to the pupa’s survival to full term? The simple answer is to refer the reader to the title, although this does somewhat avoid the question.

In practice, it is far easier to convert a total computed water loss to a corresponding steady–humidity–at–24°C\(^1\), instead of the other way around. Either way entertains the possibility of fictitious, or negative, humidities. (There are always those who are apt to find this sort of thing vaguely disturbing, however, it should be pointed out that \(E(h)\) is just a mathematical function and \(h\), a variable. One really needs to think ‘outside the box’ in these matters. What was humidity is now not so much an artefact, just something a little more abstract.)

The results of the water loss algorithm for 24°C and any, given set of steady humidities obviously constitute a monotonic decline. The problem, however, is that the complete algorithm is relatively involved and voluminous. Under these circumstances, practical considerations and not rates of convergence dictate implementation of an 1/2 interval search. (The rate of convergence is not bad in this instance.)

7 Remaining Fat Reserves

Remaining fat reserves are a more tenuous result. Water content stays constant after the 3rd and 4th instars GLASGOW [4]. Although the oxidation of fat for the specific purpose of water production is suspected, it could not be proven at a statistically significant level (BURSELL [1]). The conversion factor (by mass) is given as

\[
\text{fat oxidised} = 1.12 \times \text{water}. 
\]

\(^1\)G. tachinoides data the exception, being at 30°C
Testing the model presents something of a challenge. The emergence data at 24°C, to a certain extent, provides a test for self-consistency. Transecting the following surfaces of emergence at 24°C should come close to replicating the Gaussian curves for emergence, on page 20. “Close”, since the data were adjusted as a consequence of the inferior pupae issue.

Testing for corroboration with observed mortalities in the field is somewhat heuristic. All one can say is that predicted pupal mortalities due to water loss should, logically, never exceed any pupal mortalities observed in the field for similar conditions of humidity and temperature. For example, the computed *G. morsitans* emergence due to water loss is not lower than the 87% obtained by Hargrove and Williams [7] in their Antelope Island mark-recapture experiment.

One set of data on which the model was not based does, however, still remain. That data is the measured initial water reserve for a number of species. It has the makings of a test for consistency with reserves. In a perfect world, the measured, critical water loss contour should correspond to that of this model’s, median or 50% emergence contour. *G. morsitans* is of obvious interest as the species on which the model is based.

Figure 8: Computed pupal emergence (left) and water loss (right) for *G. morsitans*. 
Pupal Water Loss in *Glossina*

Figure 9: Computed pupal emergence (top left) and water loss (top right) for *G. brevipalpis*; computed pupal emergence (bottom left) and water loss (bottom right) for *Glossina pallidipes*. 
Figure 10: Computed pupal emergence (top left) and water loss (top right) for *G. palpalis*; computed pupal emergence (bottom left) and water loss (bottom right) for *G. swynnertoni*. 
The sensitivity of *G. brevipalpis* and *G. palpalis* pupae to dehydration makes these species arguably the most challenging tests, as well as of particular interest to this work. *G. brevipalpis* is, furthermore, of national interest to those who funded this work and *G. palpalis* is known to feed on humans in West Africa (SOLANO [10]), it being a major culprit in the spread of human trypanosomiasis. In both cases, information on the respective 4th instar excretions is available.

The critical water reserve is also known for two other species which are expected to be less challenging as tests and for which *G. morsitans*–type, 4th instar excretions are expected to suffice. The water loss associated with the 4th instar excretions only becomes relevant close to the dew point (a part of the domain in which we have little interest) and it is, furthermore, thought to be too small to be of any real consequence.

|                | *G. brevipalpis* | *G. morsitans* | *G. pallidipes* | *G. palpalis* | *G. swynnertoni* |
|----------------|------------------|----------------|----------------|---------------|-----------------|
| Initial mg     | 18.7             | 8.8            | 10.5           | 7.7           | 8.5             |

Table 3: Initial water reserves after BURSELL [11].

Given these initial water reserves, the position of the critical water loss contour should correspond to that of the median or 50% emergence contour for the model to work (Figures 8 to 10). In this regard, it is worth noting that the *G. morsitans*–based puparial duration used in the model could be as little as 83% of the *G. brevipalpis* puparial duration and the correspondence observed in the Figure 9 result should therefore not be as good as it is.

9 Conclusions

The results are certainly adequate to conclude proof–of–concept for the model (at very least).

High transpiration rates are a consequence of high temperatures and unfavourable humidities. They lead to a dehydration of the tsetse pupa which can be fatal. Although the diametrical opposite is true of transpiration rates at low temperatures, metabolic processes are slowed, the puparial duration becomes too long and the cumulative effect of transpiration can be just as fatal. The pupal development of the tsetse fly may be divided into four successive stages: The third instar, the fourth instar, the sensu strictu pupal stage and the pharate adult. Water loss rates adhere in some semblance to this timetable.

It would appear that the similarities between the various *Glossina* species are better than expected so far as pupal water loss is concerned. The correspondence between actual measured, critical, water losses and water losses calculated based on Assumption 3 is profound in most cases. No discernable error exists for some species e.g. *G. pallidipes* and *G. swynnertoni*. It would therefore appear that most tsetse species behave fairly similarly in the ground, that they actively pursue a strategy to minimise water loss for the majority of modern habitats and have hydrational mechanisms preventative of desiccation.
Figure 11: Computed daily mortality for *G. morsitans* (top left), *G. austeni* (top right), *G. palpalis* (bottom left), *G. brevipalpis* (bottom right).
Figure 12: Computed ratio of female to male emergent for *G. morsitans* (left) and *G. brevipalpis* (right). Note that this is a minimum scenario, owing to the lack of availability of any gender based data on pupal masses and surface areas (these results are based on puparial duration alone).

The *Glossina* genus very likely does derive from a common, tropical, rain–forest dwelling ancestor, adjusted to moist, warm climates and dehydration is a challenge to pupae. The fact that loss rates in BURSELL [1] were originally determined as fractions of initial pupal masses, rather than per unit of surface area, turned out to be a windfall rather than a criticism (defended in BURSELL [2]). The necessary information to convert between the two turns out to facilitate the adaption of the *G. morsitans* model to other species.

A strong school of thought is of the opinion that pupal and teneral mortality due to dehydration are either irrelevant or can be assumed constant. Do daily, pupal mortality and water loss justify this work? A cursory inspection of Figure [1] is suggestive of what the origins of such an argument might be in the case of the Morsitans group, even for *G. austeni*1. Notice, however, that even for a hardy fly such as *G. morsitans*, its prospects deteriorate rapidly once out of favourable habitat. Even for the *morsitans* group, daily pupal mortality is neither linear, nor a function of temperature alone. When it comes to some members of the *fusca* and *palpalis* categories, the situation becomes even more critical.

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1*G. austeni* is thought to have secondarily invaded moist forest areas (it is small, with all the lack of hydational inertia that a high surface area to volume ratio implies).
groups, however, that pupal mortality due to dehydration is both relevant and palpable is beyond contention. The effect of humidity is profound. Humidity defines habitat. This is despite the fact that water loss and any consequent pupal mortality are also very different things (one expects water loss to culminate in, and ultimately take its toll on the teneral).

Two gender selection effects are evident based on puparial duration alone. Under adverse conditions more females than males emerge. A less significant, male–selective phenomenon occurs close to dewpoint. Both phenomena are expected to be enhanced should the heavier female mass and lower relative surface area be taken into account (no data could be found).

The prognosis for the simplistic experimental model would seem to be better than expected (given that issues such as inferior quality pupae, differing puparial durations and the shortage of statistically significant data can be corrected at some stage).

The possibility that plots presented in this work may point to the fact that breeding sites for some species could be predicted to be very much confined in the dry season, cannot be ruled out. These would be obvious places in which to concentrate traps and one immediate application of this work.

10 Acknowledgements

Abdalla Latif and the Onderstepoort Veterinary Institute are thanked for their generosity in co-funding this work. Glyn Vale is thanked for general advice, helpfulness and enthusiasm. The usual friends, Neil Muller and Kevin Colville, are thanked for assistance in the way of technical support.

Although obviously not the original intention, this work also turns out to be something of a tribute to the late E. Bursell. Bursell’s investigation was both comprehensive and enquiring. He asked the right questions and for this we sing his praises.

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Addendum

10.1 The Issue of Sub–Standard Laboratory Pupae

In BURSELL [1] it is somewhat heuristically argued that the laboratory pupae in question were too small and that all emergence curves should therefore be displaced 10% to the left (the right in those graphs). An alternative argument can also be entertained: To bring pupae that are 10% too small up to size would mean multiplying volume by $\frac{100}{90}$, or each dimension by $\sqrt[3]{\frac{100}{90}}$. It would not be unreasonable to assume reserves are volume dependent whereas water loss is dependent on surface area.

Suppose $s$ is the initial starting reserve of the pupa and that $g(T, t)$ is some complicated loss rate function. If emergence is dependent on some critical water loss,

$$s - g(T, t) s (100 - h) = 0,$$

for the larger, wild puparium, one then has

$$\frac{100}{90} s - g(T, t) \left( \frac{100}{90} \right)^{\frac{2}{3}} s (100 - H) = 0,$$

where $H$ is the humidity pertaining to a larger, wild puparium. If equation 18 was satisfied for $h$, then equation 19 will be satisfied for the new humidity, $H$, when

$$(100 - H) = \sqrt[3]{\frac{100}{90}} (100 - h) \Rightarrow H = \sqrt[3]{\frac{100}{90}} h - 3.57.$$

Thus, replacing the argument in the old emergence relation, $E(h)$, with

$$h = \frac{(H + 3.57)}{\sqrt[3]{\frac{100}{90}}}$$

is as good as the new one,

$$E \left( \frac{H + 3.57}{\sqrt[3]{\frac{100}{90}}} \right),$$

so far as puparial transpiration is concerned. Although puparial transpiration rates are of the order of ten times bigger than pupal rates, the sensu strictu pupal period is usually of the order of ten times as long. In other words, the pupal phase is just as relevant. the same reasoning as above can be applied to the historical dependence (the coefficients for equation 6 suggest that historical effects are as important as the prevailing humidity). Dependence on $H$ is quadratic.

Of course, observed emergence is not linearly dependent on humidity, as the relationships depicted in Figure 7 show. If, however, one is talking about the relevance of size to straightforward water loss (and water loss being the predominant determinant of emergence), not variation within the species, one would question a simple, sideways shift of 10%. 

10.2 Does Generalizing the Morsitans Based Model to other Species Work?

On the face of it, Assumption 3 is certainly the most tenuous. How valid is it? Does such a simplistic approach work? Both the examples which follow suggest that the model’s general puparial rate is slightly on the low side for the first few hours, something we already know to be true.

Example 1

Consider the conversion of first day *G. morsitans* transpirational values to *G. brevipalpis*. Then

$$\frac{dk}{dt}(h, T) = \phi_{\text{puparium}}(h) \theta_{\text{puparium}}(T) \delta_{\text{puparium}} = 1.10 \times 10^{-3} \times 10.3 = 11.4 \times 10^{-3} \text{h}^{-1}.$$  

This answer is, of course, in dimensionless, *G. morsitans* pupal masses. To convert to a fraction of *G. brevipalpis* pupal mass h$^{-1}$:

$$11.4 \times 10^{-3} \text{h}^{-1} \times \frac{m_{\text{morsitans}}}{m_{\text{brevipalpis}}} = 11.4 \times 10^{-3} \text{h}^{-1} \times \frac{31}{78} = 4.51 \times 10^{-3} \text{h}^{-1}.$$  

Compare this with the measured value of $4.79 \times 10^{-3} \pm 0.05 \times 10^{-3}$ pupal masses h$^{-1}$ cited in BurSELL [1]. This constitutes a 6% error.

Example 2

Consider the conversion of first day *G. morsitans* transpirational values to *G. palpalis*. Then

$$\frac{dk}{dt}(h, T) = \phi_{\text{puparium}}(h) \theta_{\text{puparium}}(T) \delta_{\text{puparium}} = 1.10 \times 10^{-3} \times 2.54 = 2.80 \times 10^{-3} \text{h}^{-1}.$$  

This answer, again, is in dimensionless, *G. morsitans* pupal masses. To convert to a fraction of *G. palpalis* pupal mass h$^{-1}$:

$$2.80 \times 10^{-3} \text{h}^{-1} \times \frac{m_{\text{morsitans}}}{m_{\text{palpalis}}} = 2.80 \times 10^{-3} \text{h}^{-1} \times \frac{31}{32} = 2.70 \times 10^{-3} \text{h}^{-1}.$$  

Compare this with the measured value of $3 \times 10^{-3} \pm 0.4 \times 10^{-3}$ pupal masses h$^{-1}$ cited in BurSELL [1]. The 10% error is within the measured limits and tolerable by ‘engineering standards’.