

Tsetse population dynamics

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Introduction

Mosquitoes and tabanids deposit their eggs in water, stable flies and horn flies deposit them in wet dung. Most biting flies, in short, lay their eggs in a moist environment in which their larvae feed and develop. In the tsetse fly (*Glossina* spp.), by contrast, a single fertilised egg is retained in the uterus during each pregnancy and, when it hatches, the female feeds it until she deposits it as late third instar larva. The larva, which may weigh more than the female which has just deposited it, burrows into loose dry ground and forms around itself, within minutes, a hard puparial case. The adult fly develops within this case and emerges, at least three weeks later, having not fed since its deposition as a larva.

Freedom from a requirement for a moist external environment in the larval stage is matched in the adult stages by the fact that both sexes feed exclusively on blood, which provides not only the nutritional requirements but also the fly's water needs. While vegetation is required for shelter, and as food for the fly's hosts, tsetse are well suited to survive dry conditions. The behaviour, physiology and the population dynamics of the genus *Glossina* are entirely dominated and conditioned by the consequences of these adaptations in both juvenile and adult stages.

Seasonal variations in numbers are much smaller than in blood-sucking insects such as mosquitoes, stable flies and many tabanids, which depend on surface water or other moist media for breeding. On the other hand, the massive inputs of energy and raw material required by the larva mean that only one larva can be produced every 7-12 days. This is a much lower birth rate than in almost all other insects, and means that death rates must also be low if the species is to survive. The larvae and pupae, which spend virtually their entire existence either in the uterus or under the ground, are less prone to predation than their aquatic counterparts. Losses in the larval and pupal stages are generally small, both in absolute terms and in comparison with other blood-sucking flies.

The remaining, serious, problem for the fly is to minimise mortality in the adult stages. Complete reliance on blood means that adult tsetse must regularly make flights to contact host

animals and feed off them. Indeed, for female tsetse, life consists of little other than a cycle of finding a blood meal, sitting somewhere safe turning that blood into a larva, depositing said larva and flying for the next meal. But flight consumes energy at up to 100 times the resting rate (Bursell *et al.*, 1974) and feeding, moreover, carries its own risks. Optimal feeding behaviour in females thus involves balancing the requirement of getting enough blood to produce a larva, whilst using as little energy as possible, and avoiding being killed while feeding.

The imperative for males differs in that optimal behaviour consists entirely of mating with as many virgin females as possible. Rates of energy replenishment must nonetheless be balanced against the risks associated with feeding and the high costs of flight. This balance for both sexes is modified by climate. Thus, when temperatures rise, metabolic rates increase in poikilotherms such as tsetse. If flies are to maintain condition and, in the case of females, the size of the pupae they produce, they must feed more frequently, and/or modify their behaviour so as to reduce body temperature below ambient. Failure to do so will lead to increases in mortality and consequent decreases in population growth rate.

Population growth rates are determined by the interplay rates of dispersal, birth and death, as summarised by the equation:

$$\text{Growth rate} = (\text{Birth rate} + \text{immigration rate}) - (\text{Death rate} + \text{emigration rate})$$

The present chapter is accordingly concerned with a consideration of each of the components of this equation. How well do tsetse manage to minimise mortality in different environments? How do the rates of gain and loss vary with climate and with population density? Which environmental factors cause the greatest problems? And at what stages are the flies most vulnerable? Of overriding concern is the problem of how we find the answers to these questions and what confidence we have in them.

Birth rates

The reproductive rate in tsetse depends on the rate of production of larvae and on the rate at which those larvae develop, via the pupal phase, into adults. Both elements are temperature dependent but the functions involved are quite different and the processes need to be considered separately.

Rates of larval production

The massive load on the female of the late third-instar larva would be greater yet but for the fact that, while the nutritional content of the pupa is sufficient to produce an adult, the young fly which emerges has smaller fat reserves and a less well developed flight musculature than the mature fly. Before the emerging adult female embarks on reproduction she uses the first three or so blood meals to rectify this situation. As a consequence, the time (I_0) to production of the first larva is longer than the time (I) between the production of subsequent larvae.

Early laboratory work produced estimates of the effect of ambient temperature on I_0 and I (Anon, 1955). The predictive equations are not entirely satisfactory in that, at low temperatures, I_0 appears to be less than I . In the only extensive field study I was always lower than predicted by the laboratory equation (Fig. 1), particularly at low temperatures (Hargrove, 1994). The discrepancy at high temperatures is probably greater than apparent from Fig. 1 since tsetse utilise microenvironments such that they appear to live in the field at 2 - 6 °C lower than the ambient temperature (Hargrove & Coates, 1990).

Data from Rekomitjie in Zimbabwe suggest that the female generally produces her first larva when she is 14 – 17 old and at intervals of 8 – 10 days thereafter (Fig. 1). For flies introduced to Redcliff Island, Lake Kariba, Zimbabwe the periods were even shorter and suggest that I may approach a minimum of six days under optimal conditions. The trend of the data for Rekomitjie indicates, similarly, that I may take a maximum value of at least 12 days at low temperatures. While such values of I are readily observed in the laboratory they have not been measured in the field. This is doubtless due, in part, to the fact that tsetse behave in such a way as to minimise the effects of extremes of temperature – by using artificial refuges when temperatures exceed 32°C and by sitting in direct sunshine at low temperatures. Extrapolations beyond the range of field measurements should therefore be treated cautiously.

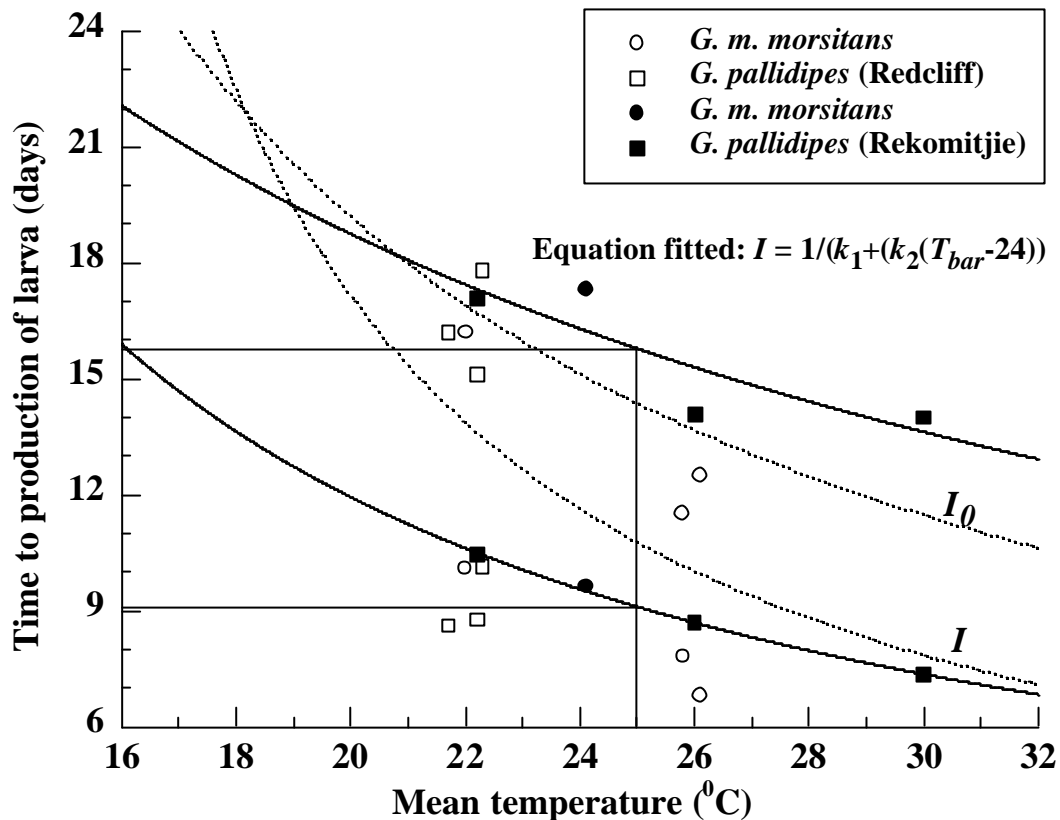


Figure 1. The relation between temperature and the observed and predicted times (I_0) to production of the first larvae and the duration (I) of subsequent inter-larval periods. Bold lines fitted to the data for flies collected at Rekomitjie Research Station, Zimbabwe (Hargrove, 1994). Estimated values, and standard errors, of the coefficients for the equation in the body of the graph were: For time to production (I_0) of the first pupa; $k_1 = 0.061 \pm 0.002$, $k_2 = 0.0020 \pm 0.0009$. For subsequent inter-larval periods (I); $k_1 = 0.1046 \pm 0.0004$, $k_2 = 0.0052 \pm 0.0001$. Faint lines show the predicted values from a laboratory study in Tanzania (Anon, 1955).

Rates of pupal development

Phelps & Burrows (1969a) produced the most complete and precise measures of the effect of temperature on the durations of the pupal phase (I_p) for field-deposited larvae kept in the laboratory at constant temperatures. While their model did not predict I_p accurately outside the temperature range 20-30°C, analysis of their data shows that this was only because they fitted the

rates of development over the entire temperature range, 8 - 32°C, of the experiment. If attention is restricted to the range 16 - 32°C, over which flies actually emerged from the pupae, then the resulting fit is near perfect (Fig. 2) with all pupal durations predicted to within 2.5 days.

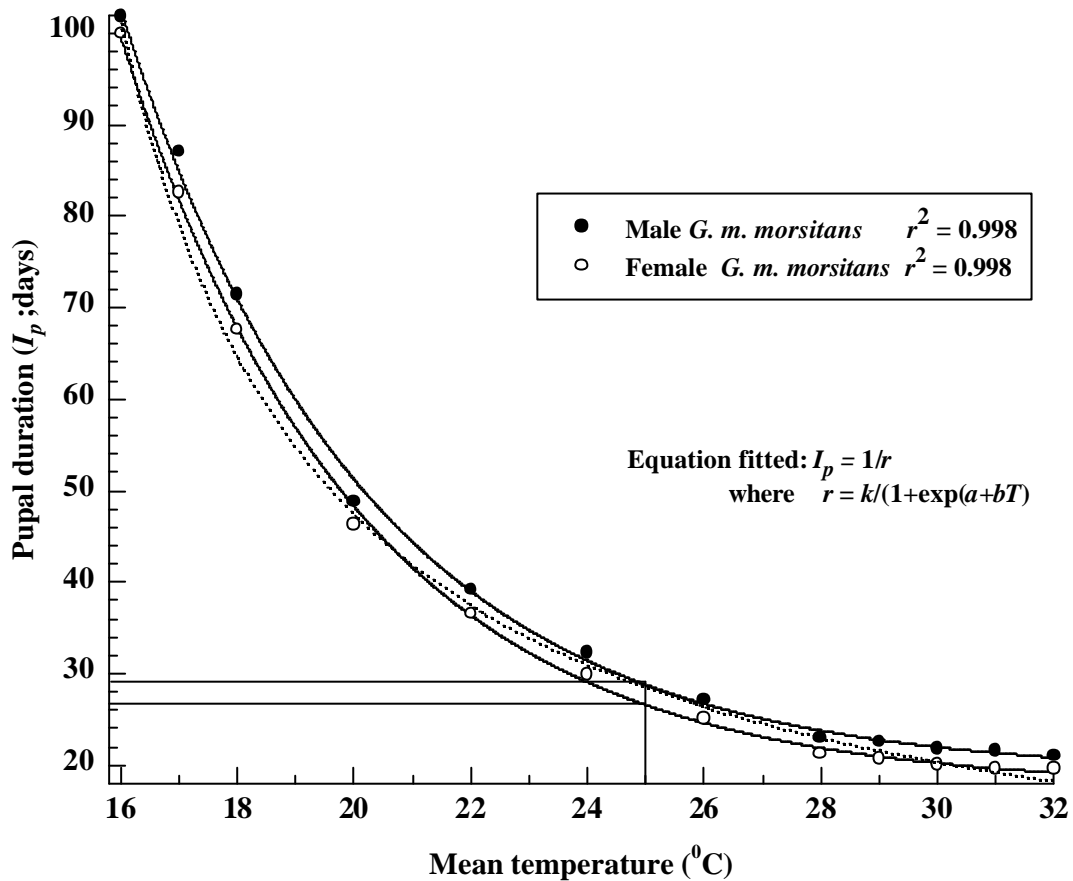


Figure 2. The relation between temperature and pupal durations of *G. m. morsitans* in the laboratory (Phelps & Burrows, 1969a). Estimated values, and standard errors, of the coefficients for the equation in the body of the graph were: Males; $k = 0.053 \pm 0.001$, $a = 5.3 \pm 0.2$, $b = -0.24 \pm 0.01$. Females; $k = 0.057 \pm 0.001$, $a = 5.5 \pm 0.2$, $b = -0.25 \pm 0.01$.

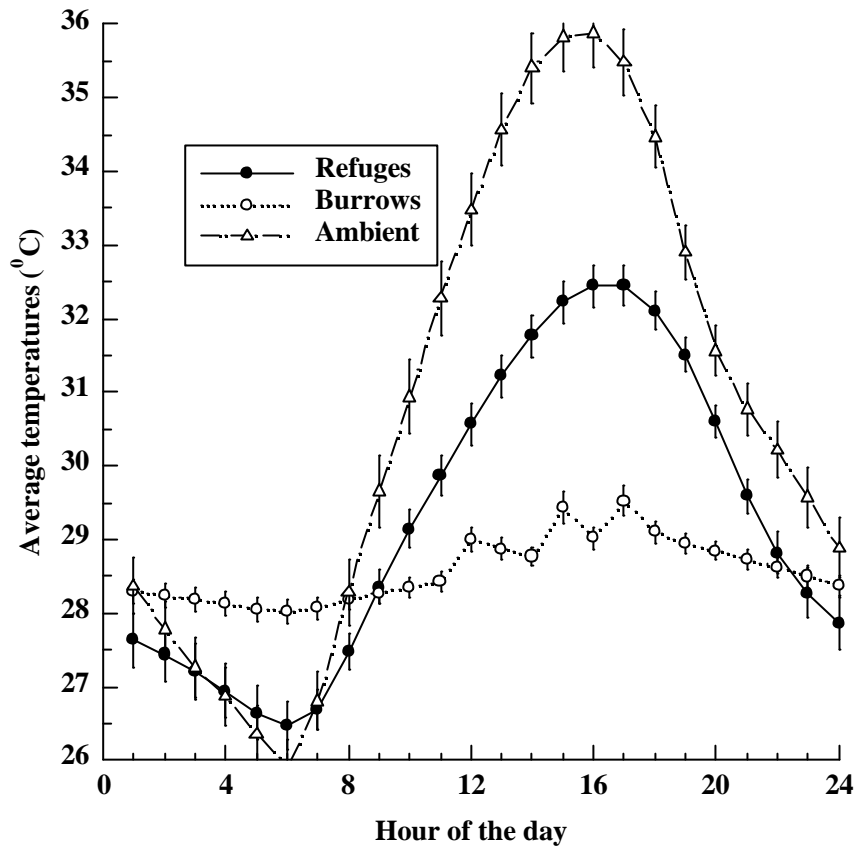


Figure 3. Mean hourly temperatures in artificial refuges and warthog burrows compared with ambient temperature at Rekomitjie Research Station in October – November 1998.

Phelps & Burrows (1969b) used their data and averages of maximum and minimum Stevenson screen temperatures in Zimbabwe to produce predictions of I_p which generally followed the seasonal changes in ambient temperature in the field. The observed variation in I_p was high, however, as a consequence of the variation in mean temperature between deposition sites. Pupae deposited under logs and rocks during winter tended to have shorter developmental times than expected, while the reverse was true for pupae deposited in ant-bear holes during the hot season. This accords with Jackson & Phelps' (1967) finding that temperatures in the former situation were often higher than ambient, and those in ant-bear burrows were lower. Recent measurements of the mean temperatures in artificial ant-bear burrows where tsetse pupae had been deposited showed that these were on average 2.2°C lower than ambient (Fig. 3).

Mortality rates

The preceding section suggests that tsetse reproductive rates are well predicted by temperature. If the population's mortality is also known then it is a simple matter to predict its growth rate - but mortality is generally not as easily estimated. It is not even generally agreed which abiotic factors are most important in determining density-independent mortality nor where and how density-dependent effects act to regulate tsetse numbers.

Since mortality varies with developmental stage the situations in the pupal, teneral (*i. e.* adults which have not yet taken their first meal) and post-teneral adult stages are considered separately. Mortality can vary even within the post-teneral phase, particularly in flies which have taken at least one meal but have not yet completed the development of their thoracic musculature. Where it is necessary to refer specifically to this class of fly they are termed post-teneral immature adults.

Mortality in utero

Ovarian dissection indicates reproductive losses, due mainly to abortion, of 1 - 2% in *G. pallidipes* Austen from two locations in Kenya (Turner & Snow, 1984). Hargrove (1999a) found abortion frequencies of < 1% in *G. m. morsitans* Westwood and *G. pallidipes* Austen at Rekomitjie Research Station in Zimbabwe. These studies indicate that *in utero* losses are not generally a major source of loss. At the hottest times of the year at Rekomitjie, however, the abortion rate rose as high as 3%. Moreover, the proportion of *G. pallidipes* found with empty uteri rose exponentially with temperature (Fig. 4) and there is some suggestion that the abortion rate at high temperatures may be higher than indicated by current methods of measurement (Hargrove, 1999a)

Pupal mortality

Pupae are generally not easily found in the field and the estimation of their numbers in a population is a problem which has so far defeated tsetse biologists. There are, consequently, few estimates of the natural pupal death rate but parasitism and predation may nonetheless be severe. In Zimbabwe, various studies have recorded maximum parasitoid frequencies of 12 - 40% in

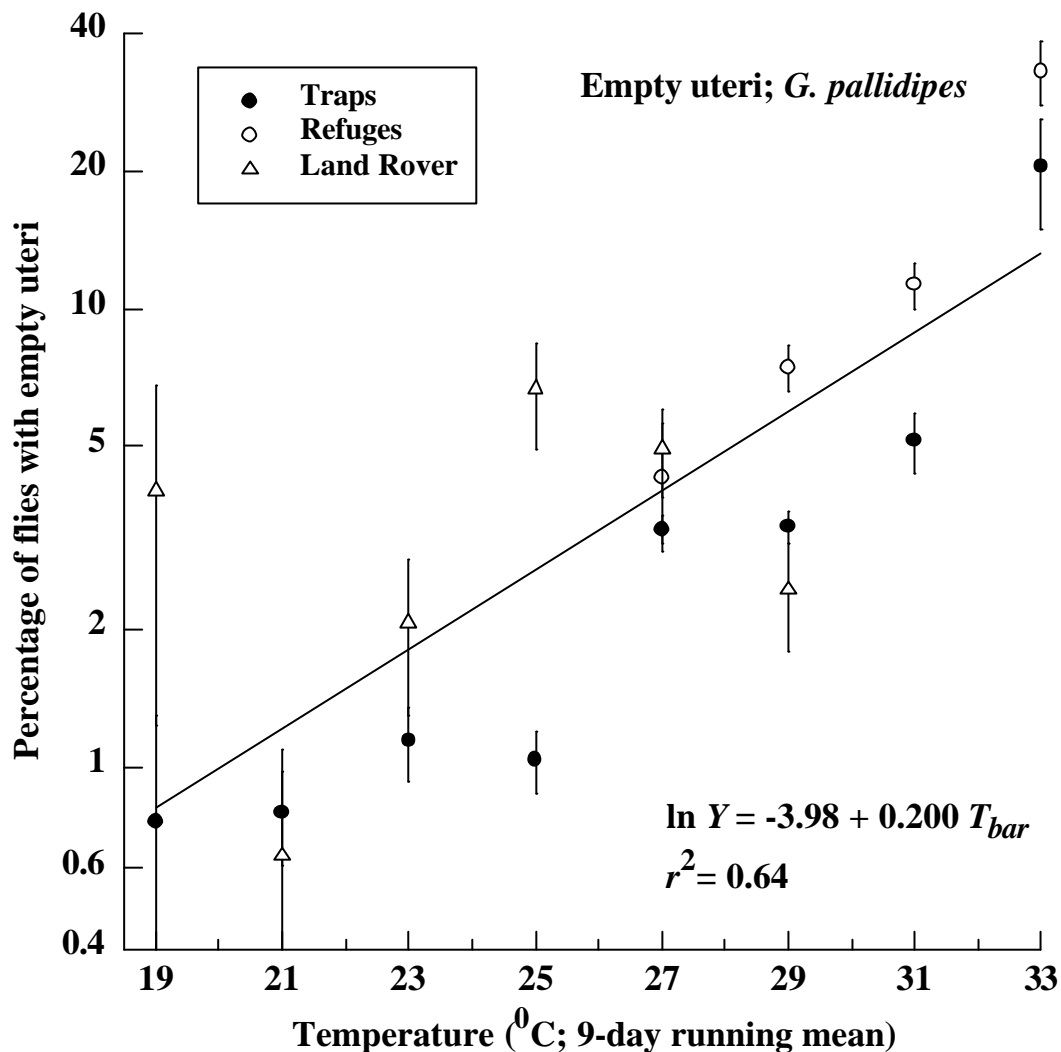


Figure 4. The relationship between temperature and the percentage of *G. pallidipes* found to have empty uteri. Flies caught at Rekomitjie Research Station, Zimbabwe using odour-baited traps, in artificial refuges and on an electric net mounted on the back of a moving vehicle. Figure redrawn from Hargrove (1999).

collections of *G. m. morsitans* and *G. pallidipes* pupae (Fig. 5) (Chorley, 1929; Heaversedge, 1969a, b; Hargrove & Langley, 1993). The maximum values over-estimate the greatest losses per pupal cohort because the duration of the intra-puparial stages of tsetse parasitoids is greater than that of their host and parasitised pupae therefore accumulate in favoured deposition sites. Nonetheless, losses can clearly be high in the hot, dry season in habitats like the Zambezi Valley

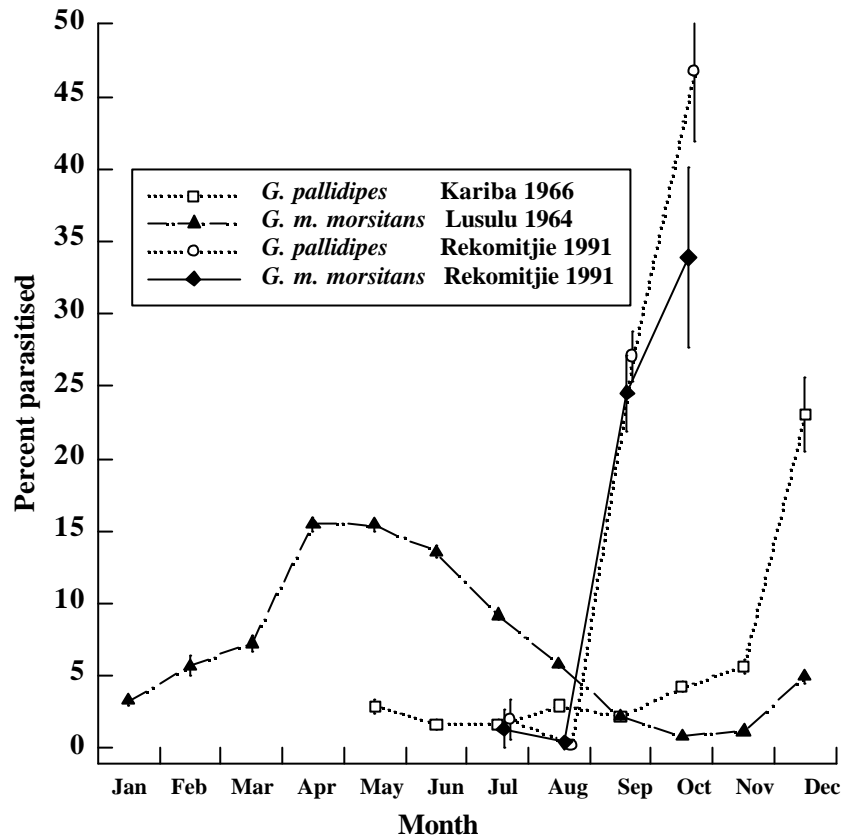


Figure 5. Percentages (\pm standard error) of parasitised pupae of *G. m. morsitans* and *G. pallidipes* collected in Zimbabwe. Data from Heaversedge (1969a, b) and Hargrove & Langley (1993).

of Zimbabwe. For the remainder of the year losses due to parasites in this environment appear to be only *c.* 1%. For a 30-day pupal period this is a daily loss rate of *c.* 0.03%, which is inconsequential compared to adult losses and even estimated pupal losses due to predation.

Jackson (1937) marked pupae of *G. m. morsitans* in field deposition sites and found that 26% (49/188) were lost or taken by predators during the whole pupal period. Using similar techniques Challier (1973) estimated pupal losses of 0.2 - 1%/day in *G. palpalis gambiensis* Vanderplank and Rogers & Randolph (1990) 1%/day in *G. pallidipes* at Nguruman, Kenya.

The effect of climatic parameters on pupal mortality is poorly understood but Phelps and Burrows (1969c) found that repeated exposures of pupae to temperatures of 36⁰C for up to 4h per day did not raise mortality above normal levels. More than half of the pupae died, however,

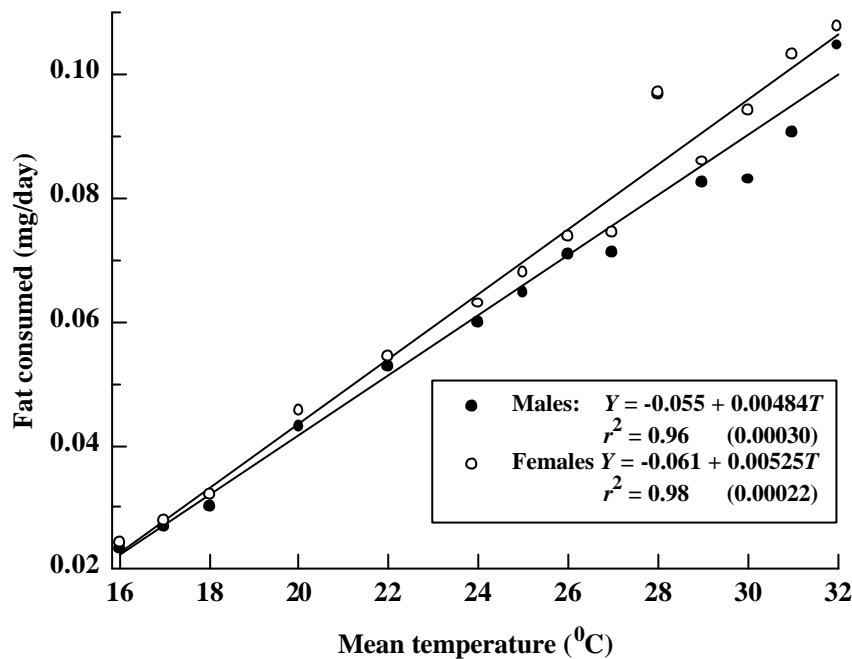


Figure 6. Effects of temperature on fat consumption (mg day^{-1}) during puparial development in laboratory male and female *G. m. morsitans*. The standard error of the regression coefficient is shown in parentheses beneath each estimate. Data from Phelps (1973).

when the pupae were subjected to the same temperature for 6h per day, or to temperatures of 38°C for anything over 4h per day. Laboratory studies also show that high relative humidities are required for good pupal survival.

Teneral mortality

Given the low fat levels and poorly developed flight muscle of teneral tsetse it is to be expected that this class will be particularly at risk from starvation. This was first inferred from field data by Jackson (1948) who released *G. m. morsitans* and *G. swynnertoni* Austen in the field on the day of their emergence. Wing-vein lengths of post-teneral females of both species, and of male *G. swynnertoni*, were significantly greater than those of recaptured tenerals. He concluded that small teneral flies were selectively eliminated, but that there was no size selection once flies had taken their first meal. Similar results were observed for *G. palpalis fuscipes* Newstead in Kenya (Bursell & Glasgow, 1960). The most complete study (Phelps & Clarke,

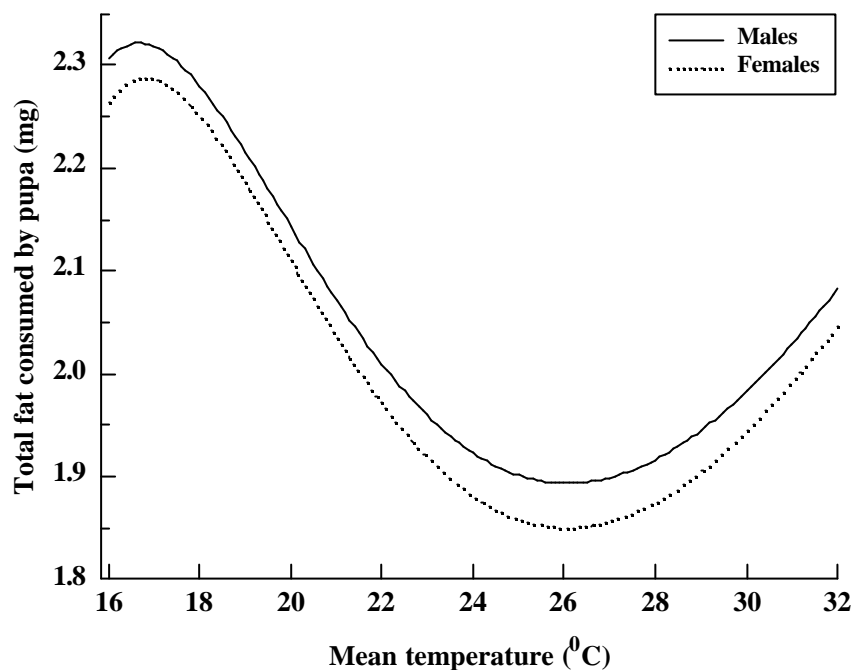


Figure 7. Estimates of the total fat consumed at different temperatures given the results in Fig. 6 and the puparial duration estimated from the functions in Fig. 2.

1974) showed that, between April and December, flies emerging in the laboratory from field-collected pupae were significantly larger than young field-caught adult males estimated to have emerged at the same time. Field losses of small flies were estimated at 35% in the cool months and up to 75% in the hot dry season.

Dransfield *et al.* (1989) concluded, from similar experiments at Nguruman in Kenya, that there were size dependent losses of young male, and female, *G. pallidipes*. The evidence is flawed, however, because these workers did not use field-collected pupae. Instead they caught wild females and used the pupae that these females produced in the laboratory. Later studies (Randolph *et al.*, 1990, 1991; Hargrove, 1999b, c) make it clear that the sizes of laboratory-produced pupae cannot be used to predict the sizes of offspring which the same females would have produced in the field under natural conditions. There is nonetheless evidence from ovarian dissection data (see below) that, at least at Rekomitjie Research Station, Zimbabwe, young female *G. pallidipes* do suffer severe mortality during the hot dry-season.

The relationships for pupae between temperature and development (Fig. 1), and between temperature and fat consumption (Fig. 6) are such that the size-specific fat contents of emerging tsetse are highest for temperatures in the region of 26⁰C (Fig. 7). Bursell (1960b) and Phelps (1973) also showed that fat levels at emergence were relatively lower in smaller flies. At the hottest times of the year, small pupal size and high temperatures combine to produce a large proportion of small flies with low fat levels at emergence, thus explaining the particularly high losses of young tsetse in this season.

The same problem can also occur at the coolest times of the year in certain habitats. This point is illustrated in Fig. 8 where annual variations in fly size are plotted for tsetse caught in the field in Zimbabwe. At Rekomitjie Research Station (altitude 510m) where the temperature seldom declines below 10⁰C, but maxima reach 42⁰C, fly sizes increase between January and August and only decline in the extreme heat prior to the rains. At Lusulu (altitude 990m), by contrast, the temperature extremes were of the order of -1 and 37⁰C, and fly sizes decreased between January and August. Mortality in young flies may therefore be expected to increase at both high and low extremes of temperature, as observed by Phelps & Clarke (1974).

Adult mortality

Since mortality changes with age, one needs to define precisely the age range over which the estimates are being made. This range depends on the method used. Mark-recapture estimates generally depend on the flies coming to a sampling team and mortality estimates exclude those teneral flies which die before they can appear in fly-round samples (Phelps & Clarke, 1974). The resulting mortality estimates are thus an *ad hoc* average of the mortalities of teneral, post-teneral immature and mature adult flies

When the ovarian dissection technique is used to provide sample age distributions, female mortalities are most often estimated using only those flies which have ovulated at least once and which can therefore be considered to be mature adults.

Estimates of mortality can also be made from series of catches of adult tsetse (Rogers, 1979). This method provides global estimates of mortality over all developmental stages. It is necessary to distinguish carefully between all these estimation methods if we are to make sense of the results of the field experiments.

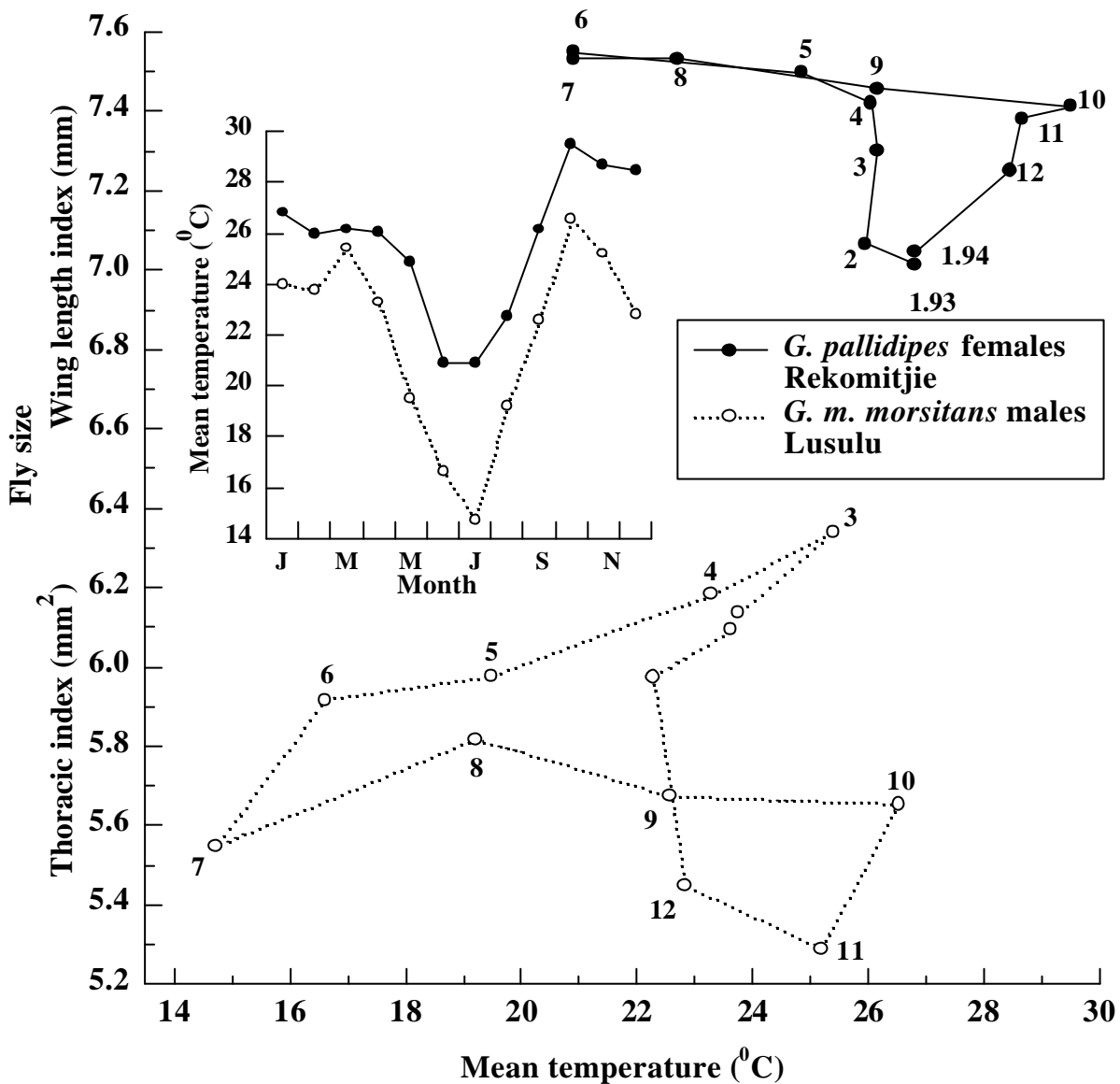


Figure 8. Seasonal changes in the indices of size of tsetse flies in Zimbabwe. Mean monthly indices of wing length for female *G. pallidipes* at Rekomitjie Research Stations and of thoracic area for male *G. m. morsitans* at Lusulu are plotted against mean temperature. Numbers in the body of the plot indicate the month and year to which the temperatures and fly sizes refer. Data from Hargrove (unpublished) and Phelps & Clarke (1974) respectively.

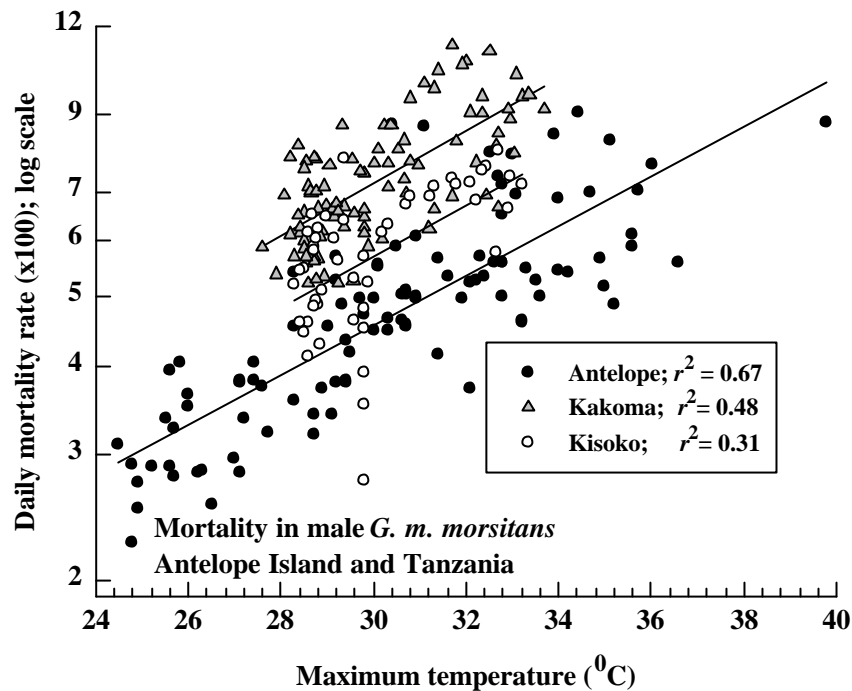


Figure 9. Mean values of weekly mortality for male *Glossina m. morsitans* plotted against maximum temperature (Hargrove, 2001b). Survival probability estimates from mark-recapture experiments carried out at Kakoma and Kisoko in Tanzania and on Antelope Island, Lake Kariba, Zimbabwe. Solid lines show the mortalities predicted by regression.

Mark recapture estimates

The most extensive and sophisticated estimates of mortality have involved the use of mark-release-recapture but, not surprisingly given the vast effort required, only a small number of long-term studies have been carried out. Jackson (1948), working in Tanzania, estimated mortality in adult male *G. m. morsitans*, initially in a rectangle of 4.6 km² and thereafter in two areas each measuring 41 km². Nash's (1933) demonstration of a correlation between tsetse numbers and saturation deficit led Jackson to look for an effect of this factor on adult mortality. The correlation was poor and improved analysis (Hargrove, 2001b) showed that mortality was no better correlated with saturation deficit than with maximum temperature (Figs. 9, 10).

Mark-recapture experiments carried out on Antelope Island, Lake Kariba, Zimbabwe provided, *inter alia*, mortality estimates for the same sex and species of fly. Maximum and, more clearly, mean temperature (Figs. 9,10, 11 a, b) accounted for more of the variance in

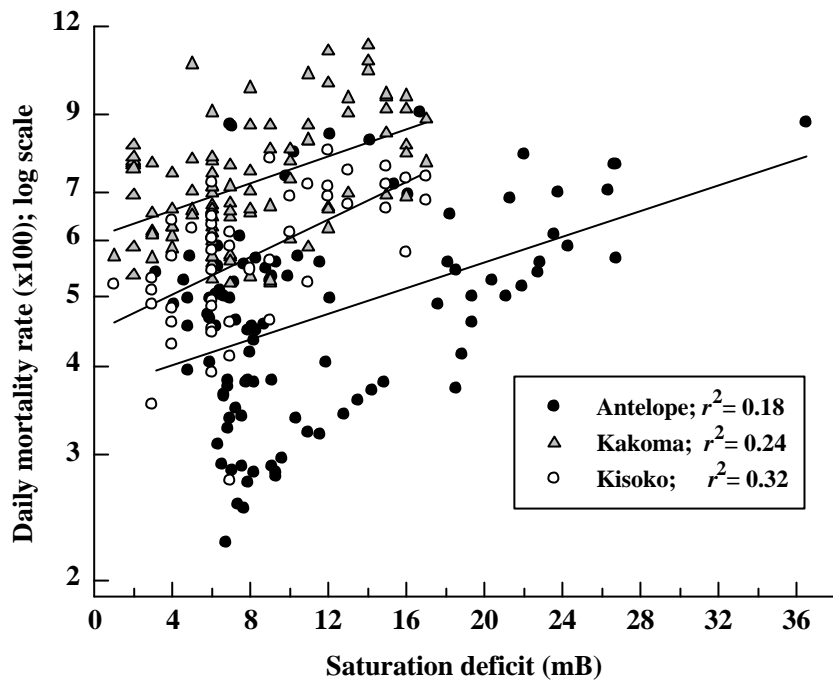


Figure 10. Mean values of weekly mortality for male *Glossina m. morsitans* plotted against saturation deficit (Hargrove, 2001b). Survival probability estimates from mark-recapture experiments carried out at Kakoma and Kisoko in Tanzania and on Antelope Island, Lake Kariba, Zimbabwe. Solid lines show the mortalities predicted by regression.

G. m. morsitans mortality than did saturation deficit (Hargrove, 2001c). These results are consistent with supports Bursell's (1961) view that tsetse are less likely to be stressed by water loss than they are by a shortage of food reserves. For *G. pallidipes* the differences between the effects of saturation deficit and of temperature were less clear, however, and mortality appeared to increase with temperature only above a threshold temperature (Fig. 11c, d).

It is unclear why adult mortality increases with temperature. At extremes values there may be a direct effect. Nash (1936) found that a temperature of 39°C was lethal for *G. tachinoides* Westwood and Potts (1933) gives a value of 40°C for an hour for *G. m. morsitans* in Tanzania. For the latter species the positive correlation between mortality and temperature is evident at < 25°C (Fig. 11) and here a direct effect seems unlikely. Since tsetse are poikilotherms, at least part of the increased mortality may stem from the increased number of

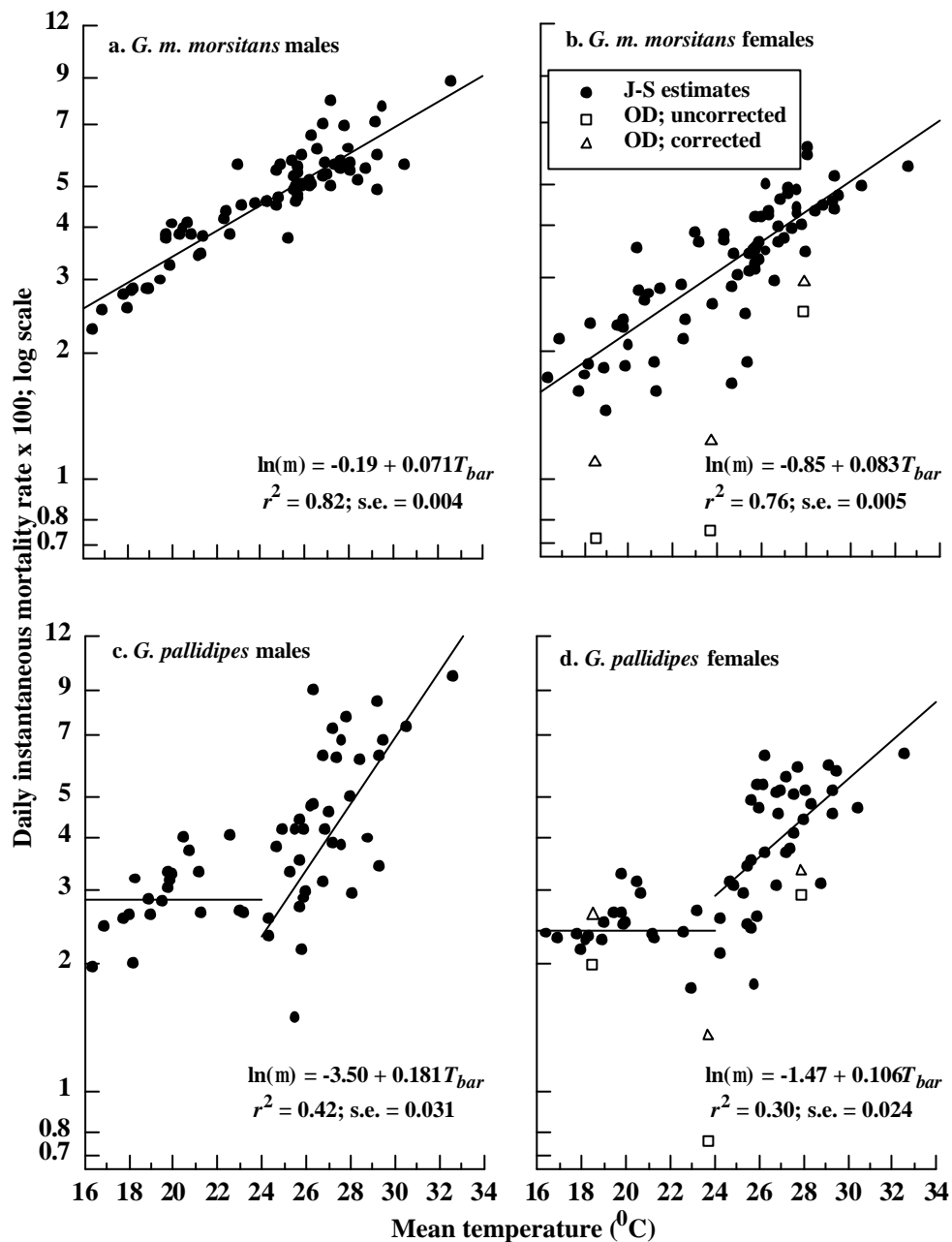


Figure 11. Daily mortality rate of *G. m. morsitans* and *G. pallidipes* on Antelope Island estimated by mark-recapture (dots) between February 1980 and November 1981 or by the analysis of ovarian dissection data collected in April, July and December 1981. The latter analysis was applied to raw ovarian age data (squares) or to data corrected for estimated biases in age-dependent probability of capture (triangles) (Hargrove, 1993)

risks taken in securing the more frequent meals required at higher temperatures. This problem would be most serious for teneral flies since high temperatures imply that the flies emerge with sub-optimal fat levels (Fig. 6, 7).

The mortalities shown in Figs. 9-11 are estimated on the assumption that adult mortality is independent of age, though early laboratory and field work suggested this was unlikely (Jordan & Curtis, 1972; Gouteux & Kiénoú, 1982). In a field experiment designed to test this assumption Hargrove (1990) released uniquely marked 218 adult female *G. m. morsitans*, on the day of their emergence, on Redcliff Island, Lake Kariba and noted the marks of these flies every time they visited twice-daily ox fly-rounds. It was thereby possible to estimate the capture probability and population (Fig. 12 a, b) at regular intervals and to estimate the changing mortality during all of adult life. The population estimates are well fitted by a model which assumes the mortality function consists of the sum of two exponentials (Fig. 12 b). Mortality declined during the first 10 days of life from an original rate > 10 to < 2 % per day and increased slowly thereafter with age (Fig. 12c).

Estimates from ovarian age distributions

Ovarian dissection data (Challier, 1965) can be used to estimate female mortality. This is best done using a maximum likelihood method (Hargrove, 1993) making due allowance for the population growth rate (Van Sickle & Phelps, 1988). Rogers *et al.* (1984) provided a series of mortality estimates from ovarian dissection data obtained from female *G. p. palpalis* (Robineau-Desvoidy) sampled at Degbézéré in the Ivory Coast using biconical traps. Daily mortality rates in any month were best correlated with mean temperature in the previous month. The estimates were not, however, corrected for rates of population change, which were marked in the Ivory Coast study particularly because the population was subjected to two aerial spraying campaigns. When such allowance is made a number of the mortality estimates are then negative (Fig. 13). These impossible values occurred most frequently after attempts to control the population by aerial spraying and could result from post-spray invasion of the area by populations of predominantly older flies.

Gouteux & Laveissiere (1982) estimated mortalities in female *G. p. palpalis* and *G. pallicera* Newstead Austen but their results are difficult to interpret because they used an inappropriate estimation method rate (Rogers *et al.*, 1984) and did not correct for growth rates.

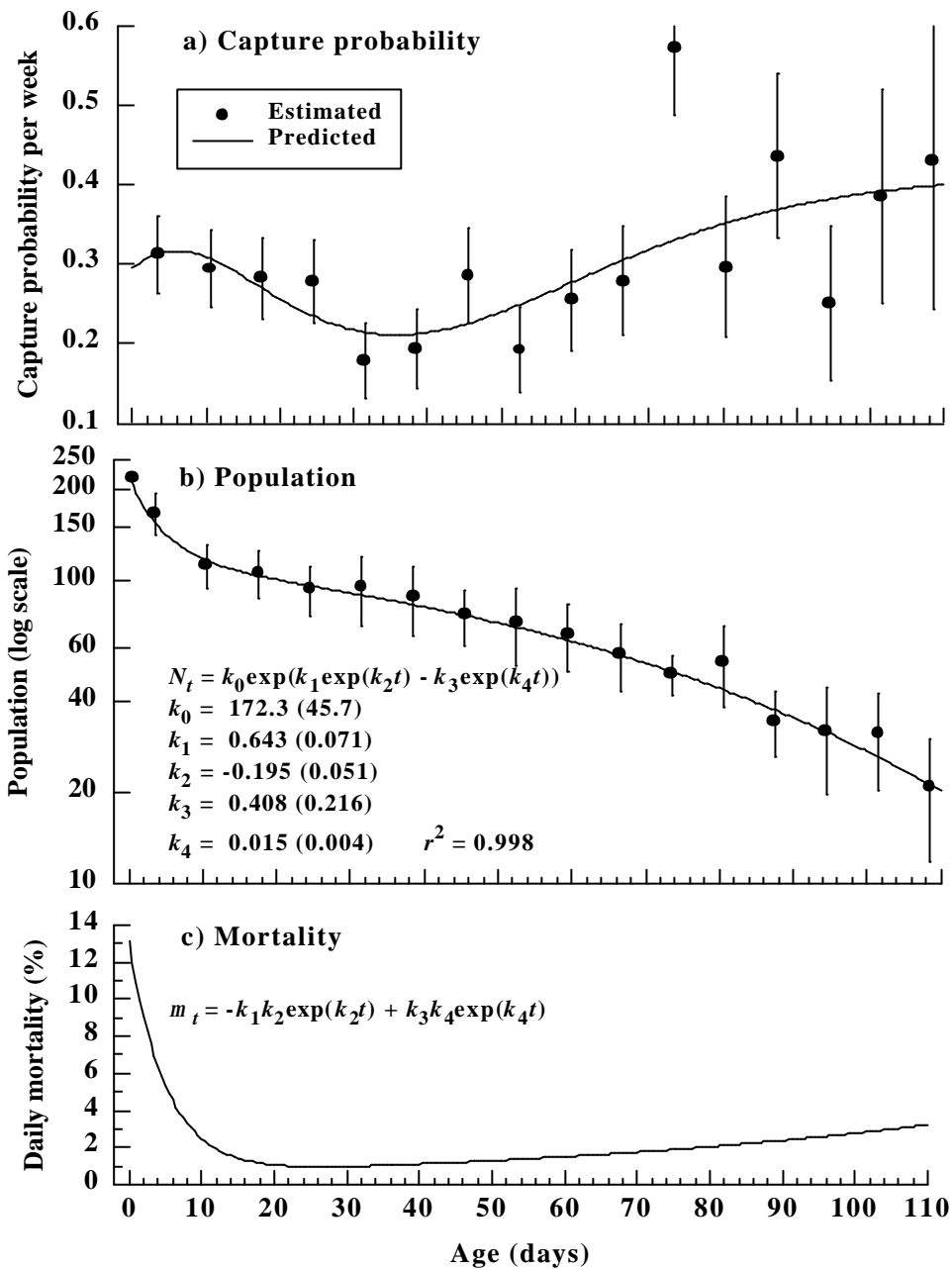


Figure 12. Population parameters for female *G. m. morsitans* marked and released at emergence on Redcliff Island, Lake Kariba, Zimbabwe, 1986. a) Probability of capture in any given week. b) Population estimates with the function used to draw the fitted solid line and the parameter estimates, with standard errors in parentheses, for this function. The same parameter estimates are used to calculate the mortality (c) at each age. c) Vertical bars in a) and b) denote the standard error of each estimate. Data from Hargrove (1990)

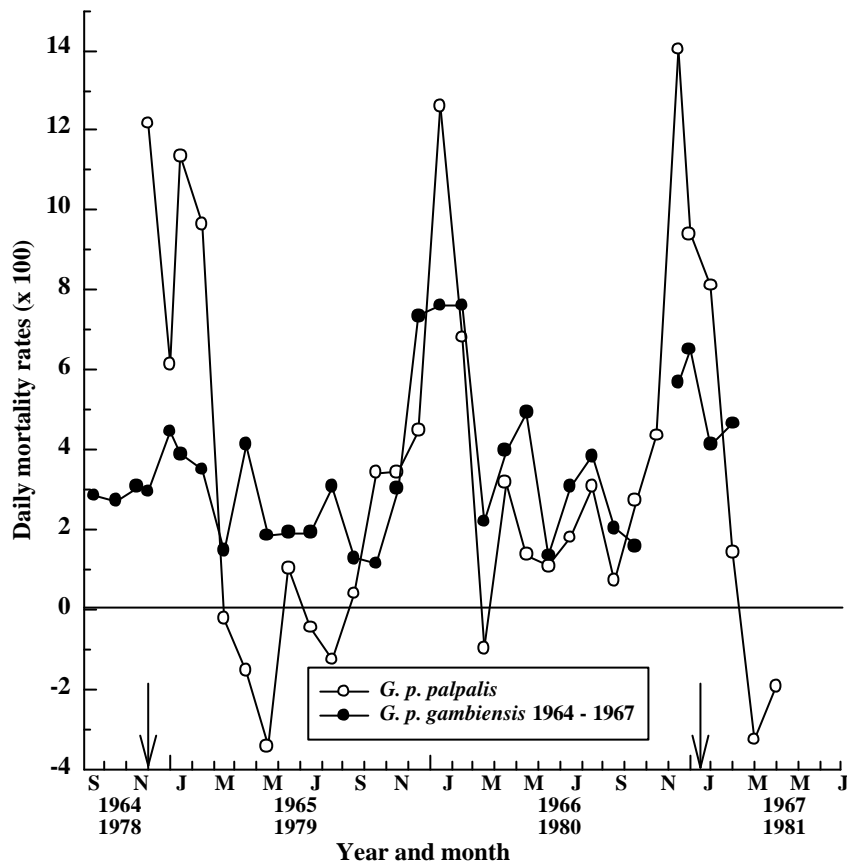


Figure 13. Mortality of adult female estimated from the ovarian age distributions.

i) (circles) *G. p. palpalis* captured in biconical traps at Degbézéré in the Ivory Coast..

ii) (dots) *G. p. gambiensis* caught on man fly-rounds in the forest of Kou, Burkina Fasso.

Graphs redrawn using data from Challier (1973), Randolph *et al.* (1984) and Jarry *et al.* (1996).

Jarry, Gouteux & Khaladi (1996) later developed the maximum likelihood method such that both adult mortality and population growth rate could be estimated, as long as pupal mortality could be estimated separately. They applied the technique to Challier's (1973) ovarian dissection data for *G. p. gambiensis* (Fig. 13). Challier (1973) buried pupae in selected field sites and estimated pupal mortality from the numbers subsequently emerging. It is not clear how closely these experimental loss rates approached the mean losses in all natural pupal sites. What is clear is that growth rates estimated in this way have high variances (Van Sickle, 1988), the levels of which were not estimated by Jarry *et al.* (1996), being highly sensitive to sampling errors. The

resulting adult mortalities show, nonetheless, a pattern similar to those estimated from the data of Rogers *et al.* (1984) (Fig. 13).

Unpublished data for *G. pallidipes* caught in odour-baited traps in Zimbabwe provide the longest series of mortality estimates from ovarian dissection. The raw mortality estimates, uncorrected for growth rate, show a consistent cyclical pattern with well-defined minima in May - June and December (Fig. 14). Given the annual changes in temperature (Fig. 15a) and the strong evidence that adult mortality increases with temperature (Fig. 9, 11) the cool season minimum makes sense. The apparent reduction in adult mortality in November – December, at the hottest time of the year, make little sense and are at variance with the contemporary decline in catches (Hargrove & Vale, 1980).

Inspection of the ovarian dissection raw data identifies the probable source of the paradox. At the end of each year there is a striking reduction in the proportion of young flies in field samples. In particular, the proportions of category zero flies, which are not used in the mortality estimation, show a rapid decline between September and the end of the year (Fig. 15b). The apparent decline in mortality is thus almost certainly an artefact consequent on a marked increase, during the hot, dry season, in the losses of immature tsetse. This could be due to increased parasite levels (Hargrove & Langley, 1993) and/or to increased losses of teneral flies due to the combined effects of high temperatures and low fat at emergence (Phelps & Clarke, 1974). These results provide a particular example of the problem raised by Van Sickle & Phelps (1988) who suspected that tsetse populations at Rekomitjie seldom exhibited the stable age distribution necessary for the reliable estimation of mortalities using ovarian dissection data.

The Antelope Island experiment provided a unique opportunity to compare contemporary mortality estimates on the same population using mark-recapture and ovarian dissection data. The former estimates, for female *G. pallidipes* and particularly *G. m. morsitans*, were almost always higher (Fig 11b, d). Part of the difference could be due to age-dependent change in capture probability (Hargrove, 1991, 1993). Correcting for this effect accounted, however, for only part of the discrepancy. At least part of the remainder could have been due to the fact (see above) that the mark-recapture method estimated mortality in all post-teneral adults, whereas the ovarian dissection estimation procedure included only those which had already ovulated and which were generally at least a week old. The discrepancy between the mortality estimates from

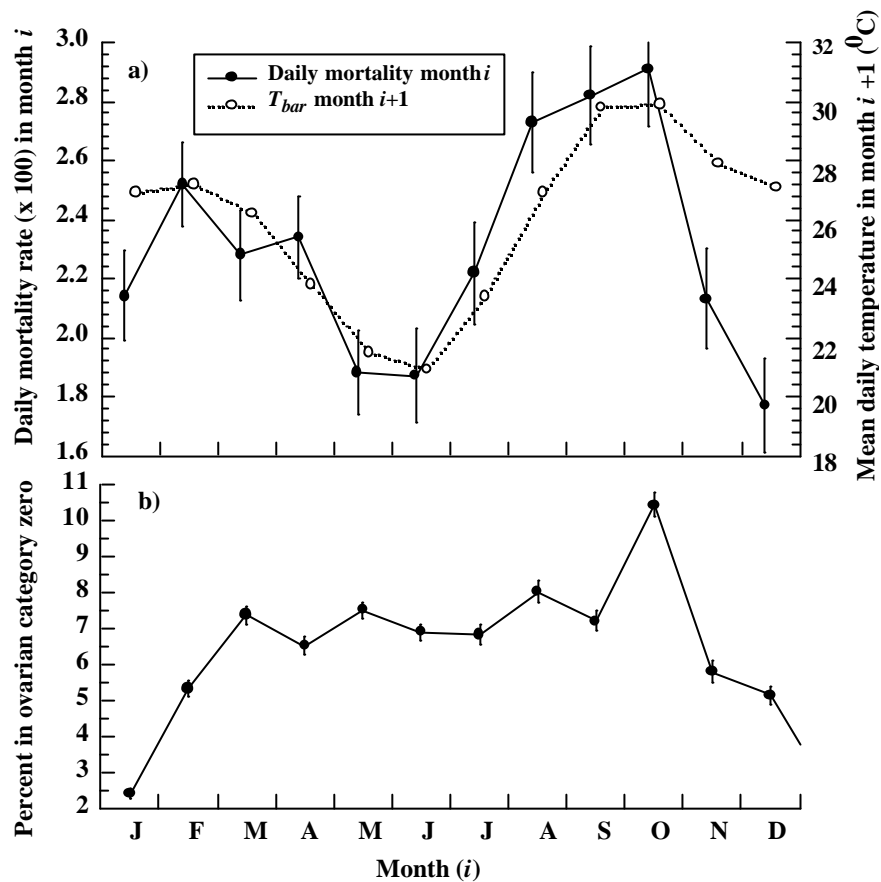


Figure 15 a) Mean daily mortality rates (\pm standard errors) of adult female *G. pallidipes* calculated by month using the data in Fig. 14. b) Annual change in the percentage (\pm standard errors) of category zero flies in samples of adult female *G. pallidipes* captured in odour-baited traps at Rekomitjje Research Station, Zimbabwe between September 1988 and January 1999.

the two methods would thus be further reduced if the mortality were markedly higher in the first week of life than at later stages, and this is clearly the case (Fig. 12).

Elevated post-emergence mortality means that category zero flies must be excluded when estimating tsetse mortality from ovarian ages using any method which assumes that mortality is independent of age. Jarry *et al.* (1996) did not exclude these flies in their analyses and would thus have over-estimated the mortality in all older flies. This tendency is further accentuated because their flies were caught in hand-nets. For female *G. m. morsitans*, at least, the probability of capture by man fly-rounds declines by an order of magnitude over the first five weeks of life.

The results reviewed above provide a warning that mortalities estimated from ovarian dissection data can be seriously misleading. Standard errors, which have never been estimated in the past, are also often disturbingly high. Thus, even for the Zimbabwe data for 1991, where estimates were based on > 800 flies each month, the standard errors averaged 23% of the mean; for Challier's (1973) data, based on only 20-160 flies, this figure rose to 74%.

Overall mortality in all developmental stages

Rogers (1979) adapted Moran's (1950) method to use time series of field samples of adult tsetse to estimate mortality across all developmental stages, as opposed to the mark-recapture and ovarian dissection, where estimates refer to adult survival only. The resulting mortality estimates are better correlated with some measure of dryness, such as saturation deficit (Fig. 16a) or an index of vegetation cover (Fig. 16b), than with temperature (Rogers, 1979, 1991; Dransfield *et al.*, 1989; Hargrove, 2001a, 2001c). Hargrove (2001c) contrasted these findings with mark-recapture estimates of adult mortality, which were generally better correlated with temperature (Figs. 9, 10). If all these findings are valid they imply, since the Moran method provides measures of mortality across a whole generation, that the immature stages must be particularly sensitive to dryness and the mature adults to temperature. This is reasonable given that the only times during the fly's life when the exoskeleton is soft, and particularly prone to water loss, are between larviposition and the formation of the puparial shell, and immediately after eclosion of the adult. It is also consistent with the finding that mortality per generation between months $i-1$ and i is more highly correlated with the saturation deficit in month $i-1$, when it is affecting the immature stages, than in month i , when the effect is chiefly on the adults.

For the Antelope Island study, Hargrove (2001a) estimated post-teneral adult mortality from mark-recapture data, and overall mortality using the Moran technique. It was thereby possible to estimate that the joint mortality in the larval/pupal and teneral adult stages was almost always markedly lower and less variable than in mature adults (Fig. 17). Since there are good reasons for supposing that teneral adults are particularly at risk (see above) their mortality was presumably higher than the level estimated for post-teneral adults. Mortality in the pupal phase is lower yet than the joint estimate. At least on Antelope Island it may have been lower than the 1%/day estimated by Jackson (1937) and Rogers & Randolph (1990).

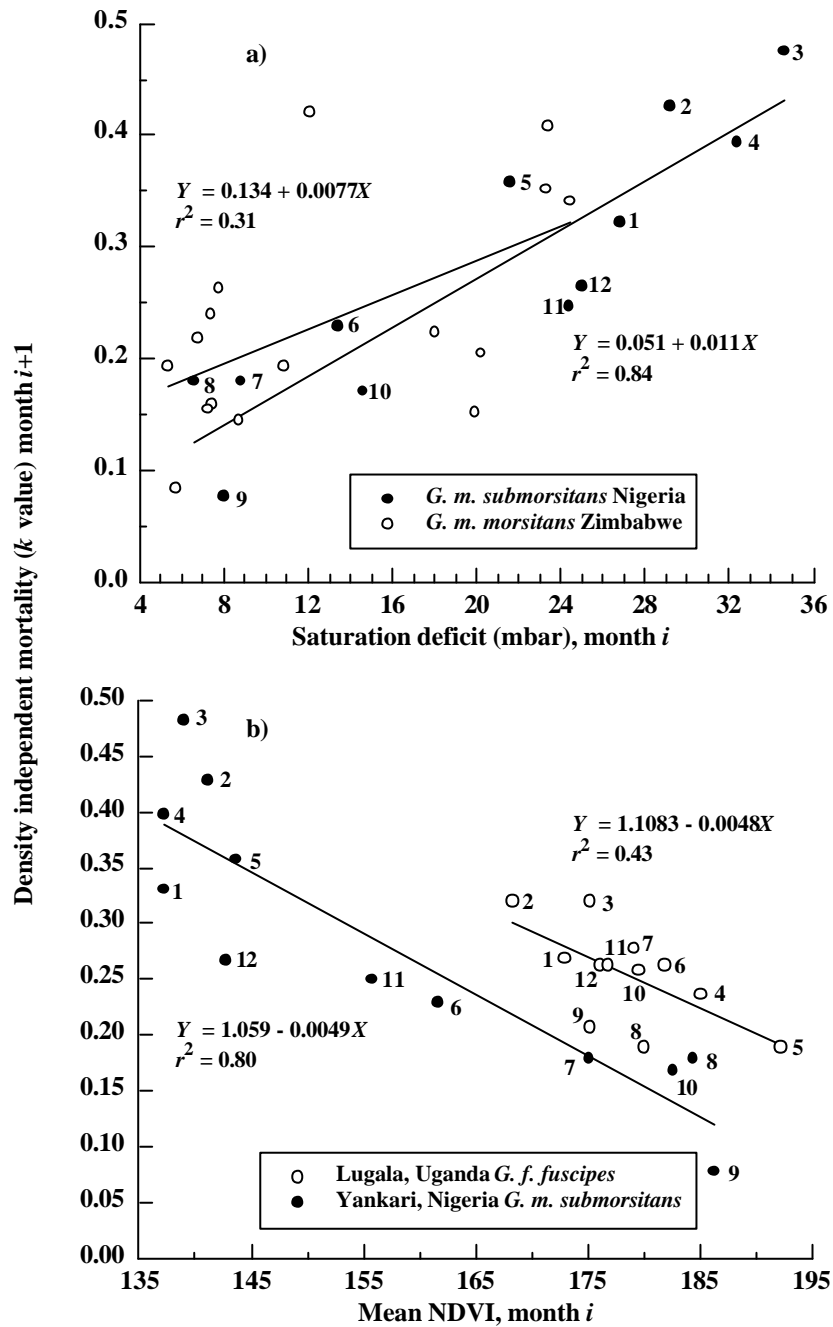


Figure 16. Survival of generations of female tsetse flies, estimated from time series of catches as described by Rogers (1979), plotted against the prevailing saturation deficit or maximum temperature. Redrawn using data from Rogers & Randolph (1991) and Hargrove (2000a).

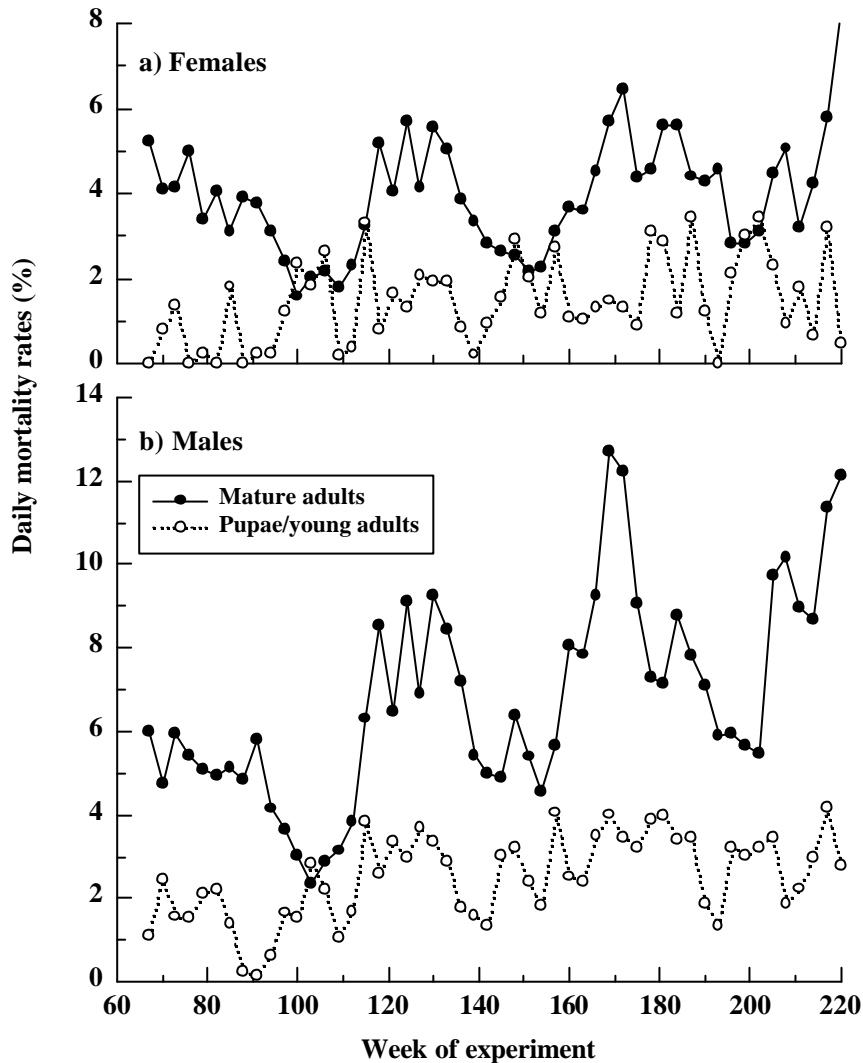


Figure 17. *Estimated mortalities of adult and immature G. m. morsitans on Antelope Island, Lake Kariba, Zimbabwe. Methods of estimation described in the text and by Hargrove (2000a).*

Growth rates of small closed populations

The relationship between growth and mortality rates

For small, closed populations, where density-dependent effects and migration can be ignored, Williams *et al.* (1990) provides a simple and powerful method for calculating the growth rate resulting from given age-dependent rates of mortality, larval production and pupal development. Since the latter two depend largely on the mean temperature (Fig. 1), the growth rate at a given temperature depends simply on mortality. For example when $T_{bar} = 25^{\circ}\text{C}$, the

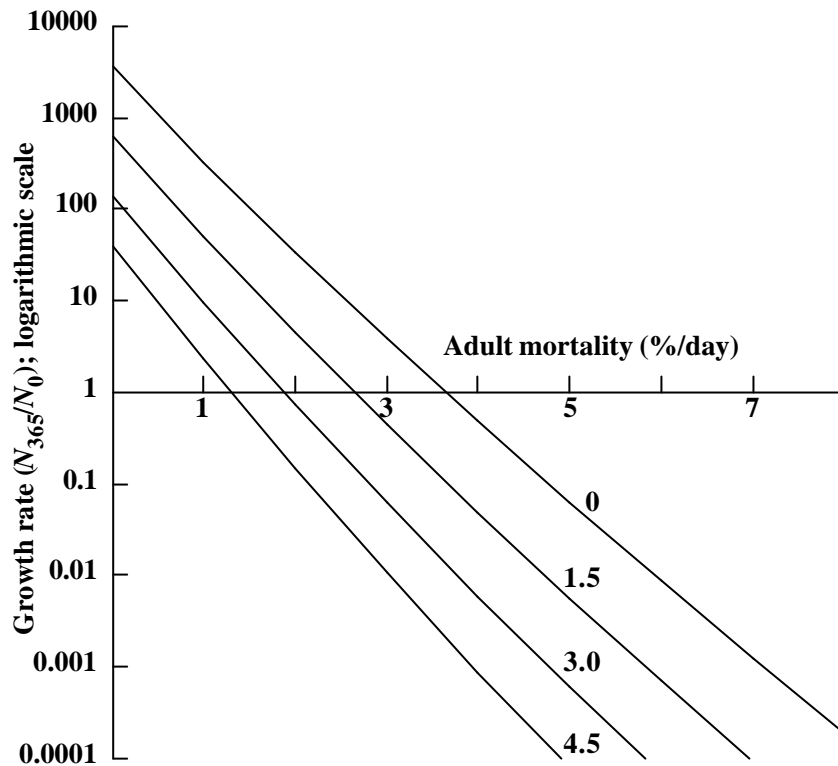


Figure 18. Predicted annual growth rates for a tsetse population living at 25°C, with various levels of daily adult and pupal mortality rates. Latter rates are shown in the body of the graph. Assumptions: Pupal duration, 27 days; first larva produced at age 7 days; subsequent pupae produced at 9-day intervals. Growth rates calculated using equation 11 of Williams *et al.* (1990).

functions in Fig. 1 predict values for I_p , I_0 and I of 29, 16 and 9 days respectively. The predicted growth rate declines exponentially with adult mortality (Fig. 18). The level of the graph varies with the pupal mortality but the slopes are approximately constant.

With zero mortality the population increases by a factor of *c.* 3500 per year or nearly doubles each month. Observed growth rates are always smaller than this, because mortality is never zero in the field, but short-term growth rates of *c.* 100 per annum have been observed (Turner & Brightwell, 1986; Vale *et al.*, 1986). Predicted maximum growth rates increase with temperature for $T_{bar} > 25^\circ\text{C}$, but these predictions grow progressively less realistic since death rates also increase with temperature (Fig. 11 and see below).

There is approximately a 10-fold change in the growth rate for each 1% change in adult mortality (Fig. 18). For the developmental periods in the previous paragraph, and assuming 20%

losses during the egg, larval and pupal phases, the population would begin to decline if the adult mortality exceeded *c.* 3.5% per day. These are important results in practical terms because they imply that if a mortality of >3.5% per day is imposed and maintained on the adult female population, the annihilation of the population is assured, regardless of the resilience of the population due to density-dependent effects. Moreover, relatively small additional increases in this imposed mortality have large negative impacts on the population.

The sensitivity of the growth rate to changes in adult female mortality stems directly from the low natural birth rate and demands that tsetse behaviour, particularly the female's, must be tailored to minimise risk. Randolph *et al.* (1992) argue that this consideration requires female tsetse to take large meals at long intervals in order to maximise lifetime fertility. It also explains the fact that female *G. m. morsitans* and *G. pallidipes*, unless they are close to starvation, do not attempt to feed on high-risk hosts such as humans (Vale, 1974). Equally, tsetse populations can be controlled and even eradicated using simple technologies which attract a small proportion (4 - 8%/day) of the female population to point sources and kill them using traps, targets or treated livestock (Vale *et al.*, 1988; Dransfield *et al.*, 1990; Bauer *et al.*, 1992).

The effect of temperature on population growth rates

Loss rates at various stages of a tsetse life are temperature dependent. Thus, the results in Fig. 4 suggest an effect of extremely high temperatures on reproductive losses, at least for *G. pallidipes* in Zimbabwe. Fat levels in emerging teneral decline at extremes of both high and low temperature (Fig. 7) and survival probabilities in this group of flies presumably follow a similar function of temperature. Density-independent mortality rates in post-teneral adult *G. m. morsitans* (Fig. 11a, b) increase exponentially with temperature.

Given these results, and the fact that reproductive rates are also temperature dependent (Fig. 1, 2), the interesting possibility arises that one can make reasonable predictions of the growth rate of a *G. m. morsitans* population in a given environment knowing nothing more than the prevailing mean temperature (T_{bar}). In doing so one needs to take account of age-related changes in female mortality (Fig. 12c) which suggest that the mortality estimates in Fig. 12 provide only an average adult mortality biased towards the mortality of the most numerous young flies. Mortality will thus be over-estimated in flies > 1-2 weeks old and under-estimated

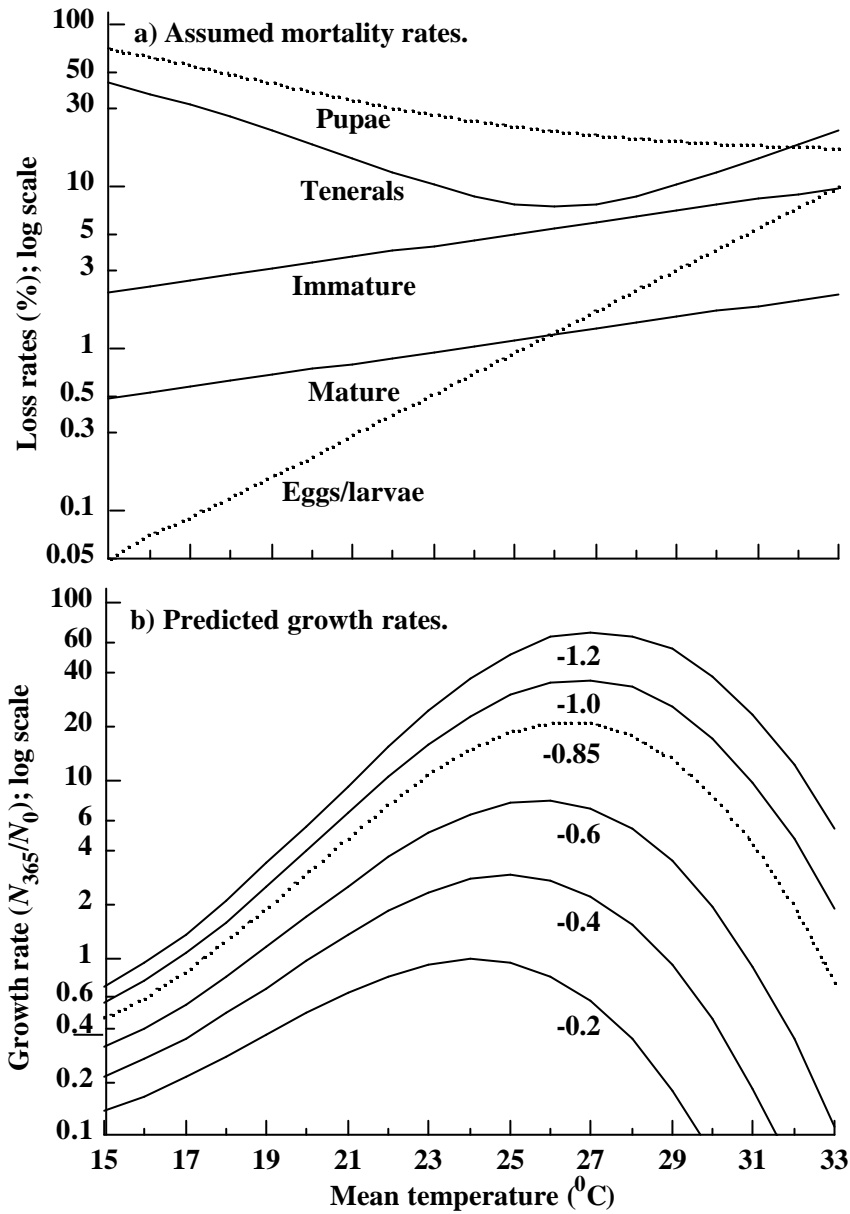


Figure 19. The relationship between mean temperature and growth rate. Developmental rates estimated using the equations in the legend for Fig. 1. **a)** Assumed mortalities. All adult mortalities (\mathbf{m}) assumed related to mean temperatures (T_{bar}) by the equation $\ln(\mathbf{m}) = A + B \cdot T_{bar}$. B is assumed to take the value 0.83 (Fig. 11b) and A is treated as a parameter which, for female *G. m. morsitans* on Antelope Island, took the value -0.85 . Pupal mortality set at 0.5% per day. **b)** Growth rates calculated using equation 11 of Williams *et al.*, 1990.

in young flies. The increased mortality in very old flies is ignored for the present since relatively few females survive to such ages.

Examples of the changes in mortality suggested by the above results, for $15 \leq T_{bar} \leq 33^{\circ}\text{C}$, are shown in Fig. 19a. Reproductive losses are assumed to increase exponentially from $c. 0$ to 10% over the given range. Losses during the pupal phase are assumed to take a constant value of 1% per day (*cf* Rogers & Randolph, 1990) independent of T_{bar} . This means of course that the total losses during the pupal period increase with decreasing temperature (Fig. 19a). Losses consequent on the increased total fat consumption at extremes of temperature are also to be expected, but these are subsumed into the teneral phase. For the post-teneral adults it was assumed that, for the first week of post-teneral life, mortality was 1.5 times the value predicted by regression in Fig. 11b. For all older flies the mortality was assumed to be only one third of the predicted value.

The dotted line in Fig. 19b shows the growth rate for the Antelope Island population of female *G. m. morsitans* predicted using the mortality data in Fig. 19a, and reproductive rates predicted from the equations in Figs. 1 and 2. This predicts that positive growth will only occur for $16 \leq T_{bar} \leq 32^{\circ}\text{C}$. A maximum rate of population increase of $c. 20$ -fold per year is predicted for $T_{bar} \approx 25 - 27^{\circ}\text{C}$. This is in good accord with the observed mean rate of increase of 23-fold per annum for the female *G. m. morsitans* population on Antelope Island between February and April 1981, for which period the temperature averaged 25.2°C .

For adult male *G. m. morsitans* the coefficient of increase in adult mortality with T_{bar} was similar for studies carried out in Zimbabwe and Tanzania (Fig. 9). Only the general level of mortality differed. In calculating the remainder of the trajectories in Fig. 19b it was assumed that the same was true for females. The figures in the body of the graph refer to the constant term (A) in the predictive equation for the mortality (see legend). As A gets closer to zero the mortality increases and the range of T_{bar} which support positive population growth decreases. Regardless of the value of A , however, maximum growth rates are always predicted to occur for temperatures in the range $24 \leq T_{bar} \leq 27^{\circ}\text{C}$.

The mortality functions used in constructing of Fig. 19b are necessarily speculative but appear reasonable given published data. The assumed maximum abortion rate of 10% is less than the observed increase in the proportion of empty uteri (Fig. 4) but greater than the 5% assumed by Williams *et al.* (1990) on the basis of ovarian dissection data from Kenya. The daily

pupal mortality was set at 0.5% given the indications of low pupal mortality on Antelope Island (see above and Fig. 17). Teneral losses are put at high levels at extremes of temperature, not unreasonably given Phelps & Clarke's (1974) estimate that up to 35% of undersized teneral are lost in the cold season and up to 75% at the height of the hot season in Zimbabwe. Partitioning the mortality between different phases of post-teneral life is again speculative but is reasonable given the age-related changes in mortality estimated on the adjacent Redcliff Island (Fig. 12).

In a recent publication on tsetse biology book Rogers *et al.* (2009) consider the relationship between climate and tsetse distribution. The present approach suggests a useful adjunct to their studies since it could be used to predict not simply the presence or absence of flies but also the potential growth rate of a tsetse population. The present model is of course a simplification of reality. Even for *G. m. morsitans*, the undoubted effect of saturation deficit or relative humidity on mortality, for some developmental stages, is ignored for the present. The qualitatively different relationship between adult mortality and temperature for *G. pallidipes* (Fig. 11) provides, moreover, a timely reminder that the situation will differ between species. Thus Rogers & Randolph (1986) have plotted three-dimensional "climograms" of overall mortality against temperature and saturation deficit and find that different species exhibit quite different climograms indicative of their differing meteorological preferences.

For any tsetse species, population growth will, in any case, be affected by food availability. Where the fly's wild hosts have been removed by, for instance, a combination of hunting and rural development, potential growth rates will be much lower than suggested by the temperature data. The model indicates, nonetheless, the potential for re-invasion of these areas should domestic livestock or alternative hosts be introduced.

Estimating the growth rate from field data

Previous sections have looked at the problem of predicting the growth rate given estimates of mortality and birth rates, or even perhaps given data on the mean temperature. Attempts have also been made to estimate the growth rate from ovarian age samples but Van Sickle (1988) showed that several such attempts were invalid because, in making the estimates, it was implicitly assumed that the growth rate was zero. The estimates are still used on occasion as if they were valid (Leak, 1998) and this can lead to misleading results. As an example, Allsopp's

(1985) growth rate estimates for *G. m. centralis* Machado in Botswana were negatively correlated with fly-round catches, and seemed therefore to be evidence in favour of density-dependence (Rogers & Randolph, 1984). The later demonstration that the growth rate estimates were invalid makes it clear that the observed correlation was in fact serendipitous.

Van Sickle (1988), Williams *et al.*, (1990) and Jarry *et al.* (1996) suggest methods whereby age distribution data can be used to provide legitimate estimates of the growth rate but, as Van Sickle (1988) pointed out, such estimates have unacceptably high variances. At present, therefore, growth rates can satisfactorily be estimated only from changes in population levels, and this normally means using changes in apparent density. This, in turn, involves the assumption that catch levels are, in general, proportional to absolute population levels and, in particular, that this proportion is indicative of weather and season.

The growth of large open populations

Dispersal

Models of normal, wild populations of tsetse, which are generally large and open must take into account the effects of movement, and the density-dependent effects which regulate the population around some characteristic level.

As with most ideas on tsetse population dynamics, early advances in the understanding of tsetse dispersal were due to C. H. N. Jackson, who concluded from his mark-recapture experiments that tsetse dispersal involved to-and-fro movements between a home range and regular feeding grounds (Jackson, 1944, 1946). Bursell (1970) argued that his data could as well be described by a random movement model, which had the advantage that it did not require tsetse to be able to navigate in what was apparently undifferentiated woodland. The model has been developed by several authors (references in Williams *et al.*, 1992), most conveniently as the equivalent formulation of a diffusion process, which is currently used as the best available description of tsetse dispersal. Estimates of the daily step length for this model are generally in the range 0.15 – 1 km. Given that the mean distance moved is approximately the product of this figure and the square root of the time since dispersal began, the average fly moves no more than 10 km from its birth place even if it lives for 100 days.

Density-dependent effects

The development so far has ignored the fact that, in a finite environment, population size has an upper limit, and when numbers approach that limit the growth rate must begin to decrease. In a closed population this means that the birth rate must decrease or the death rate increase or both. In an open population there is the further option that the net rate of emigration can increase. The important feature of the rate changes are that they are dependent on the density of the population, as opposed to the changes with temperature and saturation deficit which are density-independent. The reader is referred to papers by Rogers & Randolph (1984, 1985) for detailed discussion of the issue of density-dependence as it applies to tsetse.

Density-dependent factors are essential for the regulation of population numbers but the effects are notoriously difficult to detect (Hassell *et al.*, 1989), let alone measure, and the problem is no less severe for tsetse. Rogers (1974) placed puparia of *Glossina fuscipes fuscipes* Newstead at natural depths in the field near Lugala, Uganda and found that losses were density-dependent at densities > 4 puparia m^2 . In contrast, Rogers & Randolph (1990) found no such effect in similar experiments on *G. pallidipes* at Nguruman, Kenya.

Rogers (1974) tied adult *Glossina fuscipes fuscipes* Newstead to branches of trees with pieces of cotton and found that predation by vertebrates, but not invertebrates, was density-dependent. Given the highly artificial nature of the experiment, however, and the fact that the observed losses were 10-30 times as high as those generally observed in the field, the results of uncertain relevance to wild populations of tsetse. In fairness, however, no other worker before or since has attempted to provide experimental evidence on predation of adult tsetse. All of the other evidence on density-dependence is indirect.

In modelling tsetse populations Rogers (1990) found it necessary to include density-dependent mortality in both the adult and pupal stage in order to achieve good fits to the data (see below). Data from Zimbabwe support this indirect evidence in favour of density-dependent losses of pupae. At Rekomitjie, humans can most easily find tsetse pupae during the hot dry season, presumably because, as this season proceeds, female tsetse increasingly concentrate their larviposition activities in sites such as ant-bear burrows, under leaves on the edges of dried up river beds, and under fallen logs. This behaviour has the effect of greatly increasing the density of pupae in these larviposition sites and there is a simultaneous increase in the proportion of parasitised pupae (Fig. 5) and a marked decrease in the proportion of young flies in the

population (Fig. 15). It is reasonable to think that parasites, like humans and probably also other predators, find tsetse pupae more easily as pupal density increases and the pupae-rich sites are more easily identifiable. But the increase in pupal density is purely local. Trap catches at this time of the year suggest that adult populations, and hence presumably overall pupal density, peak in September and decline rapidly thereafter (Hargrove & Vale, 1980). Increased pupal loss rates would thus depend *directly* on local pupal density but would be *inversely* correlated with total population density. The “density-dependent” effect would thus actually work in concert with increased density-independent losses due to the increasing temperature and both would serve to drive the population below optimal levels. This interesting situation clearly merits further study

There is some evidence that feeding success is density-dependent, although Rogers & Randolph (1984) point out that this need not necessarily lead to increased mortality and, indeed, nobody has yet demonstrated such an increase. Vale (1977) found that the feeding success of *G. m. morsitans* in some field experiments in Zimbabwe, but not others, decreased as the numbers of flies visiting the host increased. Other workers, using Vale’s methods, find that the observed irritability of host animals increases with fly density but that this is not always translated into reduced feeding success (Baylis, 1996; Torr & Mangwiro, 2000; Schofield & Torr, 2001).

Indirect evidence for density-dependent effects comes from estimates of changes in growth rate with estimated changes in population size. The estimates have always been based on time series of sample catches, rather than absolute population estimates, so that an important untested assumption is that the capture probability is independent of time. For *G. p. palpalis* at Katabu in Nigeria, Rogers & Randolph (1984) found that the log of the change in fly-round catch between December and January was negatively correlated with the log of the catch in December (Fig. 20 a). Similarly, the maximum rate of increase of trap catches *G. p. palpalis* in the Ivory Coast was inversely related to catch size at the time when that increase was occurring (Fig. 20 b). In this case catches increased at a rate greater than could be explained by birth processes alone and it was concluded that density-dependent rates of invasion were involved.

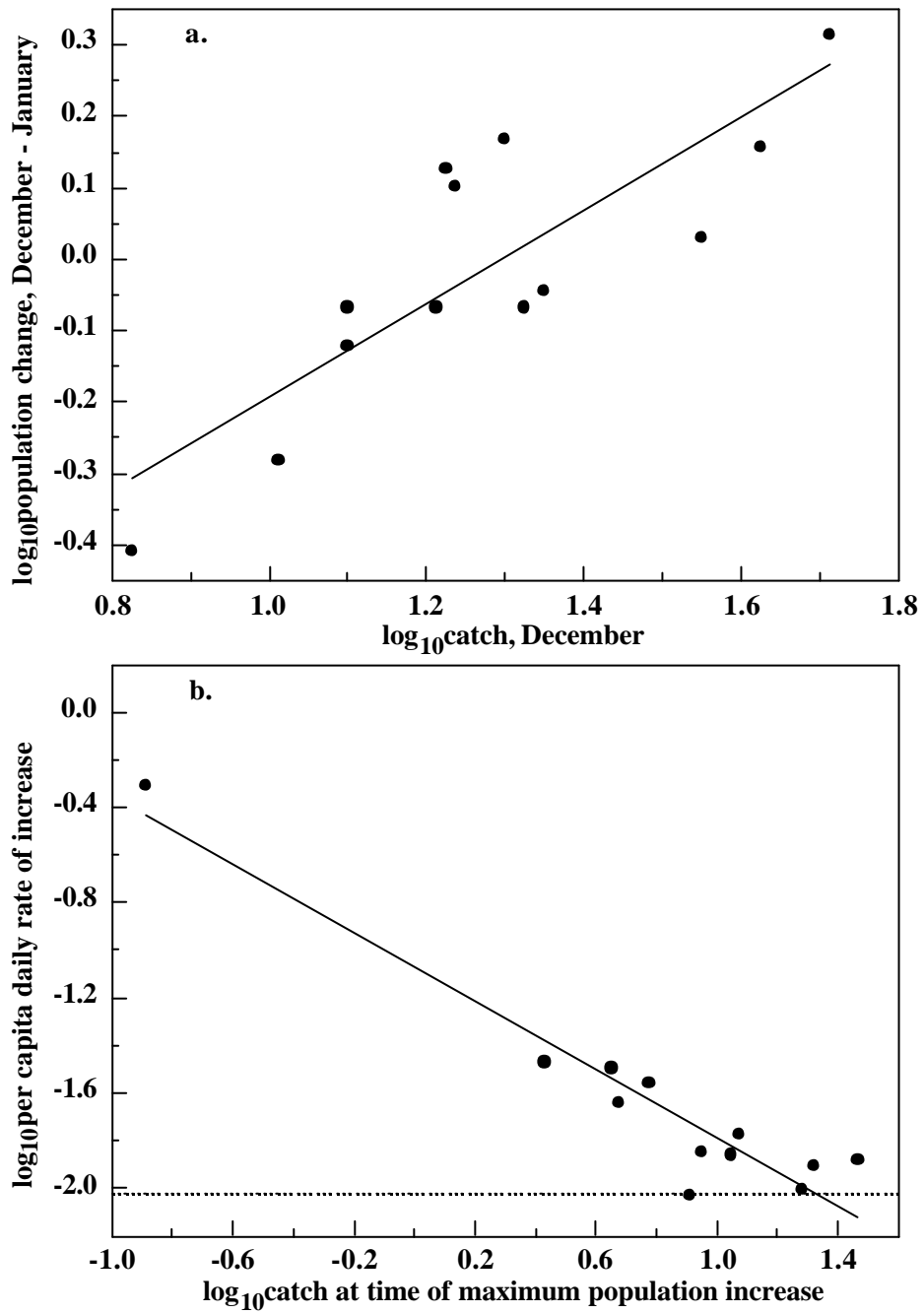


Figure 20. a) Changes in catches of *G. palpalis* at Katabu, Nigeria between months; \log January catch vs \log December catch; b) maximum rate of increase vs $1/\text{catch}$ at that time. . Redrawn from Figs. 4a and Fig. 7 of Rogers & Randolph (1984).

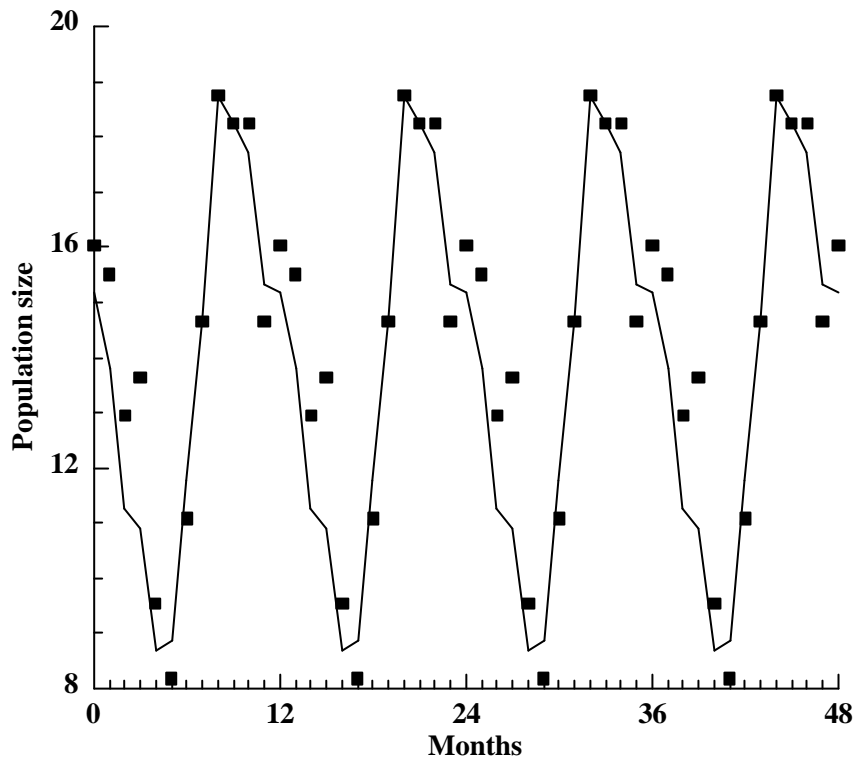


Figure 21. Simulation of changes in the population of *G. palpalis* at Katabu, Uganda. Density-independent mortalities were estimated from the data using the Moran curve method. The model included density-dependent mortality in pupal and adult phases. Redrawn from Rogers (1990).

Modelling population changes

Birth and death models

Changes in tsetse population reflect the integrated effects of numerous exogenous and endogenous factors, not all of which are fully understood, and many of which have delayed effects. These complexities make it difficult to derive analytical formulae for predicting population changes. Instead, modelling of population data has so far involved the use of computer simulation.

Rogers (1990) developed the first such model and used it to provide good fits (Fig. 21) to time series of catches of tsetse, assumed proportional to actual population levels (Rogers *et al.*, 1994). Birth rates were estimated from ambient temperatures and overall density-independent mortalities from observed changes in the population. The important result of this approach was

that it was always found essential, for population stability, to include density-dependent mortality in the model.

Hargrove & Williams (1998) developed the simulation approach further in modelling time-series of population estimates of *G. m. morsitans* on Antelope Island. By linking a simulation procedure, similar to that of Rogers (1979), to a non-linear optimisation routine it was possible to estimate, for any given model, the parameter values that produced the best fit to the data. Variables thought likely to affect mortality were entered one at a time and it was thereby possible to keep in the model only those variables which produced a significant improvement to the fit. The model was used to provide a successful fit, without any need for scaling, to estimates of changes in the absolute population of male and female *G. m. morsitans* over a period of 240 weeks (Fig. 22). This was achieved without reference to estimated mortalities, though there was a good correspondence between their predicted and observed values. Adult mortality was modelled as a linear function of maximum temperature (T_{max}) whose coefficients were estimated by the optimised simulation procedure. No other meteorological variable was required for a good fit; indeed, once (T_{max}) had been included no other meteorological variable could be included which improved the fit significantly. This result supports indications from other work (see above) of the overriding importance of temperature in controlling the density-independent growth rates of tsetse populations.

Models including migration

Williams *et al.* (1992) have made the only serious attempt at modelling the growth of large, open populations. They assumed diffusive movement and logistic growth, making no assumption about the mode of operation of the density-dependent processes, except that they applied only to the birth and death processes, not to dispersal rates. In simple terms it was assumed that each population has a characteristic carrying capacity and that the growth rate slows as this level is approached.

The resulting differential equation has no analytical solution but a solution is easily approximated using a numerical technique. The approach has been used only by Hargrove (2000) to model the re-invasion of areas cleared of tsetse and by Hargrove *et al.* (2000) to model the use of insecticide-treated livestock as a method of tsetse control. It could be used for modelling observed changes in natural tsetse population, both natural and as a consequence of

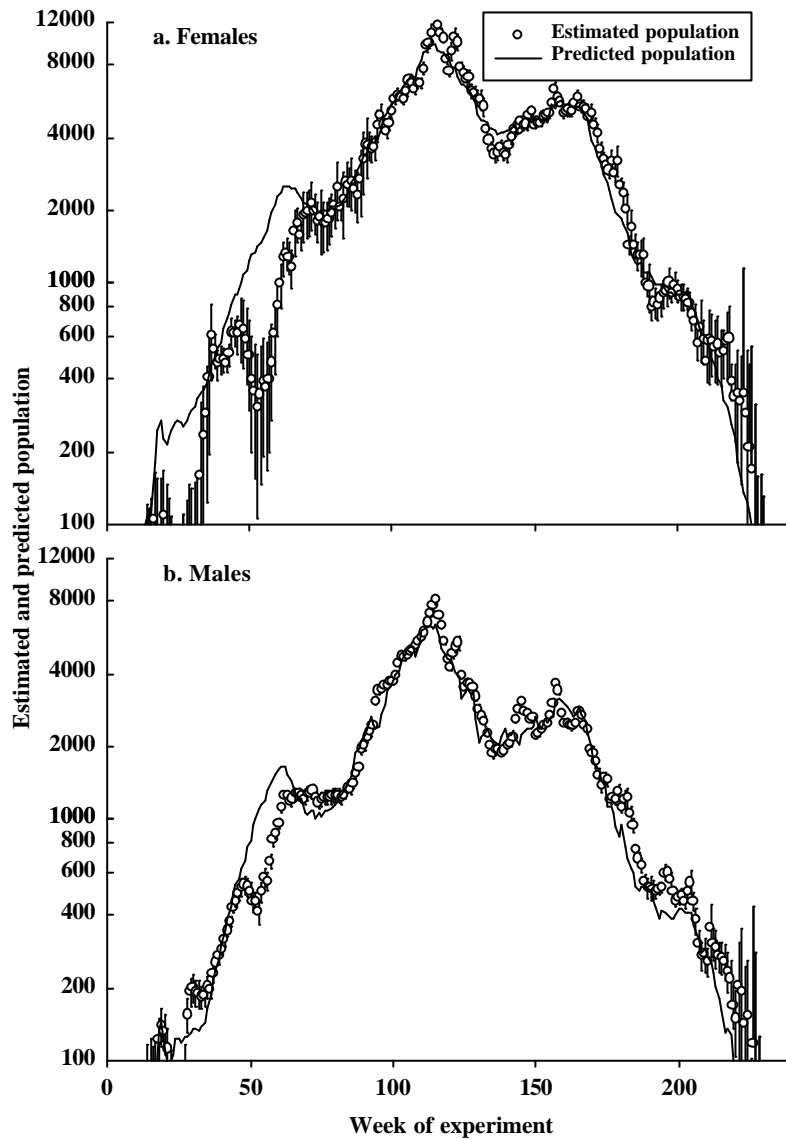


Figure 22. Simulation of changes in the population of *G. m. morsitans* on Antelope Island, Lake Kariba, Zimbabwe. Numbers in the body of the graph indicate the number of parameters in the fitted model. For the complete model, parameters related to the separate effects of maximum temperature, trapping and NDVI on mortalities of male and female flies separately. Redrawn from Hargrove & Williams (1998)

human intervention. Having obtained adequate fits to existing data it could then be used to predict the progress of other operations, needing only as input data realistic estimates of the levels of imposed mortality and rates of fly movement. As such the model provides a powerful weapon for the analysis of past, and the planning of future, control operations. It also has the potential, therefore, of providing a much-needed *objective* measure of the cost-effectiveness of different approaches to tsetse control under different circumstances.

Caveats

In the interests of simplicity, relative brevity and readability the above development has glossed over numerous difficulties associated with the estimation of the rates of birth, death, movement and growth. The scale of these difficulties is evident in an early elegant experiment in which Jackson (1946) allowed teneral *G. m. morsitans* to emerge from pupae introduced to the habitat of *G. swynnertoni* in Tanzania and captured the adults on a spiral fly-round centred on the release point. Any reasonable assumption of rates of loss of flies, by death and emigration, from the sampling area leads to the prediction of an approximately exponential decline in the numbers of flies still alive and still within the boundaries of the spiral (Fig. 23a). If the probability of capture were independent of the time (t) after release (*i.e.* the fly's age in this case) then captures should have shown a similar decline with t .

This expectation was not realised in either sex. Male catches did not decrease consistently until the seventh week after release. Females, in contrast, always showed a lower capture probability and were only caught in any numbers during the first week after emergence. Making, again, reasonable assumption of rates of loss one can estimate the probability of capture during each of the experiment. For males this increased by a factor of between five and eight during the first six weeks of life (Fig. 23b). Conversely, for females, the capture probability declined by a similar factor over the same period (Fig. 23c).

If one assumes unbiased sampling in Jackson's experiment one is led to the erroneous conclusions that male tsetse have sub-zero mortality rates and that mortality in females is higher than in males. Jackson made the point that this is not the result of random sampling error but rather to consistent sampling biases, specific to the fly-found system, which are functions of the age and the sex of the flies being sampled. This was only clear because of the sophisticated

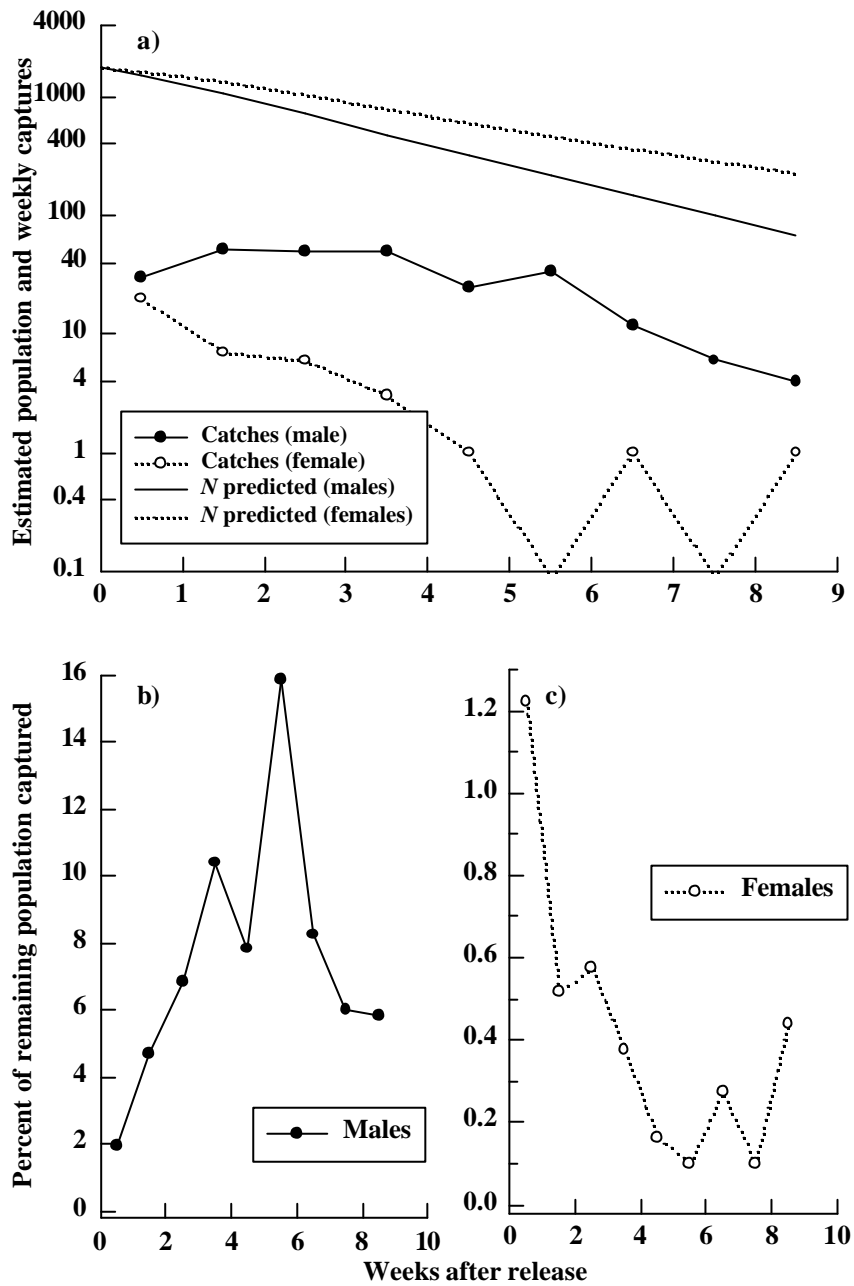


Figure 23. a) Recaptures of male and female *G. m. morsitans* on a square spiral fly-round (Jackson, 1946) and the population estimated to be alive and inside the boundary of the spiral at different ages. Constant death rates of 4 and 2% per day were assumed for males and females respectively. Both sexes were assumed to disperse according a diffusion process with a coefficient of $0.3 \text{ km}^2/\text{day}$. b), c) Estimated capture probabilities for males and females estimated from the results in a).

nature of the experiment, which served as an early warning about the dangers involved in the interpretation of tsetse sampling data.

There is no *a priori* reason to suppose that the biases inherent in other sampling systems are less severe than those seen in the fly-round method. The difficulty lies in measuring the bias, as is clear from Fig. 23. While male capture probability clearly increased with age it is not possible to provide quantitative estimates of the bias. The estimated bias functions in Fig. 23 depend entirely on *assumed* rates of mortality and dispersal, the very rates we would like to *estimate* from the data. But one can only make those estimates if one knows the bias. This manner of problem has been appreciated with respect to other fields of endeavour (Heller, 1964).

Jackson (1944, 1948) had, in fact, carried out a prodigious series of mark-recapture experiments prior to his discovery of the age-dependent sampling bias. Re-analysis of these data suggests that the anomalies which puzzled Jackson were due in part to age-related changes in capture probability (Hargrove, 1981). In order to provide a good fit to the data it also helped, however, to assume that death and dispersal rates changed with age. Independent evidence has since been presented that such changes do occur throughout adult life (Hargrove, 1990, 1991). Taking these changes into account complicates the analysis of data on tsetse population dynamics. Nonetheless, a complete understanding of the subject demands that we ultimately make sense of the reason behind, and the effect of, these interesting changes with age in the biology of the tsetse fly.

Conclusions

The preceding review, and Rogers' chapter on tsetse distribution, suggests that we are now able to predict with some confidence the behaviour of tsetse populations under a wide variety of circumstances. In particular, on the practical level of fly and disease control, we can predict how quickly fly populations grow under different levels of imposed mortality, how quickly they can re-invade cleared areas and what we need to do in order to prevent this happening. In short, advances in our understanding of population dynamics have given us the ability to predict the outcome of various approaches to tsetse and trypanosomosis control. It should therefore be possible to select the most sensible, cost-effective, approach to a given disease situation. A recent report (Hargrove, 2003) may stimulate discussion on this subject.

References

- Allsopp, R.** (1985) Variation in the rates of increase of *Glossina morsitans centralis* and their relevance to control. *Journal of Applied Ecology*, **22**, 91-104.
- Anon** (1955) *Notes for the study of tsetse flies in East Africa*, Nairobi, East Africa High Commission.
- Bauer, B., Kabore, I., Liebisch, A., Meyer, F. & Petrich-Bauer, J.** (1992) Simultaneous control of ticks and tsetse flies in Satiri, Burkina Faso, by the use of flumethrin pour-on for cattle. *Tropical Medicine and Parasitology* **42**, 41-46.
- Baylis, M.** (1996) Effect of defensive behaviour by cattle on the feeding success and nutritional state of the tsetse fly *G. pallidipes* (Diptera: Glossinidae). *Bulletin of Entomological Research* **86**, 329-336.
- Bursell, E.** (1960) The effect of temperature on the consumption of fat during pupal development in *Glossina*. *Bulletin of Entomological Research*, **51**, 583-598.
- Bursell, E.** (1961) Starvation and desiccation in tsetse flies (*Glossina*). *Entomologia Experimentalis et Applicata*, **4**, 301-310.
- Bursell, E.** (1970) Dispersal and concentration of *Glossina*. in *The African Trypanosomiasis* (Ed. H. W. Mulligan). pp 382-394. London, George Allen and Unwin.
- Bursell, E. & Glasgow, J. P.** (1960) Further observations on lakeside and riverine communities of *Glossina palpalis fuscipes* Newstead. *Bulletin of Entomological Research*, **51**, 47-56.
- Bursell, E., Billing, K.J.C., Hargrove, J.W., McCabe, C.T. & Slack, E.** (1974) Metabolism of the bloodmeal in tsetse flies. *Acta Tropica*, **31**, 297-320.
- Challier, A.** (1965) Amélioration de la méthode de détermination de l'âge physiologique des glossines. Études faites sur *Glossina palpalis palpalis* Vanderplank, 1949. *Bulletin de la Société de Pathologie Exotique*, **58**, 250-259.
- Challier, A.** (1973) Ecologie de *Glossina palpalis gambiensis* Vanderplank, 1949 (Diptera-Muscidae) en savanne d'Afrique Occidentale. *Mémoire O.R.S.T.O.M.*, No. 64, Paris. 274pp.
- Challier, A. & Turner, D. A.** (1985) Methods to calculate survival rate in tsetse fly (*Glossina*) populations. *Annals de la Société belge Médecine Tropicale*, **65**, 191-197.
- Chorley, J. K.** (1929) The bionomics of *Glossina morsitans* in the Umniati fly belt, Southern Rhodesia, 1922-1923. *Bulletin of Entomological Research*, **20**, 279-301.

- Dransfield, R.D., Brightwell, R., Kyorku & Williams, B.** (1990) Control of tsetse fly (Diptera: Glossinidae) populations using traps at Nguruman, south-west Kenya. *Bulletin of Entomological Research*, **80**, 265-276.
- Dransfield, R.D., Brightwell, R., Kiilu, J., Chaudhury, M.F. & Adabie, D.A.** (1989) Size and mortality rates of *Glossina pallidipes* in the semi-arid zone of southwestern Kenya. *Medical and Veterinary Entomological*, **3**, 83-95.
- Glasgow, P.A.** (1961) Selection for size in tsetse flies. *Journal of Animal Ecology* **30**, 87-94.
- Gouteux, J-P** (1982) Analyse des groupes d'age physiologique des femelles de glossines. Calcul de la courbe de survie, du taux de mortalite, des ages maximal et moyen. *Cahiers de l'Office de la Recherche Scientifique et Technique Outre-Mer, Serie Entomologie Medicale et Parasitologie*, **20**, 189-197.
- Gouteux, J-P. & Kiéno, J.P.** (1982) Observations sur les glossines d'un foyer forestier de trypanosomiase humaine en Côte d'Ivoire. 5. Peuplement de quelques biotopes caractéristiques: plantations, forêt et galerie forestière. *Cahiers de l'Office de la Recherche Scientifique et Technique Outre-Mer, Série Entomologie Médicale et Parasitologie*, **20**, 41-61.
- Gouteux, J-P. & Laveissière, C.** (1982) Écologie des glossines en secteur pré-forestier de Cote d'Ivoire. 4. Dynamique de l'écodistribution en terroir villageois. *Cahiers de l'Office de la Recherche Scientifique et Technique Outre-Mer, Série Entomologie Médicale et Parasitologie*, **24**, 199-229.
- Hargrove, J. W.** (1981) Tsetse dispersal reconsidered. *Journal of Animal Ecology*. **50**, 351-373.
- Hargrove, J. W.** (1988) Tsetse: the limits to population growth. *Medical and Veterinary Entomology*, **2**, 203-217.
- Hargrove, J. W.** (1990) Age-dependent changes in the probabilities of survival and capture of the tsetse fly *Glossina morsitans morsitans* Westwood. *Insect Science and its Application* **11**, 323-330.
- Hargrove, J. W.** (1991) Ovarian ages of tsetse flies (Diptera: Glossinidae) caught from mobile and stationary baits in the presence and absence of humans. *Bulletin of Entomological Research* **81**, 43-50.
- Hargrove, J. W.** (1993) Age-dependent sampling biases in tsetse flies (*Glossina*). Problems associated with estimating mortality from sample age distributions. pp. 549-556. *In*

Management of Insect Pests: Nuclear and Related Molecular and Genetic Techniques.

***pp. International Atomic Energy Agency, Vienna..

Hargrove, J. W. (1994) Reproductive rates of tsetse flies in the field in Zimbabwe.

Physiological Entomology **19**, 307-318.

Hargrove, J. W. (1999a) Reproductive abnormalities in field tsetse flies in Zimbabwe.

Entomologia Experimentalis et Applicata, **92**, 89-99.

Hargrove, J. W. (1999b) Nutritional levels of female tsetse *Glossina pallidipes* from artificial refuges. *Medical and Veterinary Entomology*, **13**, 150-164.

Hargrove, J. W. (1999c) Lifetime changes in the nutritional characteristics of female tsetse flies *Glossina pallidipes* caught in odour-baited traps. *Medical and Veterinary Entomology*, **13**, 165-176.

Hargrove, J.W. (2000) A theoretical study of the invasion of cleared areas by tsetse flies (Diptera: Glossinidae). *Bulletin of Entomological Research* **90**, 201-209.

Hargrove, J. W. (2001a) Mark-recapture and Moran curve estimates of the survival probabilities of an island population of tsetse flies *Glossina morsitans morsitans* (Diptera: Glossinidae). *Bulletin of Entomological Research* **91**, 25-36.

Hargrove, J. W. (2001b) The effect of climate on density-independent mortality in populations of male *Glossina m. morsitans* in Zimbabwe and Tanzania. *Bulletin of Entomological Research* **91**, 79-86.

Hargrove, J. W. (2001c) Factors affecting density-independent survival of an island population of tsetse flies in Zimbabwe. *Entomologia Experimentalis et Applicata* **100**, 151-164.

Hargrove, J. W. (2003) *Tsetse eradication; sufficiency, necessity and desirability*. DFID Animal Health Programme, Edinburgh, UK. 133 + ix pp

Hargrove, J. W. & Coates, T. W. (1990) Metabolic rates of tsetse flies in the field as measured by the excretion of injected caesium. *Physiological Entomology* **15**, 157-166.

Hargrove, J. W. & Langley, P. A. (1993) A field trial of pyriproxyfen-treated targets as an alternative method for controlling tsetse (Diptera: Glossinidae). *Bulletin of Entomological Research*, **83**, 361-368.

Hargrove, J. W. & Vale, G. A. (1980) Catches of *Glossina morsitans morsitans* Westwood and *G. pallidipes* Austen (Diptera: Glossinidae) in odour-baited traps in riverine and deciduous

- woodlands in the Zambesi Valley of Zimbabwe. *Bulletin of Entomological Research*, **70**, 571-578.
- Hargrove, J. W. & Williams, B. G.** (1998) Optimized simulation as an aid to modelling, with an application to the study of a population of tsetse flies, *Glossina morsitans morsitans* Westwood (Diptera: Glossinidae). *Bulletin of Entomological Research*, **88**, 425-435.
- Heaversedge, R. C.** (1969a) Insect parasites of *Glossina pallidipes* Aust. puparia in Rhodesia. *Journal of the Entomological Society of South Africa*, **32**, 225-229.
- Heaversedge, R. C.** (1969b) Levels of insect parasitism of *Glossina morsitans orientalis* Vanderplank (Diptera) in Rhodesia. *Journal of the Entomological Society of South Africa*, **32**, 231-235.
- Heller, J.** (1964) *Catch-22*.
- Jackson, C. H. N.** (1937) Some new methods in the study of *Glossina morsitans*. *Proceedings of the Zoological Society Lond.* **1936**, 811-894.
- Jackson, C. H. N.** (1944) The analysis of a tsetse fly population II. *Annals of Eugenics*, **12**, 176-205.
- Jackson, C. H. N.** (1946) An artificially isolated generation of tsetse flies (Diptera). *Bulletin of Entomological Research*, **37**, 291-299.
- Jackson, C. H. N.** (1948) The analysis of a tsetse fly population. III. *Annals of Eugenics* **14**, 91-108.
- 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.
- Jarry, M., Gouteux, J.-P. & Khaladi, M.** (1996) Are tsetse fly populations close to equilibrium? *Acta Biotheoretica*, **44**, 317-33.
- Jordan, A. M. & Curtis, C. F.** (1972) Productivity of *Glossina morsitans* Westwood maintained in the laboratory, with particular reference to the sterile - insect release method. *Bulletin of the World Health Organisation* **46**, 33-38.
- Leak, S.G.A.** (1998) *Tsetse biology and ecology: their role in the epidemiology and control of trypanosomosis*. CABI Publishing. Oxford and New York. 568pp.
- Moran, P. A. P.** (1950) Some remarks on animal population dynamics. *Biometrics*, **6**, 250-258.

- Nash, T. A. M.** (1933) A statistical analysis of the climatic factors influencing the density of *Glossina morsitans* Westw. *Journal of Animal Ecology* **2**, 197-203.
- Phelps, R. J.** (1973) The effect of temperature on fat consumption during the puparial stages of *Glossina morsitans morsitans* Westw. (Dipt., Glossinidae) under laboratory conditions, and its implication in the field. *Bulletin of Entomological Research*, **62**, 423-438.
- Phelps, R.J. & Burrows, P. M.** (1969a) Puparial duration in *Glossina morsitans orientalis* under conditions of constant temperature. *Entomologia Experimentalis et Applicata* , **12**, 33-43.
- Phelps, R.J. & Burrows, P. M.** (1969b) Prediction of the puparial duration in *Glossina morsitans orientalis* Vanderplank under field conditions. *Journal of Applied Ecology*, **6**, 323-337.
- Phelps, R.J. & Burrows, P. M.** (1969c) Lethal temperatures for puparia of *Glossina morsitans orientalis*. *Entomologia Experimentalis et Applicata*, **12**, 22-32.
- Phelps, R. J. & Clarke, G.P.Y.** (1974) Seasonal elimination of some size classes in males of *Glossina morsitans morsitans* Westw. (Diptera, Glossinidae). *Bulletin of Entomological Research*, **64**, 313-324.
- Randolph, S. E. & Rogers, D. J.** (1984) Movement patterns of the tsetse fly *Glossina palpalis palpalis* (Robineau-Desvoidy) (Diptera: Glossinidae) around villages in the pre-forest zone of Ivory Coast. *Bulletin of Entomological Research*, **74**, 689-705.
- Randolph, S.E., Rogers, D.J. & Kiilu, J.** (1990) Rapid changes in the reproductive cycle of wild-caught tsetse, *Glossina pallidipes* Austen, when brought into the laboratory. *Insect Science and its Application*, **11**, 347-354.
- Randolph, S.E., Williams, B.G., Rogers, D.J. & Connor, H.** (1992) Modelling the effect of feeding-related mortality on the feeding strategy of tsetse (Diptera: Glossinidae). *Medical and Veterinary Entomology* **6**, 231-240.
- Rogers, D.J.** (1974) Natural regulation and movement of tsetse fly populations. In: *Les Moyens de Lutte contre les Trypanosomes et leur Vecteurs*, pp.35-38. Paris: Institut Elevage Medicale Veterinaire Pays Tropicale. 387 pp.
- Rogers, D. J.** (1979) Tsetse population dynamics and distribution: a new analytical approach. *Journal of Animal Ecology*, **48**, 825-849.

- Rogers, D. J.** (1990) A general model for tsetse populations. *Insect Science and its Application*, **11**, 331-346.
- Rogers, D. J.** (1991) Satellite imagery, tsetse and trypanosomiasis in Africa. *Preventive Veterinary Medicine*, **11**, 201- 220.
- Rogers, D. J. & Randolph, S. E.** (1984) A review of density-dependent processes in tsetse populations. *Insect Science and its Application*, **5**, 397-402.
- Rogers, D. J. & Randolph, S. E.**(1985) Population ecology of tsetse. *Annual Review of Entomology*, **30**, 197-216.
- Rogers, D. J. & Randolph, S. E.**(1986) Distribution and abundance of tsetse flies (*Glossina* spp.). *Journal of Animal Ecology*, **55**, 1007-1025.
- Rogers, D.J. & Randolph, S.E.** (1990) Estimation of rates of predation on tsetse. *Medical and Veterinary Entomology*, **4**, 195-204.
- Rogers, D.J. & Randolph, S.E.** (1991) Mortality rates and population density of tsetse flies correlated with satellite imagery. *Nature*, **351**, 195-204.
- Rogers, D. J., Hendrickx, G. & Slingenbergh, J.** (1994) Tsetse flies and their control. *Revue Scientifique et Technique de l'Office International des Epizooties*, **13**, 1075-1124.
- Rogers, D. J., Randolph, S. E. & Kuzoe, F. A. S.** (1984) Local variation in the population dynamics of *Glossina palpalis palpalis* (Robineau-Desvoidy) (Diptera: Glossinidae). I. Natural population regulation. *Bulletin of Entomological Research*, **74**, 403-423.
- Schofield, S. & Torr, S.J.** (2001) A comparison of the feeding behaviour of tsetse and stable flies. *Medical and Veterinary Entomology* **15**, (submitted for publication).
- Torr, S.J.** (1994) Responses of tsetse flies (Diptera Glossinidae) to warthog (*Phacochoerus aethiopicus* Pallas). *Bulletin of Entomological Research*, **84**, 411-419.
- Torr, S. J. & Hargrove, J. W.** (1998) Factors affecting the landing and feeding responses of the tsetse fly *Glossina pallidipes* to a stationary ox. *Medical and Veterinary Entomology*, **12**, 196-207.
- Torr, S. J. & Mangwiro, T. N. C.** (2000) Interactions between cattle and biting flies: effects on the feeding rate of tsetse. *Veterinary Entomology* **14**, 400-409.
- Turner, D.A. & Brightwell, R.** (1986) An evaluation of a sequential aerial spraying operation against *Glossina pallidipes* Austen (Diptera: Glossinidae) in the Lambwe Valley of Kenya:

- aspects of the post-spray recovery and evidence of natural population regulation. *Bulletin of Entomological Research*, **76**, 331-349.
- Turner, D. A. & Snow, W. F.** (1984) Reproductive abnormality and loss in natural populations of *Glossina pallidipes* Austen (Diptera: Glossinidae) in Kenya. *Bulletin of Entomological Research*, **74**, 299-309.
- Vale, G. A.** (1974) The responses of tsetse flies (Diptera: Glossinidae) to mobile and stationary baits. *Bulletin of Entomological Research*, **64**, 545-588.
- Vale, G.A.** (1977) Feeding responses of tsetse flies (Diptera: Glossinidae) to stationary hosts. *Bulletin of Entomological Research*, **67**, 635-649.
- Vale, G.A., Hargrove, J.W., Cockbill, G.F. & Phelps, R.J.** (1986) Field trials of baits to control populations of *Glossina morsitans morsitans* Westwood and *G. pallidipes* Austen (Diptera: Glossinidae). *Bulletin of Entomological Research*, **76**, 179-193.
- Vale, G.A., Lovemore, D. F., Flint, S. & Cockbill, G.F.** (1988) Odour-baited targets to control tsetse flies, *Glossina* spp. (Diptera: Glossinidae), in Zimbabwe. *Bulletin of Entomological Research*, **78**, 31-49.
- Van Sickle, J.** (1988) Invalid estimates of the rate of population increase from *Glossina* (Diptera: Glossinidae) age distributions. *Bulletin of Entomological Research*, **78**, 155-161.
- Van Sickle, J. & Phelps, R. J.** (1988) Age distributions and reproductive status of declining and stationary populations of *Glossina pallidipes* Austen (Diptera: Glossinidae) in Zimbabwe. *Bulletin of Entomological Research*, **78**, 51-61.
- Williams, B., Dransfield, R. & Brightwell, R.** (1990) Tsetse fly (Diptera: Glossinidae) population dynamics and the estimation of mortality rates from life-table data. *Bulletin of Entomological Research*, **80**, 479-485.
- Williams, B., Dransfield, R. & Brightwell, R.** (1992) The control of tsetse flies in relation to fly movement and trapping efficiency. *Journal of Applied Ecology*, **29**, 163-179.