**Notes**

**31/05/18**

For personal benefit, read Phelps and Burrows (1969), took data and plotted along with fit from Phelps and Burrows (1969) and from Hargrove (2004). R script doing this is r\_phelps\_data\_fit.R.

Two approaches to modelling – fixed time to pupal emergence or as we did before constant rate of pupal emergence. I already have a delay differential equation model written up that includes temperature-dependent pupal duration and mortality – so going to adapt that first to the climate change model.

**Notes on Phelps and Burrows (1969) paper:  
Phelps and Burrows (1969). Puparial duration in Glossina morsitans Orientalis under conditions of constant temperature**

**Introduction**

Previous investigations confined to 16 – 30 (Potts 1933, Jack 1939, Jackson 1949, Bursell 1960, Glasgow 1963). Lower limit – metabolic activity continues (Bursell 1960; Rajagopal and Bursell 1965) adults do not emerge below 16. For predictions of puparial duration in natural breeding sites, using the relationship between rate of development and temperature, this restricted temperature range is inadequate in Rhodesian winter months when daily mean temperatures of 11 are recorded in puparial sties… The results reported here extend the range of constant temperatures for which rate of development in puparia of Glossina morsitans orientalis Vanderplank is known, to a lower limit of 8o and an upper limit of 32o. Additionally relationship between rate of development and temperature has been examined for both insectary and field populations.

**Methods**

Puparia collected at Lusulu field station established colony in Salisury. Test temperatures using water jacketed incubators… for test temperatures of 8, 10, 12 and 14 batches were held at constant temperatures for 24 hour periods, such periods being alternated between the test temperature and 25o. Knowing the rate of development at 25 and the proportion of the puparial duration spent at each of the alternating temperatures the rate of development at these low test temperatures could be inferred…. Lusulu colony discontinued after two years and a new colony maintained in same way from Kariba. Batches from this colony incubated at test temperatures 16, 20, 25 and 30 and also at 12 alternating with 25 every 24 hrs. Compared development of puparia from field and colony adults. Also compared pupae from females at 20 and 25.

**Results**

Rate of development (**r per day**) has been treated as the **reciprocal of puparial duration** (d days). Thus **values of r at particular test temperatures refer to the mean rate of development** over the puparial duration and make **no account of the variation in rate of development of different stages within the puparium**. Nevertheless, r is an appropriate and simple measure for the purpose of predicting puparial durations.

Table 1 – mean puparial durations and rates of development obtained from the tests of the Lusulu colony.

Table 2 – observed and predicted values of r

It is important to recognise there is considerable variation in duration between individual puparia incubated under identical conditions.

**A logistic curve in the form r = k/(1+e^a+bt) where r is the rate of development at constant temperature t was fitted to the test temperature results from Lusulu colony by the interative procedure of Aitchinson and Silvey (196) for each sex separately. The resulting estimates of k, a and b are given in table 3.**

K - 0.05415 males and 0.05884 females

a – 4.8184 males 4.8829 females

b - -0.2149 males -0.2159 females

Predicted values from these fitted curves are tabulated in Appendix A for the temperature range 8 to 32. T**he calculated curves do not fit the experimental data as well as might be desired outside the range 20 to 30 and the curves shown in Figs 1 and 2 are fitted by eye. The illustrated curves may be useful for experimental purposes at the extremes of the temperature range. The fitted curves have been accepted as adequate for field work where great variation is known to exist between temperature regimes in breeding sites (Jackson and Phelps 1967) even at the same season.**

**GV 29/04/18:**

Find attached the **latest Met data**, completed up to **Oct 2017,** as requested by John. I will add the data for Nov 2017 onward when it becomes clear what can be salvaged for that time onward.

Given that the plan for the proposed latest modelling by the ladies seems to be to recognize that the true temperature experienced by adult flies in their habitat is unlikely to be exactly the same as the screen temperatures, you MIGHT, MAYBE, PERHAPS be interested in the input slots I made to allow for that in my own ClimatChange2017 model. A copy of those slots is on the second sheet of the attached file -- the macros have been deleted from th blue buttons.. The main thing is that I allowed the difference between screen and habitat temperatures to vary according to month of the year, and allowed that in any month the difference might vary according to the max and min temperatures

By the bye, although I allowed for differences between screen and habitat temperatures I did not allow, in the main modelling, for any difference between the mean temperatures ((max+min)/2) in the habitat and pupal sites, This was partly because I was not sure what the difference might be, but mainly because I thought, conveniently, that although the max temp in the pupal sites might be less than in the adult habitat, the min in the pupal sites would probably be higher than experienced by the adults -- so that the mean daily temperature would be much the same for pupae and adults.

**JH:**

Glyn is working on a little update of the temperature data, which he will undoubtedly get to me early next week. And Faikah has made some nice progress with the R script – putting some **stochasticity into the pupal site temperatures.** This is important because we know, from Fido’s work, that there is a **lot of variability in the temperatures that pupae experience**. Will get this updated information to you as soon as I have it.

**JH:**

Here is Faikah’s **R script** for generating the **pupal duration** and **pupa mortality** for a pupa deposited on a day when the **temperature is known for that day and for the sequence of following days** while it is in the ground. The runs are done both for the situation where it is **assumed that the pupa experiences the temperatures** as recorded on the **Stevenson screen** thermometer, **or where we assume that the pupal sites are 3 degrees cooler at 35C**, and the same temperature at 10C, with a linear function between those two points. One can easily change the inputs to change the relationship between screen temperature and pupal site temperature. Faikah is also working on an extension, **where the pupal site temperature will be selected at random from a normal distribution about the mean selected site temperature**. That work is in progress so you should ignore the code in question. Hopefully you can easily apply the R programme to the complete sequence of temperature data provided for you by Glyn.

**JH 26/04/18**

Dear Jennifer

Reference your reply to my last email re the population modelling you confirmed that:

“adult flies emerge at rate 0.03 per day – i.e. with a mean pupal duration of 1/0.03 ~ 33 days”.

In other words, the **pupa duration is considered independent of temperature**. You comment: “Again – identifiability issue – if start adding in more temperature-dependent effects/ parameters and not enough information in the data to separate out what is from what – so why have a more complicated model.”. OK, I hear what you are saying – but I think the bad news is that **making pupal duration a function of temperature is not negotiable**. Making it a constant will cause more trouble than it is worth. More importantly, from our own point of view, we really *must* account for the variation. And if we don’t we will keep getting flak from people like Reviewer 1: moreover, I have to handle his criticism – to wit:

“***Why do the authors not allow for a temperature dependent fertility rate (given that they do allow for a temperature dependent pupal mortality rate)?***”In answering this we could use the argument you have used above re identifiability and the number of parameters – but I don’t think it will wash, and it doesn’t sit well with the rest of the rebuttal I am writing, where I have been able to show that the Reviewer has made some schoolboy-type blunders. That being the case I don’t want us to be seen in the same sort of bad light. So what I think we have to do – *if we can* – is to rejig the model slightly so that we **DO account for the temperature dependent pupal duration**. Then show that this does not affect the conclusions.



**Figure 1 P**redicted pupal duration for pupae experiencing temperatures as record in a Stevenson screen

And the good news is that I CAN see (I think) a fairly easy way of incorporating more realistic values of adult emergence rate into the model: (i) *without* increasing the number of parameters; and, thus, (ii) *without* increasing problems of identifiability. The approach simply follows the same sort of approach that you have already used to include time and temperature pupal *mortality* into the model.

The inclusion of temperature in this case is really quite straightforward – **because Phelps & Burrows (1969) established such a nice relationship between temperature and rates of pupal development. So if we know what the temperatures are on a sequence of days we can predict the progress of pupal development quite nicely.** No need for any new parameters. To set this up for you I have prevailed on the lovely and awesome Faikah Bruce, at SACEMA, to write a little *R* programme to **work out the expected pupal duration for a pupa deposited on a given day** – with a known sequence of daily temperatures thereafter. Even for the limited time period Faikah and I have looked at (1992 and the first chunk of 1993, see below) the pupal duration varies by a factor of >2. The variation is obviously going to be quite a bit bigger than this over the whole time period 1959 – 2018 …… Sorry, but we simply cannot sweep such big differences under the carpet. We have to allow that the rate of emergence varies with temperature and hence time. What Faikah has done for me is to **use Fido’s results to calculate, for any given day, the rate of pupal development on that day, given the mean temperature for the day.** These rates are then accumulated over a series of days and, when the accumulation hits 1.0, bingo, your pupa emerges and you have the pupal duration for a pupa deposited on any particular day. And the inverse of that duration is the (average) rate of development for a pupa deposited on the day in question.

As a concrete example, a pupa deposited on 1 January 1992 experienced a sequence of daily mean temperatures (Tbar) that went: 28.50, 29.25, 28.00, 26.50, 27.50, 28.75, 30.50, 29.00, 28.50, 29.25 etc. Adding up the development rates for each day in that sequence showed that the expected pupal duration was 21 days: the inverse of that (1/21 = 0.0476) can then be used as the emergence rate for pupa deposited on 1 January 1992. [This is still not a very nice approximation: there are fairly easy ways of improving on this in the medium/long term but, in the meantime, it will better than taking the rate of pupal development as a temperature-independent constant]. So what you can do in your modelling is simply to have, as before, β as the rate of adult emergence – but now, instead of having it as a constant, you actually have a table look-up to get the rate appropriate for that day. So, as things are presented here, there are no additional parameters. By the way, you may have noticed – from the above example of the pupal duration for pupae deposited on 1 January 1992 – that the calculated mean Tbar for the whole of the pupal period (28.54) was almost identical to the Tbar for the first day of the period (28.50) – and may have been tempted to ask why one couldn’t just use this first-day temperature as the mean for the pupal period. The similarity is, however, purely serendipitous – as is clear from Figure 2.



**Figure 2** Mean Stevenson screen temperatures over all of the pupal duration plotted against the mean temperature on the first day of that period

There is one caveat to all of this – and that is that we don’t actually know what temperature the pupae are actually living at. But we may be sure that it is not, in general, at the temperature indicated on the Stevenson screen. Looking at the paper of Jackson & Phelps (1967) we see that tsetse basically manage things such that their pupae are deposited in sites that are cooler than ambient during the hottest season and closer to ambient when it is cool.

As a first approximation Faikah I have supposed that pupal sites are at the same temperature as ambient when the latter is 100C, and 30C cooler than ambient when ambient gets to 350C – and that there is a linear function joining those two points. If we play that game we find, of course (Figure 3), that puparial durations are always rather longer than indicated in Figure 1. Notice that, whereas the temperature difference between screen temperature and estimated pupal site temperature is biggest at high temperatures, the difference between the pupal durations tends to be largest at low temperatures. This is because of the very rapid increase in pupal period as temperatures decrease.



**Figure 3 P**redicted pupal duration for pupae experiencing temperatures as recorded in a Stevenson screen (red lines) or on the assumption that temperatures in pupal sites are lower than Stevenson screen temperatures.

**Rate of larval production**

In this case it is true that, as you say, the change in inter-larval period with temperature is fairly modest and, for the time being we can ignore. But – as with the pupal duration – we good ways of predicting the inter-larval period, so we could also include that nicety into your model without introducing any more parameters to be estimated.

**Pupal mortality**

As you have explained things in the paper, and in our correspondence, you have done the following with respect to pupal mortality/survival:

For a pupa deposited on a given day in a given month you use the (mean) temperature for that month to decide the proportion of the pupae that will survive until emergence. So you *are* including the temperature effect. But, with reference to what has gone on above, I suggest that there is a better way, using the fact that we can use Faikah’s programme to tell us – for a pupa deposited on a given day:

1. How many days that pupa will be in the ground;
2. What temperature that pupa is experiencing each day;
3. Then, using data from Phelps & Burrows (1969) and Phelps (1973) we calculate the pupal mortality rate on each day while it is a pupa.

I think this should give a better approximation to the pupal mortality, and show quite nicely how it ought to change with temperature. Faikah and I have used the same temperature data as used for the outputs in Figures 1 and 3 to calculate the pupal mortalities for pupae deposited on the sequence of days throughout 1992 and the first half of 1993 (Figure 4).



**Figure 4** Predicted pupal mortalities for pupae experiencing temperatures as recorded in a Stevenson screen (red lines) or on the assumption that temperatures in pupal sites are lower than Stevenson screen temperatures.

As before, when calculating pupal durations, we have made the calculations based on: (i) Stevenson screen temperatures; (ii) the cooler temperatures we expect the pupa to experience in the various larviposition sites selected by the pregnant female.

Figure 4 shows some interesting features. For the vast majority of the year pupal mortality *due to temperature effects* is extremely low. It is only at the hottest times of the year that things go ballistic. And, even then, it only happens if we assume that the pupae are experiencing temperatures as high as those indicated by the Stevenson screen.

As with the pupal duration, I think you can use this information to improve your modelling of the pupal mortality – which will also increase realism without increasing the number of parameters over the number you already have.

I hope this makes some sort of sense. Once you have had a good read of it all please feel free to set up a Skype or WhatsApp call to discuss.

Faikah is busy tidying up the R code. Once she has it looking pretty, we will forward it to you and you can use it to generate the pupal duration and mortality look-up tables for the entire period 1959 – 2018.

In the meantime I attach an Excel file with the output used to generate the above Figures.

Then try setting up the new model and see how you go with the fitting.

Bon chance. Have fun.

John Hargrove

Stellenbosch

26 April 2018

**References**

**Jackson, P. J. & Phelps, R. J.** (1967) Temperature regimes in pupation sites of *Glossina morsitans orientalis* Vanderplank (Diptera). *Rhodesia, Zambia and Malawi Journal of Agricultural Research* **5**, 249-260.

**Phelps, R.J. & Burrows, P. M.** (1969) Puparial duration in *Glossina morsitans orientalis* under conditions of constant temperature. *Entomologia Experimentalis et Applicata*, **12**, 33-43.