The effect of temperature and saturation deficit on mortality in populations of male *Glossina m. morsitans* (Diptera: Glossinidae) in Zimbabwe and Tanzania

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Abstract

The methods of Bailey and of Jolly and Seber were used to provide maximum likelihood estimates of population parameters for Jackson's classical mark–recapture experiments on males of the tsetse fly *Glossina m. morsitans* Westwood. These were compared with Jolly-Seber (J-S) estimates for the same fly from more recent work on Antelope Island, Lake Kariba, Zimbabwe. The Bailey estimates of birth and death rates and total population size had markedly lower variances than Jackson's originals. Both sets of estimates provided moving averages over 6-week periods, whereas the Jolly-Seber analysis provided independent weekly estimates and their variance is consequently higher. Saturation deficit and maximum temperature (T_{max}) accounted for 11 and 16% respectively of the variance in independent 4-week means of the weekly J-S survival probabilities. Analysis of covariance, carried out on a joint data set of smoothed J-S estimates of the survival probability in Tanzania and Zimbabwe, showed a significant effect of T_{max} on survival. When this effect was removed, the survival probability in the Tanzania studies was found to be 8% lower than on Antelope Island. The two effects accounted for 50% of the variance in the joint data. When saturation deficit was substituted for T_{max}, regression only accounted for 35% of the variance. If saturation deficit is important in determining tsetse survival, it must act on stages other than the post-teneral adult. Given the continuous increase in mortality, even at moderate temperatures, it is hard to envisage a direct effect of T_{max}. There may be an indirect effect, however, via the number of hunger-related deaths resulting from the increase in the feeding rate with increasing temperature.

Introduction

Between 1935 and 1940, in Tanzania, Jackson (1937, 1941, 1944, 1948) carried out a prodigious series of mark–release–recapture experiments using male tsetse (*Glossina m. morsitans* Westwood) (Diptera: Glossinidae). At their peak, the experiments involved the labours of several hundred people, catching and marking flies over an area > 80 km^2.

They were the first of their type carried out on any insect and among the first on any animal. The resulting estimates of the rates of birth, death and movement, and of changes in population level, have had a profound impact on our understanding of tsetse biology.

Bailey (1951) pointed out, however, that Jackson's estimation procedure was unsatisfactory and he developed maximum likelihood estimates for the loss and recruitment rates, population size and their variances. The calculation procedures involve iterative techniques not easily performed without a computer. Perhaps for this reason, nobody has applied Bailey's solutions to the original data. The data can

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also be analysed using the model developed by Jolly (1965) and Seber (1965) but, again, this analysis has never been applied to Jackson's full data set.

With advances in satellite imagery and related technology it is possible to provide excellent assessments of the geography of tsetse habitat. There is considerable interest in linking such data to mortality rates, which are an important factor in deciding the fly's distribution (Rogers, 1991; Rogers & Randolph, 1991). Since good field estimates of the mortality are rare, Jackson's data are important for such studies and merit proper analysis. They are also important for comparison with more recent mark–recapture estimates, obtained in Zimbabwe, for the same sex and species of fly (Hargrove & Williams, 1998; Hargrove, 2001 and unpublished). Maximum likelihood estimates derived using Bailey's method and the Jolly-Seber (J-S) approach are accordingly presented below and are shown to be markedly better than the originals. The results provide an opportunity to re-assess the importance of different climatic variables as determinants of mortality in tsetse.

Methods

Between January 1935 and April 1938 captures of male tsetse were made throughout an area of 1.8 square miles at Kakoma, Tanzania (5°47′S, 32°30′E) (Jackson, 1944). From July 1938 until May 1940 the experimental area was expanded to 16 square miles (c. 41 km^2). These areas are referred to as the small and large squares respectively. Between August 1938 and August 1939 identical experiments were also carried out in another (4 × 4)-mile square at Kisoko, 8 miles from the square at Kakoma.

Each fly was marked according to the week of capture, and released, a note being taken of any mark which the fly might already bear from previous weeks. For flies released in a given week, the change in the proportion of recaptures in the samples of subsequent weeks allows the estimation of the population level and the rate of recruitment. Using the same data, records in a given sample of the recaptures from a series of previous marked releases provide another estimate of the population and one of the loss rate. Jackson termed these the 'positive' and 'negative' methods respectively.

Wet and dry bulb mercury thermometers were housed in a Stevenson screen at Kakoma. At 0800 h each day, maximum and minimum temperatures were recorded for the previous 24 h period, together with the wet and dry bulb readings. These were used to estimate the daily saturation deficit, though Jackson only presented weekly means for this variable.

Bailey (1951) developed maximum likelihood estimates for the mortality and birth rates and the total population. The same data can also be used to generate a complete set of population parameters using the J-S model. This approach is generally thought of as being applicable to situations where animals are repeatedly marked and recaptured, so-called 'multiple-recapture' exercises. Jolly pointed out, however, that the word 'multiple' is misleading. Only the most recent mark on a recaptured fly is of importance in the J-S analysis. There is thus no difference, in terms of the analysis, between situations where animals are marked and recaptured either once or many times. The benefit of the latter approach is simply that there is an increase in the information available from the data. Jackson (1948) did in fact present data on flies which had been marked and recaptured on more than one occasion. Data on flies recaptured twice were pooled according to the month of the first recapture (Jackson, 1948; table 7), whereas the single recaptures were pooled according to the week of marking and recapture. In order to use the former data, their weekly distribution was estimated on the assumption that their recapture probability was the same as for flies marked and released at the same time, but recaptured only once. Information relating to the relatively small numbers of flies captured more than twice was not available.

Preliminary analysis showed that the means and variances of the J-S estimates differed little whether re-recaptures were excluded or included, despite the increased information available in the latter data. Inaccuracies would have been introduced in any attempt to reconstruct the weekly distribution of re-recaptures and, since they accounted for only 11% of all recaptures, the analysis below is restricted to estimates derived from single recaptures.

Jackson (1941) described how he split the large experimental square into quadrants and marked flies according to their quadrant of capture. From the distribution of recaptures within and between these quadrants he estimated emigration and immigration rates of 3% per week, with a standard error of c. 0.6% (Hargrove, 1981). For the small square, which was not divided into quadrants, no such estimate was possible but, given the difference in the areas of the large and small squares, Jackson estimated emigration and immigration rates of 10% for the latter. He subtracted these figures from the recruitment and loss rates to produce estimates of birth and mortality. The same procedure has been followed here.

In mark–recapture experiments carried out on Antelope Island, Lake Kariba, Zimbabwe all of the information on every mark on every fly is available and it was possible to produce a full set of J-S estimates. Experimental details are given by Vale et al. (1986) and estimates of survival probability and total population, covering the full 220 weeks of the experiment, are given by Hargrove & Williams (1998). Estimates for the marked population, marked fraction and probability of recapture were corrected using the procedure described by Hargrove & Borland (1994). Since analysis is complicated by added artificial mortality imposed through the introduction of odour-baited traps and targets (Vale et al., 1986) the present analysis is restricted to results for the period February 1980 to December 1981 when there was no significant trapping pressure.

Survival probability, mortality rate and instantaneous mortality rate

Jackson and Bailey's developments give rise to estimates of instantaneous mortality rates whereas Jolly and Seber estimate survival probability. The relationship between these two measures needs to be defined explicitly to avoid confusion. If a fly survives a unit of time with probability ϕ then it is said to have a mortality of $1 - \phi$, often expressed as a percentage. If the probability that the fly dies in some small unit of time (δt) is approximately $\mu \delta t$ then μ is termed the instantaneous mortality rate (units time^{-1}) and:

$$\phi(t) = \exp(-\mu) \tag{1}$$

When μ is small $\phi \approx 1 - \mu$ or $\mu \approx 1 - \phi$ so that the mortality and the instantaneous mortality rate are approximately the

same. Thus if $\mu = 0.03$ per day then $\phi = 0.9704 \approx 0.97 = 1 - \mu$ and the mortality is approximately 3% per day. When the instantaneous mortality rate is large, and/or the time over which the mortality is measured is large, this approximation does not hold and the mortality must then be calculated using equation 1. Thus a value of $\mu = 1.6$ per week (see below) does not imply a mortality of 160% per week nor a survival probability of -0.6. Using equation 1 the actual survival probability is $\exp(-1.6) \approx 0.2$ and the mortality is thus 0.8 or 80% per week.

Results and Discussion

Bailey estimates from Jackson's data for the Kakoma and Kisoko squares

The benefit of using a maximum likelihood technique, compared to Jackson's approach, is immediately obvious from the results on the weekly mortality and birth rates (fig. 1a,b). The former are less variable and show clearer trends than Jackson's originals in following seasonal changes in maximum temperature (T_{max}) and saturation deficit (fig. 1 d–f). For the maximum likelihood estimates there was only one (impossible) negative estimate, whereas for Jackson's there were five negative estimates of the birth rate and nine of the instantaneous mortality rate. Negative estimates are omitted from fig. 1b since their inclusion necessitates extending the scale to -0.6 and this obscures the detail in the remainder of the plot.

The positive and negative methods provided similar population estimates (fig. 1c) and both were less variable than Jackson's originals. Population estimates are given as densities since there was a factor of 8.9 difference between the areas of the two squares. Continuity in the results suggests that the population density was similar in the small and large squares.

Bailey estimates of mortality and birth-rate, for male tsetse released in the large squares at Kakoma and Kisoko, showed similar trends (fig. 2 a,b). This was not evident from Jackson's weekly estimates, even when he smoothed the data. There were only minor differences between the positive and negative Bailey estimates of the population for the Kisoko square (fig. 2c). Both were generally lower than the corresponding estimated population at Kakoma, but the difference rarely exceeded a factor of two. This finding does not therefore conflict with the similarity between the death and birth rates, particularly given the sensitivity of tsetse population growth rates to changes in adult mortality (Hargrove, 1988). Male population levels are also, of course, strongly affected by the survival of the female population, for which there is no information in Jackson's study.

Jolly-Seber (J-S) estimates for the Kakoma and Kisoko squares

Jolly-Seber and Bailey estimates of various population parameters for the Kakoma data followed similar patterns but the former were generally more variable (cf. figs 1 and 3). Thus, the standard deviation as a percentage of the mean, i.e. the coefficient of variation, for all estimates of the survival probability was only 20% for the Bailey estimates but was 30% for the J-S estimates, with a greater number of illicit values where the survival probability was greater than one. This is a natural consequence of the difference between the models. In the J-S model, survival probabilities are calculated from independent weekly estimates of the numbers of marked animals in the population. The survival estimates are thus independent of each other. In Bailey's and Jackson's models, the weekly mortality is estimated from the decline in the number of marked recaptures over a six week period. It is explicitly assumed that the mortality is constant over this period. The resulting 'weekly' estimates are therefore actually 6-week moving averages, with unknown weighting on the various weeks.

Recapture probability and the marked fraction followed almost identical time-courses, fluctuating between c. 15 and 30% in the small square and c. 5 and 20% in the large square (fig. 3a). Patterns of changes in survival probability were also similar, as is to be expected since the longer a fly lives the greater is its chance of being captured, and then recaptured. Recapture probability, in relatively stable populations such as Jackson's, depends on the value of the survival probability over several weeks. There is thus a smoothing effect on the probability of recapture, which is thus less variable than the weekly estimates of survival. The lower variability of estimates from the large, compared with the small, square is a natural consequence of the larger numbers of marked flies released and recaptured.

Jolly-Seber estimates for Kisoko were similar to those for Kakoma (fig. 4). Estimates of the birth rates and population levels tended to be higher in the Kakoma square, but only during 1938 (cf. figs 2 b,c and 4 b,c) and, as with the Bailey estimates, the differences were small in absolute terms. Survival and recapture probabilities and the fractions of marked flies followed closely similar time courses (fig. 4a). Survival probabilities at Kisoko, and in the other study areas, are of particular interest and are now analysed in greater detail.

Correlation of survival probability with climatic parameters

Given the earlier results of Nash (1933, 1937), Jackson (1944) expected that the death-rate would correlate with saturation deficit but, not surprisingly given the variance in his results, could find no such relationship when he used the weekly estimates of mortality. Even in his monthly pooled estimates, saturation deficit accounted for only c. 20% of the variance in mortality, despite the obvious following of one on the other (fig. 1 a,b). He also found little relationship between changes in the mortality at Kakoma and Kisoko.

Apparent differences between the patterns of mortality in Jackson's results, and much of the short-term fluctuation, are due in part to the fact that he was not using an optimal estimator. Variation was consequently so great that it obscured the true trend in either data set and the relationship between mortality and climate. There are also questions about the statistical methodology since the weekly estimates were running means and were not thus independent. While Bailey's method results in a marked reduction in the variance, the problem of statistical probity remains because his estimates are also running means over 6-week periods.

In the present study the J-S estimates of survival probability are independent. Because there is now no smoothing effect of using running means the variances are, however, higher than in Bailey's method and preliminary analysis showed that neither saturation deficit nor T_{max} removed a significant proportion of the variance in the
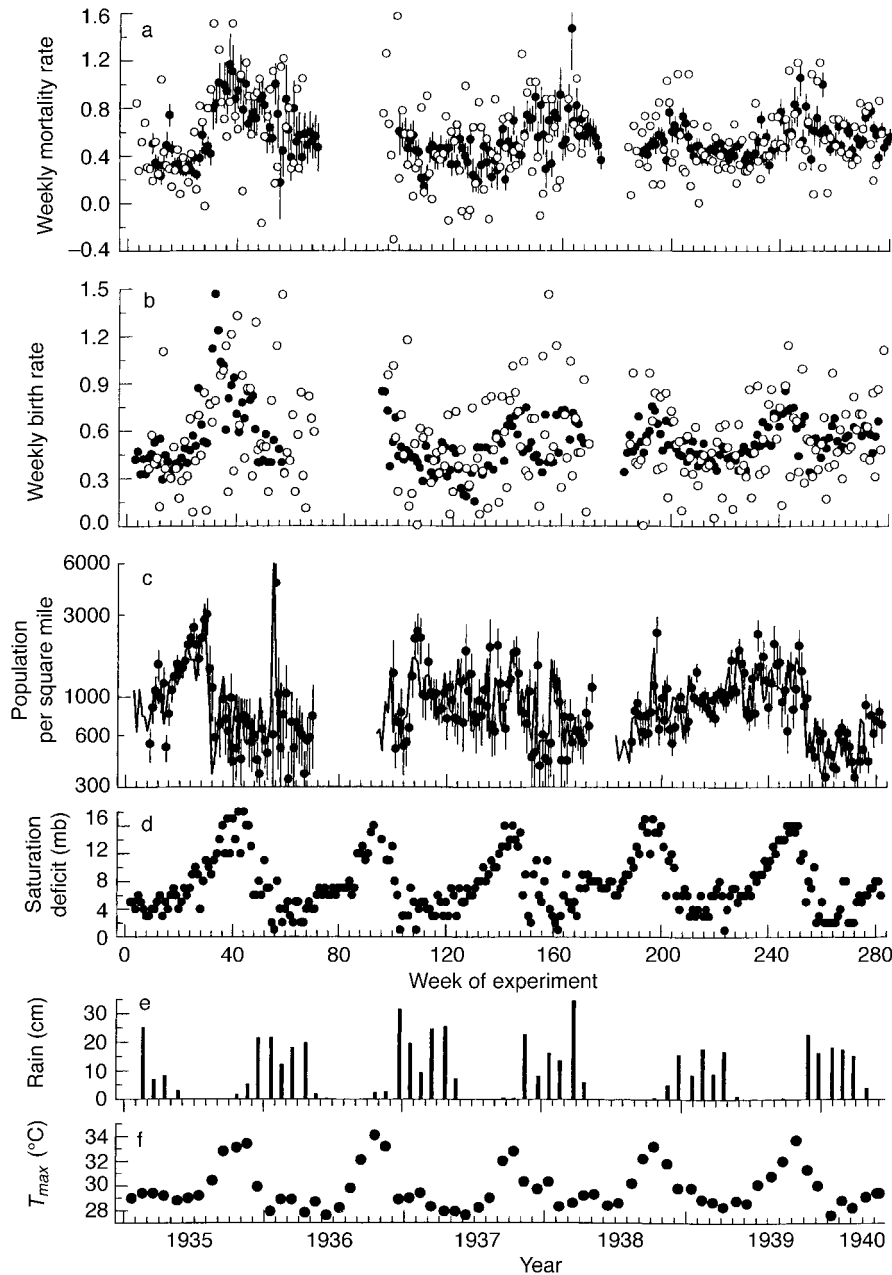
Fig. 1. Estimates using the equations of Bailey (1951) (●) and Jackson (1948) (○) of a) weekly mortality rates, b) weekly birth rates and c) population densities (●, negative; —, positive) for male *Glossina m. morsitans* at Kakoma, Tanzania (1935–1940) together with d) the mean weekly saturation deficit from daily measurements at 0800 h, e) the monthly rainfall and f) the mean monthly maximum temperature. Data from Jackson (1944; tables 5 and 6); his estimates for mortality and birth rates are from Jackson (1948; table 1). Standard errors calculated according to Bailey (1951).

weekly estimates of survival probability ($P > 0.05$; F test). Mean survival probabilities were accordingly calculated over 4-week periods, weighting each weekly estimate by the inverse of its estimated variance. The resulting independent estimates, when regressed against saturation deficit and T_{max} averaged over the same periods, were significantly correlated with both factors ($P < 0.05$; F test) but regression accounted for only 11 and 16% of the variance respectively.

With regard to the Antelope study, J-S estimates of the population size and numbers of births frequently include figures which cannot be accounted for by the natural birth rate (Hargrove, unpublished). Given that there was no immigration onto the island the problem is presumably the result of sampling error. Whatever the cause, the high variance complicates the problem of identifying the relationship between survival probability and climatic
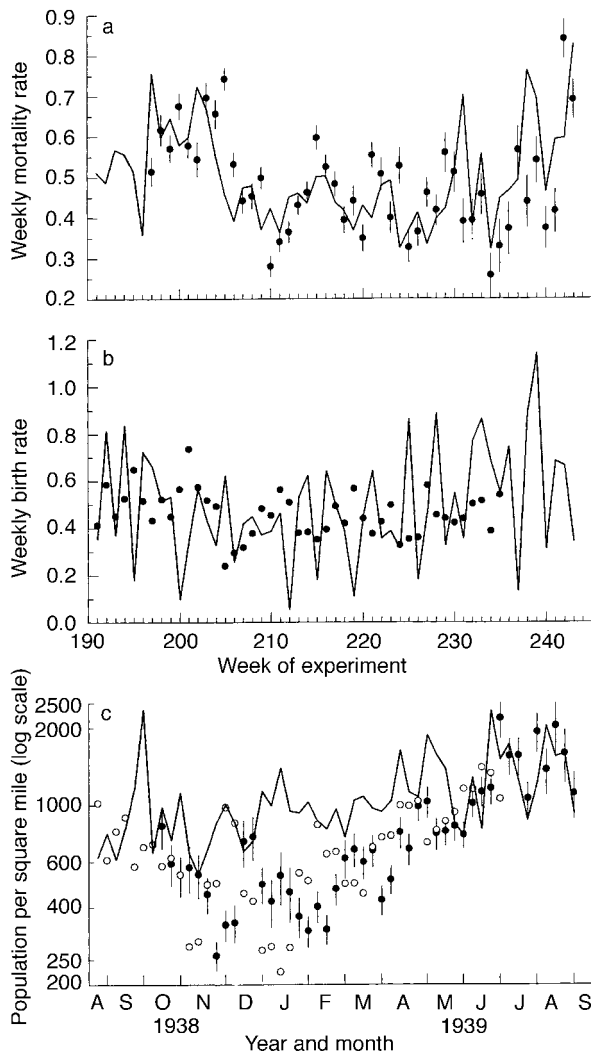
Fig. 2. Estimates of a) weekly mortality rates, b) weekly birth rates and c) population levels for male *Glossina m. morsitans* in the large squares at Kakoma and Kisoko, Tanzania (1938–1940). (●, Kisoko, negative; ○, Kisoko, positive; —, Kakoma, negative.) All estimates and standard errors calculated according to Bailey (1951).

factors. The problem was overcome by smoothing the population (N_i) and birth (B_i) estimates using a first order low pass recursive filter. If the smoothed estimates for week i are denoted $N_i(s)$ and $B_i(s)$ respectively, a new set of estimates of the survival probability can be calculated from:

$$\Phi_i(s) = (N_{i+1}(s) - B_i(s))/ N_i(s) \qquad (2)$$

This procedure was applied to the Kakoma, Kisoko and Antelope Island data set and the joint data were subjected to analysis of covariance. Preliminary analysis of the Kakoma data showed that, once the variance due to T_{max} had been removed, there was no significant difference between the survival probability in the small and large squares ($P > 0.05$; F test). Similarly, there was no significant difference between the survival probability in the Kakoma and Kisoko squares ($P > 0.05$; F test). There was, however, a significant difference

between the survival probability on Antelope Island and in both of the Tanzanian study areas ($P < 0.05$; F test) once variance due to T_{max} had been removed (fig. 5). Survival in the Tanzania experiments was 8% lower on average than on Antelope Island. Regression accounted for 50% of the variance in the joint data, but only 35% if saturation deficit was used in the regression instead of T_{max}. There was no significant interaction between location and either T_{max} or saturation deficit ($P > 0.05$; F test).

The greater effect of T_{max} than saturation deficit on survival probability supports Bursell's (1961) conclusion, from levels of fat and of hydration in male flies, that tsetse would always die of starvation before their water content fell to dangerous levels. There was no need to suggest, therefore, that increases in saturation deficit, which presumably tend only to dehydrate the fly, should be important as a determinant of adult mortality.

Rogers (1979, 1990) and Rogers & Randolph (1986, 1991) have, nonetheless, suggested that saturation deficit is generally more important than temperature in determining mortality in tsetse. Their estimates referred, however, only to females and to total mortality per generation. Mortality in the teneral and mature adult, larval and pupal phases were thus all confounded, whereas the present mark–recapture estimates refer only to mortality in post-teneral adult male flies. The results of the different studies are thus not necessarily contradictory, but the present study suggests that, insofar as saturation deficit mediates mortality, it must do so at stages other than the mature adult. This matter has been investigated in greater detail by Hargrove (2001 and unpublished).

Since survival probability declined with increasing T_{max} even in the apparently equable range $< 28°C$ (fig. 5) it is unlikely that T_{max} has a direct effect on adult tsetse mortality. There could, however, be an indirect effect via, for example, hunger-related deaths. Tsetse use food reserves more quickly as temperatures increase and must therefore feed more frequently if they are to maintain both condition and the energy reserves required for movement. If hosts are scarce, the problem of feeding will be particularly exacerbated at high temperatures.

Differences between survival probabilities at Kakoma and on Antelope Island

Survival was significantly lower at Kakoma and Kisoko than on Antelope Island, at every level of saturation deficit or T_{max} but it is not clear why this should be. To the human eye the island vegetation did not appear in any way optimal for tsetse populations, being comprised largely of deciduous woodland of the type which is typically vacated by tsetse in the hot-dry season (Hargrove & Vale, 1980).

Given that tsetse were introduced to the island in 1979 after an absence there of *c*. 10 years it is possible, particularly given the isolated nature of the habitat, that there were fewer predators and parasites than in an established, open population. An alternative explanation is that the differences between the estimates, which are anyway small in absolute terms, are an artefact resulting from errors in Jackson's estimate of the rate of emigration. If this rate were underestimated then so too would be the survival probability. Previous analysis of Jackson's data shows the estimate of the mean emigration rate has a small standard error (Hargrove, 1981; fig. 3) but also highlighted the fact
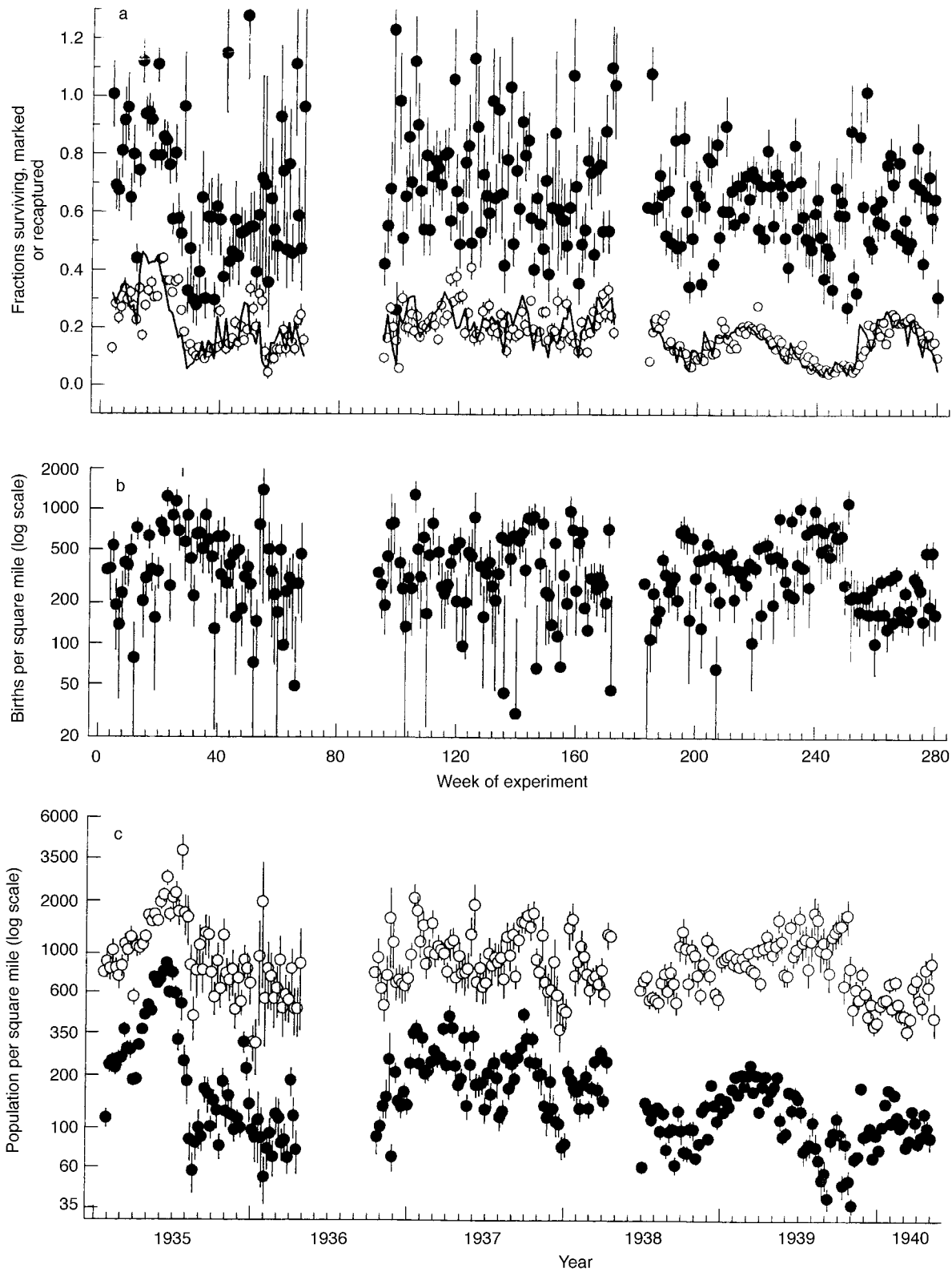
Fig. 3. Population parameter estimates and their standard errors for male *Glossina m. morsitans* at Kakoma, Tanzania (1935–1940). a) survival probabilities (●), marked proportion (○) and probability of recapture (—); b) births per unit area; c) marked (●) and total (○) population densities. All estimates and standard errors calculated according to Jolly (1965).
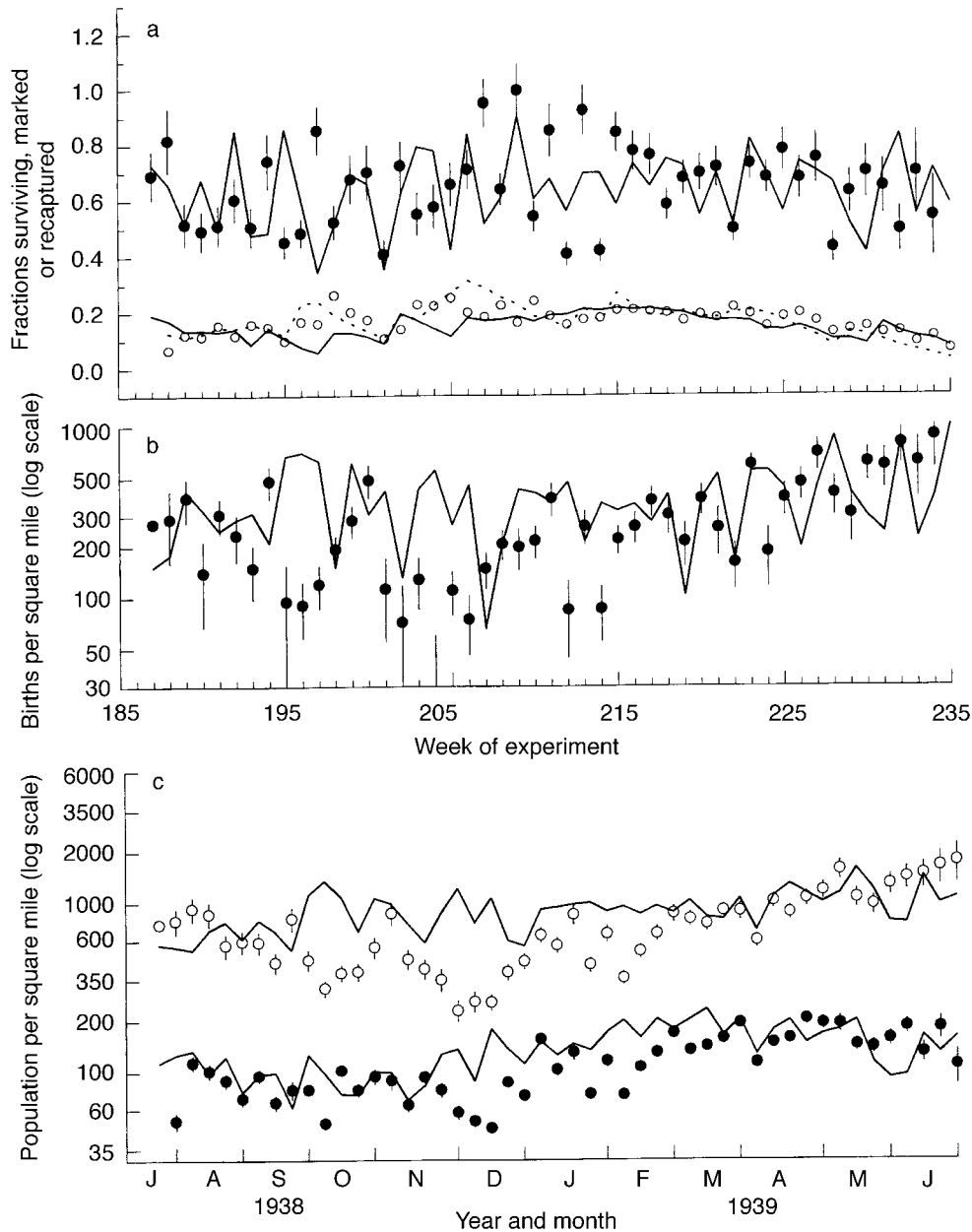
Fig. 4. Population parameter estimates for male *Glossina m. morsitans* in the large squares at Kakoma and Kisoko, Tanzania (1935–1940). a) Survival probabilities (●), marked proportion (○) and probability of recapture (----); b) births per unit area; c) marked (●) and total (○) population densities. Solid lines in each part of the figure represent the results from Kakoma. All estimates and standard errors calculated according to Jolly (1965).

that the estimation procedure would be greatly complicated if, as seems likely, there were age-related changes in the rate of tsetse dispersal.

Part of the explanation might also lie in the fact that, in addition to natural hosts, the 5 km² island was stocked during the experiment with 32–45 cattle (i.e. 6–9 per km²) distributed evenly around the island. Hosts were thus always readily available to the tsetse, which is rarely the case in natural situations. Observed differences in mortality would be explained if, in Jackson's study, tsetse had greater difficulty in finding food and this factor was sufficient to cause starvation in a significant number of cases, or induced the flies to take undue risks while feeding, and suffer elevated mortality as a consequence. The importance of starvation as a factor in tsetse biology is still an issue which has not been satisfactorily resolved (Randolph *et al.*, 1992; Hargrove & Williams, 1995) but the results presented here suggest, at least, that it should not be discounted.
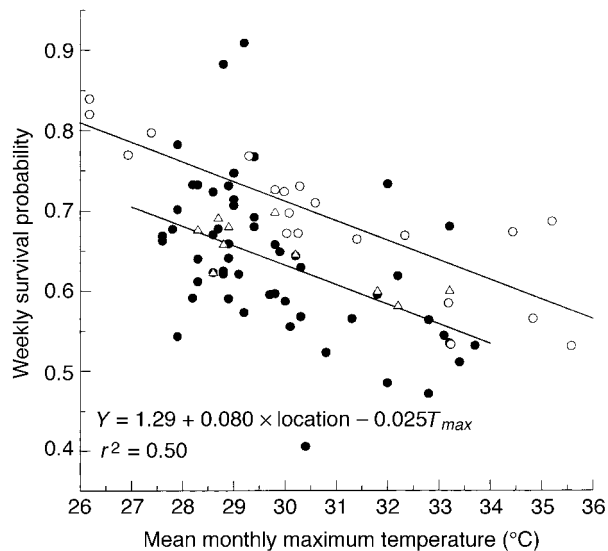
Fig. 5. Survival probability for male *Glossina m. morsitans* regressed against maximum temperature. Means were calculated from smoothed Jolly-Seber estimates of the weekly survival probability. Original data collated from mark–recapture experiments carried out at Kakoma (●) and Kisoko (△) in Tanzania (1935–1940) and on Antelope Island (○), Lake Kariba, Zimbabwe (1980–1981). Solid lines show the survival probabilities (upper line for Antelope Island, lower for Kakoma and Kisoko) predicted by the regression model. The standard errors for the regression coefficients for location and maximum temperature were 0.015 and 0.003 respectively.

Acknowledgements

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