

## PROBLEMS OF FIELD TESTING THEORETICAL MODELS: A CASE STUDY

by

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*Summary.* — The problems of field-testing models are discussed with reference to a population simulation model for the tsetse fly *Glossina pallidipes* Austen developed by us at Nguruman in southwestern Kenya. Model predictions showed a reasonable fit to the changes in the biconical trap index of population size, but tended to overestimate some changes and underestimate others. A more rigorous test for the model is to manipulate one of the population parameters and compare model predictions with the observed population trends. This revealed that some changes in population size resulted more from fly movement than from changes in mortality rates. Fly movement must therefore be incorporated in the model for it to be a useful tool in the development of appropriate control strategies.

### Introduction

«We believe that the current “state of the art” in population dynamics is that at present we can make quantitative testable models only of laboratory systems» (9).

«There is no sense in producing theories if they are not to be tested in the field. An ecological relationship observed in the laboratory can and does differ so much from the same relationship in the field that conclusions drawn solely from laboratory work are quite misleading» (8).

These two opposing views serve to highlight both the difficulties in modelling field systems and the necessity to do so. In the area of applied entomology and epidemiology, models have not only to inform but also to predict, so that they can be used in developing control strategies for pests and diseases. They must therefore be tested and validated under field conditions.

But how easy is this to do? There are at least three approaches to field testing models. The first is to see how well the model mimics the performance of the natural population being studied. Secondly the population can be manipulated, for example by adding a known level of mortality, to see how well the model predicts the behaviour of the system. Lastly the model needs to be applied in different localities under different environmental conditions to assess its wider applicability. The first two of these approaches are considered here with reference to a population simulation model developed for the tsetse fly *Glossina pallidipes* Austen, an important vector of both human and animal trypanosomiasis in Kenya.

## The population simulation model

Intensive field work on *G. pallidipes* started at Nguruman in southwestern Kenya in 1983, with the aim of identifying and quantifying the key density-independent mortality factors and relating them to environmental factors. We also tried to identify density-dependent factors which regulate population size.

Relative estimates of adult population density were obtained using biconical traps (5). These were calibrated using absolute population estimates obtained by mark-release-recapture. This was complicated by cyclic availability of tsetse to traps due to feeding and pregnancy cycles (12) and by abnormal dispersive behaviour immediately after marking, but reasonable estimates were obtained using the method of Parker (10). Relative estimates of pupal densities were obtained by time-constant searches.

Since immigration was initially assumed to equal emigration, and the tsetse reproductive rate is fairly constant with one larva produced every 8-10 days, it was only necessary to determine mortality rates at the various stages in the life cycle. The larval abortion rate was monitored by dissecting female flies. Pupal mortality rates were determined by examination of pupal age

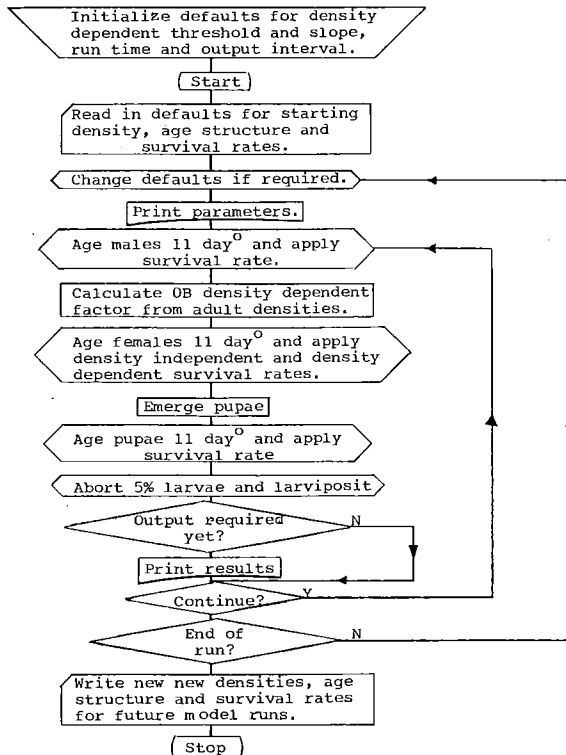


Figure 1.  
Flow diagram of tsetse population simulation model.

structures and also by burying pupae for two week periods and then determining loss rates. Adult loss rates were determined using three techniques, age dissections (4, 7), Moran curves (11) and mark-release-recapture (2). All three methods showed the same trends in the dry season, but diverged during the rains.

The abortion rate was found to vary between 1-5%. The loss rate between the pupal and teneral adult stages was density-dependent (1), possibly because of pupal predation. There was some evidence that rainfall over 100 mm per month increased pupal mortality owing to flooding of larviposition sites (1). It was also shown that the loss rate between age category OB flies (3-8 days old) and age category 1 flies (9-17 days old) was density dependent (Dransfield, unpubl. data), probably resulting from starvation or emigration after competition at the host. There was a significant ( $P < 0.05$ ) inverse relationship between generation mortality rate (from Moran curves) and relative humidity, which reflects a positive relationship between female survival rate and humidity (6).

The life table simulation model, written in Fortran 4, was constructed using the above relationships between mortality rates and biotic and abiotic factors; a flow diagram is given in Fig. 1. Initially the model ran on a physiological time scale with a step length of 11 day degrees (equivalent to one day at 25°C). This has proved to be an unnecessary complication since behavioural thermoregulation enables *G. pallidipes* to maintain an interlarval period of 9 days at Nguruman irrespective of interlarval temperature (6). All mortalities in the model were expressed as  $k$  values (see 13) and flies were assumed to have a maximum adult lifespan of 200 days at 25°C.

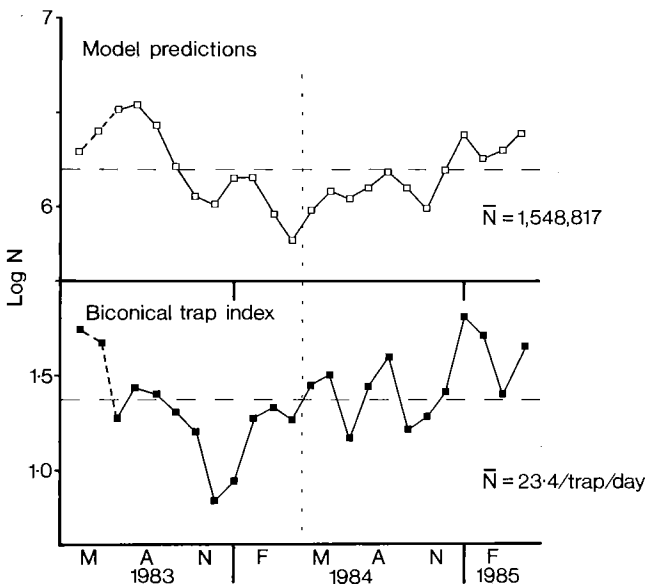


Figure 2. Model predictions and daily biconical trap catches of female *G. pallidipes* at Nguruman from May 1983 to March 1985.

## Field testing of the model

### Comparison with past data

The normal seasonal trend in *G. pallidipes* at Nguruman was for the population to increase shortly after the rainy seasons in April/May and November/December and then enter a decline phase during each dry season. Meteorological data were input to the simulation model for the period 1983-1985, and the output compared to observed population trends (Fig. 2). The model provided a reasonably good fit to the changes in biconical trap catches, although it underestimated some changes and overestimated others. In 1985, trapping mortality imposed on the population increased to about 0.7-1.0% per day because of experimental work on developing new trap/odour bait systems. This coincided with a drought at Nguruman, leading

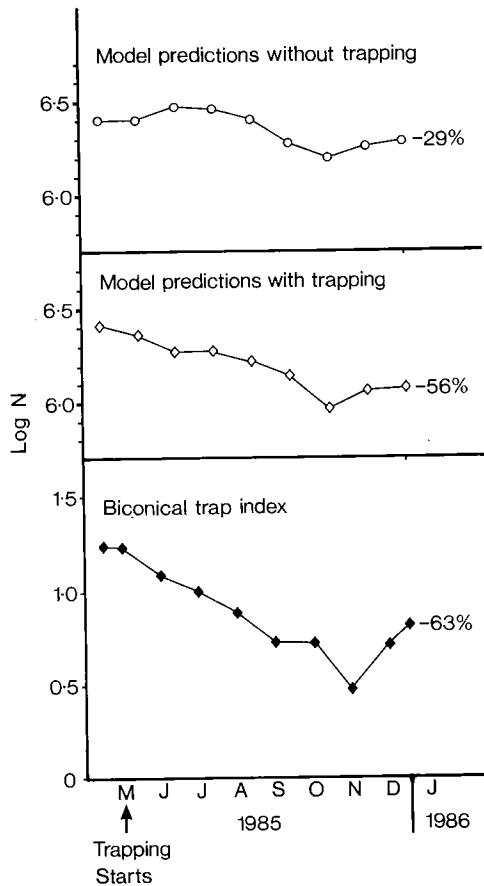


Figure 3.

Model predictions and daily biconical trap catches of female *G. pallidipes* at Nguruman from March 1985 to January 1986 when population was subjected to a low (< 1% additional mortality per day) level of trapping.

to a sharp decline in the tsetse population, in good agreement with model predictions (Fig. 3).

### Population manipulation

It was then decided to increase the population mortality rate substantially as a more rigorous test of the model and compare the outcome with that predicted by the model. The predictions for various levels of additional mortality expressed as  $k$  values are shown in Fig. 4.

The adult tsetse mortality rate was increased by deploying 100 of the newly developed NG2B traps (3) concentrated in woodland in the study area of about 100 km<sup>2</sup> at the base of the Nguruman escarpment. The highest density of traps was put on the northern periphery in an attempt to reduce invasion pressures. Based on mark-release recapture estimates of population size and estimates of the total number of tsetse removed from the population in the first month, the increase in daily mortality rate was estimated to be about 3.5% (equivalent to a  $k$ -value of about 0.015). According to model predictions, this would lead to about a 99.9% reduction within a year.

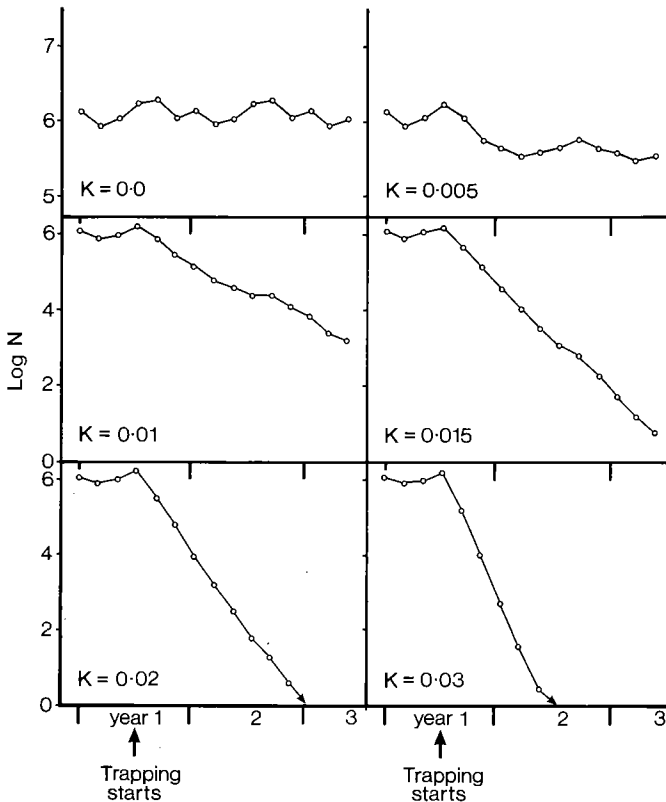


Figure 4.  
Model predictions for the response of a *G. pallidipes* population to varying levels of imposed trapping mortality.

During the dry season (June to October) the population did indeed decline at the rate predicted by the model, giving a 97-99 % reduction by October (Fig. 5). During the rains however the barrier was less effective, and from March to June there was considerable immigration, especially of females, both from the north and from the top of the escarpment, an unexpected source of reinvasion. The resident population was still high at this time and the net immigration balanced the trapping mortality, so the overall density remained fairly constant. In the short rains (November), however, the resident population had been greatly reduced, so catches increased sharply for a short period with immigrants constituting the greater part of the population. The rate of invasion was apparently related to climatic conditions with mass movements of mainly females taking place during cool, wet periods. Surprisingly we have not yet found any relationship between fly density and movement.

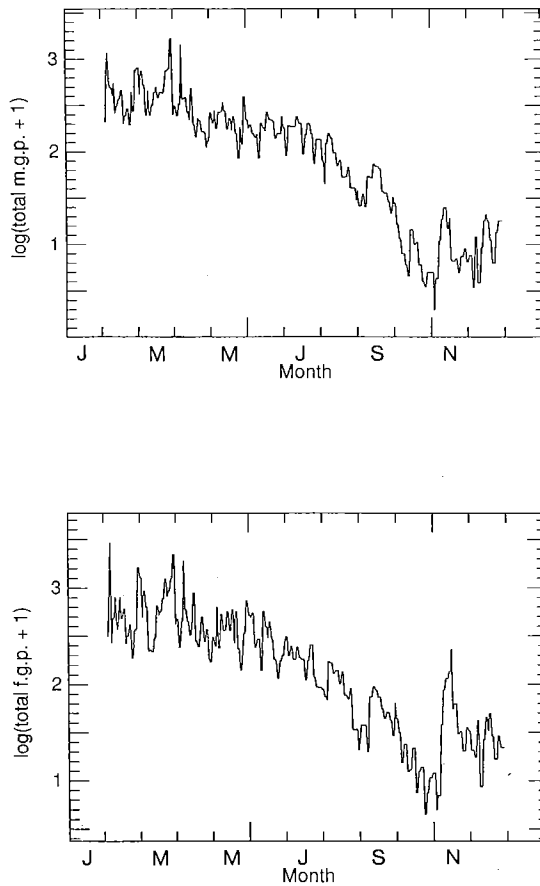


Figure 5.

Decline in catch of male (above) and female (below) *G. pallidipes* along the Oloibototo River in the suppression zone at Nguruman from February 1987 to January 1988 when population was subjected to a high intensity of trapping.

## Conclusions

Although the simulation model appeared to adequately describe the seasonal fluctuations, it is now clear that some of these changes resulted from net movement from one area to another, rather from changes in the mortality rate. The value of population manipulation as a method of validating simulation models is therefore emphasised since these movements were difficult to detect before the population was reduced by trapping. The top of the escarpment has proved to be an important reservoir of flies which «restocks» lowland areas after long dry periods. Fly movement and spatial heterogeneity must now be incorporated into the model for it to be a useful tool in developing control strategies.

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### Problèmes pour tester les modèles théoriques sur le terrain: une étude de cas.

Résumé. — Les problèmes pour tester des modèles sur le terrain sont discutés en référence à un modèle de simulation de la dynamique de population des mouches tsétsés *Glossina pallidipes* Austen, développé par nous à Nguruman dans la région du Sud-Ouest du Kenya. Les prédictions du modèle s'accordaient raisonnablement aux changements de l'index de la taille de population déterminé au moyen du piège biconique, mais tendaient à surestimer certains changements et à sous-estimer d'autres. Un test plus rigoureux du modèle consiste à manipuler un des paramètres de la population et à comparer les prédictions du modèle avec les tendances observées sur le terrain. Ceci révélait que certains changements de la taille de la population résultaient plutôt des mouvements des mouches d'un endroit à l'autre, que des changements des taux de mortalité. Le mouvement des mouches doit alors être incorporé au modèle pour qu'il soit un outil utile dans le développement des stratégies de contrôle appropriées.

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