



A model of teneral dehydration in *Glossina*

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ABSTRACT

The results of a long-established investigation into teneral transpiration are used as a rudimentary data set. These data are not complete in that all are at 25 °C and the temperature-dependence cannot, therefore, be resolved. An allowance is, nonetheless, made for the outstanding temperature-dependent data. The data are generalised to all humidities, levels of activity and, in theory, temperatures, by invoking the property of multiplicative separability. In this way a formulation, which is a very simple, first order, ordinary differential equation, is devised. The model is extended to include a variety of *Glossina* species by resorting to their relative, resting water loss rates in dry air. The calculated, total water loss is converted to the relevant humidity, at 24 °C, that which produced an equivalent water loss in the pupa, in order to exploit an adaption of an established survival relationship. The resulting computational model calculates total, teneral water loss, consequent mortality and adult recruitment. Surprisingly, the postulated race against time, to feed, applies more to the mesophilic and xerophilic species, in that increasing order. So much so that it is reasonable to conclude that, should *Glossina brevipalpis* survive the pupal phase, it will almost certainly survive to locate a host, without there being any significant prospect of death from dehydration. With the conclusion of this work comes the revelation that the classification of species as hygrophilic, mesophilic and xerophilic is largely true only in so much as their third and fourth instars are and, possibly, the hours shortly before eclosion.

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1. Introduction

The teneral stage of the tsetse fly is defined to commence immediately after eclosion and it terminates with the taking of the first blood-meal. Water loss continues after eclosion and dehydration becomes progressively, more critical, up until the moment the teneral fly has its first meal. Once fed, it is essentially no longer in jeopardy. The severely depleted, pupal reserves are replenished and, from then on, dehydration assumes a far lesser importance. The adult fly is far better equipped to fend for itself and, to a certain extent, is a master of its own destiny. It can avoid dehydration through behavioural strategies, for example, by modifying its level of activity, by temporarily retreating to deep shade, or by locating an host on which to feed; all activities that the severely depleted reserves of the teneral fly may not allow enough time for. Work on adult flies, by Hargrove (2004), is strongly supportive of such reasoning in that humidity was found to be insignificant with regard to adult mortality. Dehydration is therefore a phenomenon usually only associated with the pupal and teneral stages in tsetse. The ultimate toll on a given cohort is cumulative and, likely, best assessed in terms of the proportion of original larvae which still have sufficient reserves to achieve their first feed, as tenerals.

Since combined dehydration and fat loss are thought to culminate in massive teneral mortality (Hargrove, 1990), pupal and teneral mortality rates are crucial in deciding the viability of any tsetse population. The vastly different dynamics of water loss during the pupal and teneral phases, however, afford both the status of topics in their own right. It seems likely that the high mortality which usually characterises the teneral phase is essentially determined during the pupal phase. While teneral water loss rates are generally several times higher than pupal rates, it can be argued that pupal rates prevail many times longer (comparing the Bursell, 1958 and 1959, data). To give some idea of the relative importance, while teneral water loss rates are probably around 40 times sensu strictu pupal-stage rates and around seven times the unprotected rates which prevail prior to and immediately following the sensu strictu pupal-stage, the unprotected rates generally prevail six times longer than teneral rates and sensu strictu pupal-stage rates 24 times longer. Thus, any teneral that dies of dehydration could be said, very likely, to have died as a result of pupal water loss. Water loss during the pupal phase can decide the fate of the teneral and one possible criticism of the Bursell (1959) work is that it does not take the state of the inherited, pupal reserves into account enough.

A general model of teneral water loss is developed in the same vein as the pupal water loss model of Childs (2013a) and Childs (2009). It is largely based on the investigations of one experimentalist (Bursell, 1958 and 1959) and it otherwise relies heavily on the pupal dehydration model for its initial values. The main challenge

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to exploiting Bursell's results for the purposes of a computational model, could be said to be in three, very specific respects: A function for transpiration, extending the *Glossina morsitans*-based model to the rest of the *Glossina* genus, then formulating a satisfactory criterion for survival that is dependent on total water loss. In the latter instance, a surprisingly simple solution is found to lie in the form of the pupal emergence data and the challenge then becomes one of utilizing the dependence of pupal survival on humidity, at 24 °C, when only the cumulative water loss for the teneral has been calculated. Transpiration is activity-dependent in the case of the teneral and an allowance for the future acquisition of temperature-dependent data must be made in generalising transpiration to all humidities, activity levels and temperatures. The Bursell (1959) teneral work was all carried out at 25 ± 0.8 °C. In the pupal case, the *G. morsitans* model was extended to other species on the basis of the puparium's surface area and its transpiration rate per unit of surface area, a strategy which predicted the critical water losses of all species with remarkable success in Childs (2009 and 2013a). Bursell (1959) presents a convincing argument that, within a single species, recording transpiration in units of residual dry mass is a superior means to that utilizing units of total mass per surface area. It is claimed that such a measurement is more resilient to phenotypic plasticity. It is based on such data that the *G. morsitans*-based, teneral model must necessarily be extended to other species. Extending a *G. morsitans*-based model to other species is work that can best be described as exploratory, however, the success of the same approach in the pupal model is cause for optimism. The results at the end make it an interesting and justifiable exercise, nonetheless. This model takes no account of the vagaries of phenotypic plasticity although there is no reason why relevant data would not facilitate the incorporation of such detail.

The final formulation, hence solution to the problem, is predicated on five major assumptions which are explicitly stated and explored. Another is taken for granted. It is assumed that the Bursell (1958 and 1959) investigations are comprehensive, to the extent that they encapsulate all salient aspects of pupal and teneral water loss. The problem of teneral transpiration is then reduced to a first order, ordinary differential equation for water loss. Although this equation is in itself extremely simple, the other equations, which constitute the combined pupal and teneral scheme, are both numerous and voluminous and there are issues pertaining to differentiability and continuity. This fact and the anticipated accuracy of such models render preferred integration schemes, such as the fourth-order-accurate Runge–Kutta–Fehlberg (RKF45) method, slightly impractical. Since the problem is not intractably large from a computational point of view, expedience takes precedence over taste and the more pedestrian midpoint rule is the preferred integration technique, in keeping with the pupal-stage model. It is in this way that the resulting problem is transformed from a mathematical one, to a computational one.

The goals and broader applications of this work are threefold. In order of priority, the first is the completion of the most challenging compartment of an early mortality model, the second is habitat assessment, while the third is a better comprehension of tsetse biology, particularly the Bursell (1958 and 1959) endeavours. Most of the experimental work needed for a model of early stage mortality has long been complete. The main causes of mortality could be summed up as dehydration, fat loss, predation and parasitism. The relationship between pupal fat loss and temperature has been extensively studied by Bursell (1960) and Phelps (1973). A cursory inspection of that work suggests that a few data points pertaining to teneral fat consumption's dependence on activity (at either fixed or variable temperature) are required. Quantitative work linking predation and parasitism to the density at pupal sites has been carried out by Rogers and Randolph (1990), although the topic can almost certainly be predicted to require some stochastic treatment.

The completion of this work could be supposed to leave the way open to a comprehensive model of early mortality, based either on a joint probability density function, or, more likely, a Markov chain. Once a model of early stage mortality is completed, matters should become a lot simpler. Adult mortality is lower (Hargrove, 1990) and thought to be trivial, likely a simple, linear dependence on temperature with population density becoming relevant at its higher levels.

The question of habitat assessment is a topic of intense interest to entomologists and parasitologists. Although environmental degradation militates against the tsetse fly ever making any significant return to its former status, health officials might have become over-reliant on work such as Ford and Katondo (1977) and the implications of climate change for traditional habitat (as well as other, geopolitical factors) could find them complacent. The presently perceived incursion of *G. austeni* into previously unrecognised, South African habitat (Hendrickx, 2007), for example, requires an explanation. Accurate determination of a greatly more confined pupal and teneral habitat, as well as early mortality, will facilitate a greatly more effective application of the various kinds of control measures contemplated by an integrated approach to pest management (Barclay and Vreysen, 2010), aerial spraying being the possible exception (Childs, 2011 and 2013b). Habitat assessment and tsetse biology are, of course, intricately entwined. The implications of tsetse biology for the habitat assessment of hygrophilic species in general, as well as South Africa's two, extant tsetse species, *G. brevipalpis* and *G. austeni*, are elucidated in this work. Certainly there are surprises in store so far as to what truly sets hygrophilic species apart from their mesophilic and xerophilic counterparts.

2. Generalising the transpiration data to a function of humidity, activity and temperature

The transpiration rate resorted to in this work is measured in residual dry masses per hour, rather than as a percentage of the same which was the preferred choice of Bursell (1959). All other units conform to those of Bursell (1959). Both the level of activity and the relative humidity used are percentages and the temperature is in degrees centigrade. Bursell (1959) obtained one set of transpiration data for variable activity (at 0% r.h. and 80% r.h.) and another for variable humidity (at 0% activity and 30% activity) during his investigations into teneral water loss (Fig. 1 of Bursell, 1959). Both data sets were measured at a temperature of 25 ± 0.8 °C. No temperature-dependent data are presently known to exist, however, this need not preclude one from making provision for such data coming into existence at some stage in the future. The question as to how one generalises these and as yet unknown data to all temperatures, humidities and levels of activity therefore arises. The prospect of some, temperature-dependent data set coming into existence in the future lends itself favourably to an assumption of multiplicative separability.

Assumption 1. Transpiration rate is a multiplicatively, separable function of activity and temperature. That is, if dk/dt is the transpiration rate, then there exist two functions ϕ and θ , dependent exclusively on activity and temperature respectively, so that

$$\frac{dk}{dt}(h, a, T) = \phi(h, a)\theta(h, T), \quad (1)$$

in which a denotes activity, T is the temperature and h is the humidity.

Such an assumption supposes that transpiration's dependence on humidity at one temperature, is simply a temperature-dependent multiple of that same dependence at another temperature i.e. that there is no coupling of the independent

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