Short communication

# Networks of habitat patches in tsetse fly control: Implications of metapopulation structure on assessing local extinction probabilities

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### A R T I C L E   I N F O

### A B S T R A C T

Controlling tsetse fly populations in much of sub-Saharan Africa is one of the great challenges in stopping the spread of trypanosomosis diseases in both humans and domestic livestock. Mathematical models have been used for informing control efforts against this fly. However, often these models are too simple and do not address spatial complexity. In this brief communication, network theory is used to construct a metapopulation model to test standard results from some of these models that derive female extinction probability and show that by adding spatial complexity of metapopulation theory the extinction probability of the flies change in biologically significant ways.

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## 1. Introduction

The tsetse fly complex (*Glossina* spp.) is considered a key contributor to the African continent's continuing struggle to emerge from deep economic, social and political challenges. It has been christened "The Poverty Fly" (Leak, 1998) and "Africa's Bane" by Nash (1969), because these insects affect both human health, as a vector of human trypanosomosis; and food and agriculture in terms of livestock – which are used as a source of protein and fertilizer, and for tilling the soil in African agricultural systems. The removal of the tsetse and trypanosomosis problem would generate substantial direct benefits and numerous rural development opportunities.

Control efforts for the tsetse fly have resulted in successes in suppressing or reducing the presence of the tsetse fly to acceptable levels of economic damage or completely eradicated: e.g. the permanent removal of *Glossina morsitans submorsitans*, *Glossina palpalis palpalis* and *Glossina tachinoides* from 200,000 km² in Nigeria (Spielberger et al., 1977), of *Glossina pallidipes* from Zulu Land, South Africa (Du Toit, 1954), of *Glossina austeni* from the Island of Unguja, Zanzibar (Vreysen et al., 2000), and of *Glossina morsitans centralis* from the Okavango Delta, Botswana (Kgori et al., 2006). However, some interventions also have resulted in failures in which the tsetse fly populations were not reduced to levels wherein

the tsetse fly might be considered controlled (De La Rocque et al., 2001; Hargrove, 2003).

Because of the cost of these efforts, informed choices guided by mathematical models have helped in decision-making. Most of these assessments rely on a small group of mathematical models developed by a variety of researchers, each with a different focus on aspects of tsetse control.

One of the leading tsetse researchers using mathematical modeling was John Hargrove (Barclay and Hargrove, 2005; Hargrove, 1981, 1988, 1990, 1993, 1994, 2000, 2001, 2003, 2005) who developed a suite of biologically realistic models based on stochastic birth–death theory, age-structured transition matrices, and standard population genetics models. In particular, Hargrove's derivation of the extinction probabilities for female tsetse flies (Hargrove, 2005) has been important for informing efforts to control the tsetse fly. Most of these models, however useful, have not adequately addressed the complex spatial context in which tsetse flies are found (Peck, in press), which includes structured metapopulations of suitable habitat such as certain vegetative types and landscape features that increase the tsetse fly probability of movement and survival (Bouyer et al., 2009; Guerrini et al., 2008; Leak, 1998; McCord et al., 2012).

The ecological differences in the way individual tsetse species perceive their environment is dependent on the spatial complexity of the environment (Peck, 2009). The relevance of spatial complexity of the different savannah-, forest-, and riverine-tsetse species are well-known and even different species within the same group

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show strong habitat divergences. For example, *G. tachinoides* and *G. p. gambiensis* showed different responses to riverine forest ecotypes and disturbance intensity in Burkina Faso. A phyto-sociological analysis of the distribution of riverine tsetse flies in Burkina Faso (Bouyer et al., 2005) indicated that the same level of habitat fragmentation (Guerrini et al., 2008) had decidedly different impacts depending on this structuring (Bouyer et al., 2007; Kone et al., 2010).

How much does spatial substructuring matter for looking at tsetse fly population ecology? Metapopulation theory has continued to be a useful way of exploring ecological relationships in substructured populations (Elkin and Possingham, 2008; Hanski and Ovaskainen, 2000; Holyoak and Ray, 1999; Ovaskainen and Hanski, 2004; Xu et al., 2006).

In this paper, a spatial metapopulation model of tsetse fly population dynamics using network theory is used to create random metapopulations linked with migration among patches (Bodin and Norberg, 2007; Bunn et al., 2000; Emily and Minor, 2008; Newman, 2003). This short communication demonstrates that adding metapopulation theory to Hargrove's (2005) theoretical derivation of female extinction probability dramatically changes those probabilities. This observation suggests that care must be taken in using Hargrove's extinction probabilities when making management decisions in tsetse control.

## 2. Methods

Consider Hargrove's extinction probabilities in a metapopulation context. Allow the transition probabilities in a grid of populations all under the assumptions used by Hargrove (2005) to be:

$$X_i[t+1] = 0 \,|\, X_i[t] = 1 \sim \text{Bernoulli}(k) \Rightarrow pr\{X_i[t+1] = 0 \,|\, X_i[t] = 1\}$$
$$= \kappa \quad \text{and} \quad pr\{X_i[t+1] = 1 \,|\, X_i[t] = 1\} = 1 - \kappa$$

where $X_i$ is the $i$th patch value where $1 \Rightarrow$ the patch is occupied and $0 \Rightarrow$ otherwise and $\kappa$ is the extinction rate. Similarly,

$$X_i[t+1] = 1 \,|\, X_i[t] = 0 \sim \text{Bernoulli}(\varphi) \Rightarrow pr\{X_i[t+1] = 1 \,|\, X_i[t] = 0\}$$
$$= \varphi \quad \text{and} \quad pr\{X_i[t+1] = 0 \,|\, X_i[t] = 0\} = 1 - \varphi$$

where $\varphi$ is the colonization rate.

The extinction rate, $\kappa$, is calculated from Hargrove's equation (2005) in which he derives the probability of extinction of an individual female tsetse fly as the solution of the quadratic equation:

$$\kappa = \frac{1 - \Phi^l(1 - \zeta\psi^T(1 - \eta\Phi^u))}{\zeta\Phi^l\psi^T},$$

where $\Phi$ is the daily survival probability of adult females, $\psi$ is the daily survival probability of the female pupae, $u$ is the days between female adult eclosion and first ovulation, $\eta$ is the probability of a female being inseminated, $l$ is the interlarval period (days), $\zeta$ is the probability that a deposited pupa is a female, and $T$ is the pupal duration.

The colonization rate, $\varphi$, for individual patches was calculated as a modified Hanski's Incidence Function Model (mIFM) (Etienne et al., 2004):

$$\varphi_i = \frac{S_i^2}{S_i^2 + y^2}$$

where $y$ is an estimated parameter, and $S$ is calculated as:

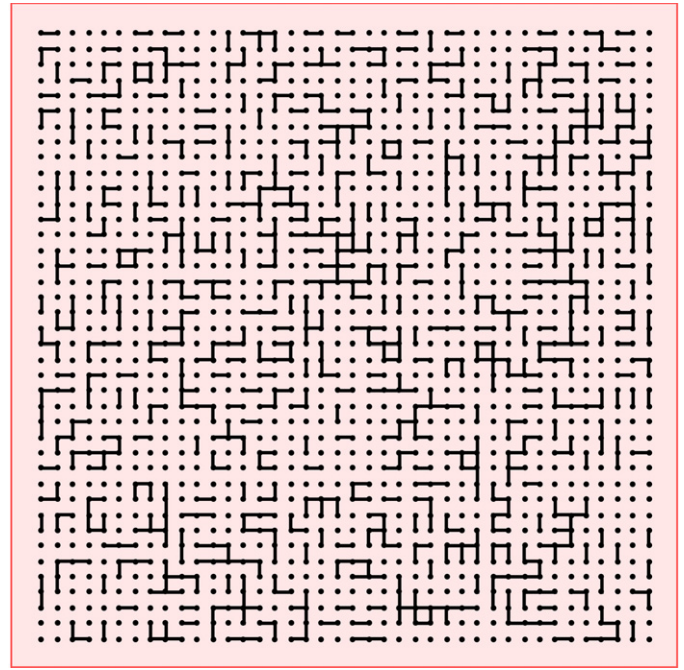$$S_i(t) = \sum_{i \neq j} X_j(t) B_{ij} \exp(-\alpha d_{ij})$$



**Fig. 1.** Model landscape over which Hargrove female tsetse fly extinction rates are applied. Each node represents a patch with its connectivity with other patches represented by edges in the graph. In this graph 75% of the edges have been removed creating isolated metapopulations of nodes not connected to other nodes by any edge.

where $B_{ij}$ is a measure of network connectivity (explained below), $\alpha$ is the area of the patch, and $d_{ij}$ is the Euclidian distance between the patches.

### 2.1. Model space testing

A metapopulation is represented by an undirected lattice-grid with each patch represented by a node of the grid. The parameter $B_{ij}$ is constructed by creating a complete grid graph among patches (Fig. 1). From this graph random edges are removed with probability $v$, creating a random graph. From this an $N \times N$ matrix $\mathbf{B}$ of $N \times N$ index matrices is created where:

$$B_{ijkl} = \left\{ \begin{array}{l} 1 \quad \text{if there exists a path from node } ij \text{ to node } kl \\ \phantom{1} \quad 0 \quad \text{otherwise} \end{array} \right\}$$

It was too computationally expensive to calculate the length of the path between nodes in the context of this model, so it was assumed in the model that tsetse fly movement is fast enough relative to the path length and that Euclidean distance acts as an adequate surrogate of movement within a habitat patch.

Because of the number of variables being explored (Table 1), a sensitivity analysis of that parameter space was conducted in order to test which of the parameters in the model were most influential in effecting the extinction probability of the flies. The model was implemented in *Mathematica* (Wolfram Research, 2010) and run 1000 times with random uniformly distributed draws from the parameters over ranges thought to be biologically relevant for tsetse fly. These were taken from Hargrove (2005), Leak (1998) and from tsetse fly biologists (Udo Feldmann, UN-IAEA, personal communication). ANOVA was used to examine the influences on the mean number of patches colonized. In addition, logistic regression was used to determine which variables influenced whether flies went extinct throughout the region.