

## A dynamic species distribution model of *Glossina* subgenus *Morsitans*: The identification of tsetse reservoirs and refugia

MARK H. DEVISSER,<sup>1,2,†</sup> JOSEPH P. MESSINA,<sup>1,2,3</sup> NATHAN J. MOORE,<sup>1,2</sup> DAVID P. LUSCH,<sup>1,4</sup>  
AND JOSEPH MAITIMA<sup>5</sup>

<sup>1</sup>Department of Geography, Michigan State University, Michigan 48824 USA

<sup>2</sup>Center For Global Change and Earth Observations (CGCEO), Michigan State University, Michigan 48823 USA

<sup>3</sup>Michigan Agricultural Experiment Station (MAES), Michigan State University, Michigan 48824 USA

<sup>4</sup>Remote Sensing and Geographic Information Science Research and Outreach Services (RS&GIS), Michigan State University, Michigan 48824 USA

<sup>5</sup>International Livestock Research Institute (ILRI), Nairobi, Kenya

**Abstract.** Tsetse flies are the primary vector for African trypanosomiasis, a neglected tropical disease that affects both humans and livestock across the continent of Africa. In 1973 tsetse were estimated to inhabit 22% of Kenya; by 1996 that number had risen to roughly 34%. Efforts to control the disease are hampered by a lack of information and costs associated with the identification of infested areas. To aid control efforts we have constructed the Tsetse Ecological Distribution Model (TED Model). The TED Model is a raster based dynamic species distribution model that predicts tsetse distributions at 250 m spatial resolution, based on habitat suitability and fly movement rates, at 16-day intervals. Although the TED Model can be parameterized to any tsetse subgenus/species requirements, for the purpose of this study the TED Model was parameterized to identify suitable habitat for *Glossina* subgenus *Morsitans*. Using the TED Model we have identified where and when *Glossina* subgenus *Morsitans* populations should be constrained by unfavorable ecological conditions to particular parcels of suitable habitat. It is our hope that by utilizing the predicted locations of tsetse reservoirs and refugia, control efforts will be better able to target tsetse populations when they are spatially constrained, thus maximizing limited available resources.

**Key words:** African trypanosomiasis; niche model; species distribution model; tsetse fly; tsetse reservoirs.

**Received** 29 March 2010; revised 25 June 2010; accepted 23 July 2010; published XX July 2010. **published** 00 Month 2010. Corresponding Editor: T. Stohlgren.

**Citation:** DeVisser, M. H., J. P. Messina, N. J. Morre, D. P. Lusch, and J. Maitima. 2010. A dynamic species distribution model of *Glossina* subgenus *Morsitans*: The identification of tsetse reservoirs and refugia. *Ecosphere* 1(1):artX. doi:10.1890/ES10-00002.1

**Copyright:** © 2010 DeVisser et al. This is an open-access article distributed under the terms of the Creative Commons Attribution License, which permits unrestricted use, distribution, and reproduction, in any medium, provided the original author and source are credited.

† **E-mail:** devisse6@msu.edu

### INTRODUCTION

#### *African trypanosomiasis and the tsetse fly*

African trypanosomiasis, otherwise known as sleeping sickness in humans and nagana in livestock, is caused by a single-celled protozoan (trypanosome) and is a neglected tropical disease (Yamey 2002, Hotez et al. 2006, 2007, WHO 2009). Trypanosomiasis is generally lethal if left

untreated, and in regions where the disease is present, livestock productivity decreases by 20% to 40% (Hursey 2001, Rogers and Randolph 2002), costing livestock producers and consumers in Sub-Saharan Africa an estimated \$4.5 billion annually (Oluwafemi 2009). Due to the trypanosomes' use of long-lived wild ungulate populations as natural hosts (e.g., cape buffalo, warthog, bushbuck), most modern control efforts have

focused on the disease vector, the tsetse fly, genus *Glossina* (Jordan 1986, Grant 2001).

Tsetse are diurnal biting flies between 6–14 mm in length and naturally feed on wild ungulate and ruminant populations (Pollock 1982*a, b*). Efforts to control tsetse have been chronically hampered by identification of infested areas, reinvasion of tsetse into previously controlled regions, and substantial costs associated with the means of control (Brightwell et al. 1992, Williams et al. 1992, Hargrove 2003, Maitima et al. 2007). Traditionally, tsetse distributions have been aggregated and mapped into contiguous “fly belts,” which can contain one or more tsetse species with boundaries set by a wide variety of physical, biological, and anthropogenic barriers (Ford 1971, Ford and Katondo 1977, Rogers and Robinson 2004, Muriuki et al. 2005). Fly belts, although useful in delineating where tsetse were historically found, are of limited use to control efforts due to the lack of information on the likelihood and timing of tsetse presence. More recent attempts to map tsetse distributions have implemented spatial modeling techniques, which have succeeded in producing maps with both higher spatial resolutions than the fly belt maps, and estimates on the probability of tsetse presence (e.g., Rogers and Williams 1994, Gilbert et al. 2001, Wint 2001). Although an improvement over the fly belt maps, the modeled predictions thus far have provided little information about intra- and inter-annual fluctuations in tsetse distributions, despite numerous studies that discuss such phenomenon (e.g., Austen and Hegg 1926, Nash 1933, Bursell 1956, Brightwell et al. 1992, Hargrove 2001, Odulaja et al. 2001, Bett et al. 2008).

To aid control efforts, we constructed the Tsetse Ecological Distribution Model (TED Model), which is a dynamic species distribution model that uses remotely sensed climate and land cover data, combined with fly movement rates, to map and track fluctuations in tsetse distributions. By using the TED Model we identified the season, approximate date, and geographic location of tsetse populations constrained to ecologically suitable habitat. Throughout the rest of this paper, the parcels of suitable tsetse habitat in which tsetse populations are predicted to survive seasonal fluctuations in temperature and moisture will be referred to as

tsetse reservoirs; habitat deemed crucial to long term tsetse survival will be called tsetse refugia. It is our hope that by utilizing the predicted locations of tsetse reservoirs and refugia, control efforts will be better able to target tsetse populations when they are spatially constrained, thus maximizing limited available resources.

### *The tsetse fly in Kenya*

The geographic distribution of tsetse is limited to Sub-Saharan Africa, where they infest 8.5 million km<sup>2</sup> in 37 countries (Allsopp 2001). This study focuses on Kenya (582,650 km<sup>2</sup>), where in 1973 tsetse were estimated to infest 22% of the country (129,229 km<sup>2</sup>) (Ford and Katondo 1977). By 1996, the amount of Kenya estimated to be infested with tsetse had risen to approximately 34% (202,774 km<sup>2</sup>) (KETRI 2008). In addition to the potential change in tsetse distributions within the country, Kenya also contains a variety of physiographic and climatic regions (e.g., cool moist highlands above 1,500m elevation, near-desert conditions in the north, and a warm humid coastal plain) and four distinct seasons (the long and short rains, and the hot and cool dry seasons).

As described in Gatebe et al. (1999) and Awange et al. (2008), seasonal climate conditions in Kenya are primarily driven by the oscillation of the Intertropical Convergence Zone (ITCZ) over the equator. The long rains coalesce as the ITCZ moves north over the equator and last from early March to late May. Following the long rains is the cool dry season, which lasts from early June to late October, and ends with the onset of the short rains in late October or early November. The short rains coalesce as the ITCZ moves to the south of Kenya in late October, can last until late December and produce one third of the annual precipitation in Kenya. Following the short rains is the hot dry season, named for having average temperatures warmer than that of the longer cool dry season. At the end of the hot dry season in late February, the long rains return and the seasonal cycle begins anew. Although the general description of the four seasons in Kenya portrays the timing, duration, and climate conditions as relatively constant, there is often a high degree of intra- and inter-annual variability from location to location (Awange et al. 2008).

Tsetse are divided into three subgenus groups

based on their physiology and general ecology, with each group requiring different land cover, temperatures regimes, and moisture levels. Although all three subgenus groups of tsetse occur within Kenya and the TED Model can be parameterized to any tsetse subgenus/species requirements, for the purpose of this study the TED Model was parameterized to identify suitable habitat for subgenus *Morsitans/Glossina* (also called the *morsitans*-group). The *morsitans*-group, commonly considered the woody savannah tsetse species, has the most expansive spatial distribution in Kenya. The subgenus *Palpalis/Nemorhina* (also called the *palpalis*-group) is restricted to the shore of Lake Victoria and along the Kenya-Uganda border, while the subgenus *Fusca/Austenina* (also called the *fusca*-group), whose distribution overlaps that of the *morsitans*-group, is found primarily in isolated patches of forest and along the Kenya-Tanzania border (Pollock 1982a, Wint and Rogers 2000). Hereafter, our reference to “tsetse” will be specific to the *morsitans*-group.

#### Tsetse ecology

Tsetse are one of the few k-strategist insects, and thus have low fecundity and over all low mortality rates relative to other insect species (Leek 1999, Rio et al. 2006). Of particular importance to tsetse survival is the availability of ecologically suitable habitat, which must include acceptable climate conditions and land cover types (Pollock 1982b, Leak 1999). With regards to climate, tsetse populations are generally found in regions with mean annual temperatures between 19–30°C (Pollock 1982b). As temperatures increase, the rates at which tsetse consume fat and water also increase, requiring the fly to either seek out a host on which to feed or risk dying of starvation or desiccation (Leak 1999, Hargrove 2001). The probability of survival drops to 50% when tsetse are exposed to temperatures greater than ~36°C for three hours (Terblanche et al. 2008), and temperatures greater than 40°C are considered lethal (Knight 1971, Torr and Hargrove 1999).

Unlike high temperatures, low temperatures slow tsetse physiology and induce a “chill coma” (Terblanche et al. 2008). The chill coma effect sets in when temperatures drop below 17–20°C, preventing tsetse from flying, carrying out

normal life activities, and, eventually, leading to starvation (Mellanby 1936, 1939, Knight 1971, Hargrove 1980, Pollock 1982b). Colder temperatures will kill tsetse outright, with the probability of survival dropping to 50% when exposed to temperatures below ~10°C for 3 hours (Terblanche et al. 2008).

Low moisture levels compound the threat of high temperature by increasing the rate of water consumption leading to desiccation in adult tsetse (Leak 1999). A significant negative correlation has been reported between fly populations and saturation deficits (Nash 1933, Rogers 1979, Hargrove 2001). However, the question of whether or not tsetse in dry conditions die from starvation or desiccation has been debated for some time (see Nash 1937, Buxton 1955, Bursell 1961, 1963, Rogers 1979, 1990, Hargrove 1980, 2001, Rogers and Randolph 1986, 1991). Regardless, it is clear that low moisture levels have a serious negative impact on tsetse populations, with optimum saturation deficits between 6.0–17.3 hPa (Rogers 1979).

To prevent possible starvation/desiccation, tsetse utilize various micro-habitats provided by particular land cover types that contain what is referred to as “woody vegetation” (Leak et al. 2008). Woody vegetation can be generally defined as woody plant material greater than 1–3 cm in diameter, a height of 1–4 meters, and with a coarse surface (e.g., rough/loose bark) (Austen and Hegh 1922, Jordan 1986). Tsetse use the various micro-habitats associated with woody vegetation (e.g., loose bark, underside of branches or logs, hollows in tree trunks or logs) to mitigate high temperatures, and provide preferred moisture levels (Austen and Hegh 1922, Pollock 1982a, b). When temperatures rise above ~32°C, tsetse seek out woody vegetation refuges (Pilson and Pilson 1967), which can be up to 4.5°C cooler than ambient air temperatures (Torr and Hargrove 1999, Muzari and Hargrove 2005).

## METHODS

### *The tsetse ecological distribution model*

To explore the spatio-temporal fluctuations of tsetse distributions, we constructed the TED Model, a raster based dynamic species distribution model (see Guisan and Zimmermann 2000, Guisan and Thuiller 2005, Peterson et al. 2008,

Kearney and Porter 2009) that predicts tsetse presence at a 250m spatial resolution based on habitat suitability and fly movement rates. The model outputs individual, binary presence/absence maps for 16-day periods, from 1 January 2001 to the acquisition date of the most recently available Moderate Resolution Imaging Spectroradiometer (MODIS) remotely sensed data products that are inputs to the model (approximately one month previous to the current date). At its simplest, the TED Model can be described in two separate parts: 1) a spatially explicit fundamental niche model that identifies all potentially suitable tsetse habitat (see Guisan and Zimmermann 2000, Peterson et al. 2002, Soberón and Peterson 2005, Kearney and Porter 2009) and 2) a fly movement model that integrates tsetse distributions and fly movement rates (Fig. 1).

The fundamental niche model uses four

separate MODIS products: 1) Normalized Difference Vegetation Index (NDVI) as a surrogate for available moisture (see Williams et al. 1992), 2) day land surface temperature (LST), 3) night LST, and 4) Land Use Land Cover (LULC). Each of the four data sets was recoded to a binary suitable (1) vs. unsuitable (0) habitat classification scheme. These four binary habitat suitability maps are then combined using Boolean logic to create a tsetse fundamental niche map for each 16-day epoch.

Although the first part of the model determines the fundamental niche of tsetse, the expansion of suitable habitat might be greater than tsetse movement rates. To identify the location of tsetse distributions (i.e., the realized niche) a fly movement model was coupled to the fundamental niche model, which expands the previous tsetse distributions by an assigned fly movement rate. When tsetse distributions expand into cells determined ecologically suitable, the TED Model predicts tsetse to be present at those new locations. If tsetse distributions expand into cells that are designated as unsuitable habitat, then the TED Model predicts tsetse would not be present at those locations. The same rules apply for cells that change from suitable to unsuitable where existing tsetse distributions were previously predicted, hence allowing for the contraction of tsetse distributions when the amount of suitable tsetse habitat declines. Thus the TED Model produces a unique tsetse species distribution map every 16 days, and is able to predict/track tsetse distributions over time and space.

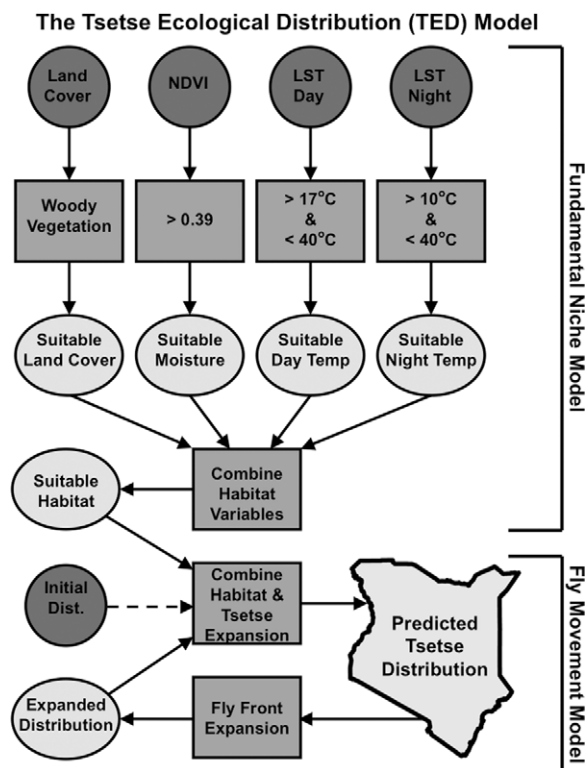


Fig. 1. The Tsetse Ecological Distribution (TED) Model Flow Chart; dark grey circles are input variables, grey squares are conversions/calculations, light grey ovals are derived auxiliary variables, and the Kenyan shaped Predicted Distribution is the model output for each date.

**Data, parameters, and initialization**

*Moisture.*—Representing available moisture in the TED Model is problematic since no publicly available, in situ, remotely sensed, or modeled measure of moisture with a temporal resolution greater than 16 days and a spatial resolution equal to or greater than 1km currently exists for Kenya. Humidity can be predicted using precipitation and temperature data, but Williams et al. (1992) demonstrated that using remotely sensed NDVI data as a surrogate for humidity outperformed predicted humidity data with regards to modeling tsetse populations. NDVI, the normalized difference ratio of Red and Near-infrared (NIR) wavelengths ( $NIR - Red / Nir + Red$ ),



essentially measures the presence and condition of green vegetation (Lillesand et al. 2008). If green vegetation is present and healthy, remotely sensed NDVI values will be higher than if vegetation is not present or unhealthy. The findings of Williams et al. (1992) that NDVI can be used as a surrogate for moisture data logically follows since healthy green vegetation generally requires water to exist. For this reason the TED Model uses NDVI as a surrogate for available moisture when predicting suitable habitat.

NDVI data were acquired from NASA in the form of the MODIS Terra NDVI Vegetation Indices 250m (MOD13Q1) product. The MODIS NDVI product is available at 16-day increments, from 1 January 2001 to approximately one month from the current date. Since our current study covered a period of nearly nine years (i.e., 1 January 2001–19 December 2009) 207 scenes of the MODIS NDVI were downloaded, compiled, reprojected, and clipped to the borders of Kenya using the MODIS Reprojection Tool (MRT), United States Geological Survey (USGS) Earth Resources Observation and Science (EROS) Center, Sioux Falls, South Dakota, USA, and ArcGIS 9.2, Environmental Systems Research Institute (ESRI), Redlands, California, USA.

Multiple models have used NDVI as a variable to predict suitable tsetse habitat in the past (e.g., Rogers and Williams 1994, Gilbert et al. 2001, Wint 2001), but these models used NDVI as a land cover descriptor, not as a surrogate for moisture. Therefore, the NDVI threshold values reported by these models are not considered appropriate for the TED Model. Williams et al. (1992) reported a Zimbabwe dry season NDVI threshold value of 0.39 based on several statistical tests (a linear regression, a non-linear regression, discriminate analysis, k-nearest neighbor analysis, and experiments using a neural network). Given that the two species of tsetse studied in Williams et al. (1992) are two of the *moristans* group species found in Kenya, the woody vegetation types found in Zimbabwe are similar to those found in Kenya (Vale et al. 1988, Rogers and Williams 1994, Muzari 1999), and high synchronicity between NDVI and precipitation events in semiarid environments (Park 2009), we adopted 0.39 as the threshold value for NDVI-based moisture suitability. Furthermore, to distinguish our use of NDVI as a surrogate for

moisture as opposed to previous studies that have used it as a land cover descriptor, the NDVI variable will henceforth be referred to as the moisture variable.

*Land surface temperatures.*—Temperature data were acquired from NASA in the form of the MODIS Terra Day and Night LST 1km (MOD11A2) V005 products. The MODIS LST products are available at 8-day increments; however, to match the same temporal resolution as the MODIS NDVI product (i.e., 16-day), only scenes with the same date as the NDVI were used. The LST products were downloaded and processed in the same manner as the MODIS NDVI product, with an additional step of filling “no data” gaps caused by the presence of clouds by using inverse distance weighted (IDW) interpolation (Li 2004). Scenes containing data gaps too large to perform an accurate interpolation (e.g., ordinal date 81, 2002) were filled with an average of the scenes 8 days before and after.

It is generally accepted that temperatures above  $\sim 36^{\circ}\text{C}$  and below  $\sim 17^{\circ}\text{C}$  will greatly hinder normal tsetse activity (Mellanby 1936, 1939, Knight 1971, Hargrove 1980, Pollock 1982b, Leak 1999, Terblanche et al. 2008). However, behavior of seeking micro-habitats to cope with temperature extremes buffers the maximum day and night temperature threshold by  $\sim 4^{\circ}\text{C}$  (see e.g., Torr and Hargrove 1999, Muzari and Hargrove 2005). The nighttime minimum temperature threshold was also altered from the accepted  $\sim 17^{\circ}\text{C}$ , below which tsetse enter into a “chill coma” (Mellanby 1936, 1939), down to  $10^{\circ}\text{C}$  to account for the diurnal nature of tsetse. The resulting suitable temperatures were between  $17^{\circ}\text{C}$  and  $40^{\circ}\text{C}$  during the day and between  $10^{\circ}\text{C}$  and  $40^{\circ}\text{C}$  at night.

*Land cover.*—The TED Model uses an externally generated LULC product to account for land cover. Based on the results of DeVisser and Messina (2009), the MODIS type 1 Global Land Cover product with a spatial resolution of 1 km was used in the TED Model. However, the MODIS type 1 Global Land Cover was only produced annually from 2001 to 2004. As a result, land cover remained static in the TED Model for the period 2005–2009. We considered, but rejected, using the MODIS 500m Global Land Cover product, which has been updated annually post 2004. The 500m Global Land Cover

product grossly overestimated the extent of grassland in southern Kenya which had a serious negative effect on the tsetse distributions predicted by the TED Model in known tsetse infested regions.

The suitability of the various LULC classes was based on the methods outlined in Cecchi et al. (2008), which compared the LULC class descriptions with published land cover requirements for tsetse (DeVisser and Messina 2009). The LULC data sets were classified into binary suitable vs. unsuitable maps.

*Fly movement rates.*—The rate of tsetse movement can be modeled in two ways: 1) maximum daily movement rate of an individual fly or 2) advancement of tsetse populations (Vale and Torr 2005). An individual fly can move up to 800 m per day (Vale et al. 1984), while fly populations with a typical 1% growth rate tend to advance much more slowly at ~11.7 km per year or roughly 513m per 16 days in what has been called a “fly front” (Hargrove 2000). Since the TED Model is designed to predict tsetse distributions as a whole, the potential movement rate of individual flies is less important. As such, the fly front was selected to model tsetse expansion rates. Due to the 250 m spatial resolution of the TED model, the advancement of the fly front was parameterized with a movement rate of 500 m (i.e., an expansion of 2 grid cells from the previous distribution) every 16 days, rather than the 513 m estimated by Hargrove (2000).

*Model initialization.*—The TED Model requires initialization with a starting tsetse distribution. Originally the TED Model was initialized using an existing tsetse distribution map (e.g., 1996 fly belts). However, due to the influence of an externally generated tsetse distribution on the outputs of the TED Model, and the possibility of excluding potential reservoirs and refugia, the TED Model was initialized with tsetse present in all of Kenya. Considering the obvious overestimation of tsetse in Kenya when the TED Model is first initialized, a one-year initialization period (1 January 2001–31 December 2001) was run before any outputs from the model were used to identify tsetse reservoirs and refugia.

### Model outputs

*Individual scenes and percent probability map.*—The TED Model produced 207 unique tsetse

distribution maps that predict the distribution of tsetse within Kenya at a 16-day temporal resolution between 1 January 2001 and 19 December 2009 (the last scene acquisition date for data used in this paper). Due to the one-year initialization period (1 January 2001–31 December 2001), only the 184 scenes between (1 January 2002–19 December 2009) were used for analysis. The total area of tsetse infestation predicted by each of the 184 individual binary scenes was then sequentially plotted to analyze their temporal patterns. The individual scenes were also summed and divided by 184 (the total number of scenes) to create a percent probability map of tsetse presence. This map was then used to compare the TED Model output to other tsetse distribution maps and to quantify the sensitivity of each variable in the TED Model.

*Tsetse reservoirs and refugia.*—The identification of tsetse reservoirs was accomplished by examining the sequentially plotted predicted tsetse surface area in each scene, and identifying the scene in each year that predicted the minimum area. The timings of these eight minimum infestation area scenes were analyzed to determine whether they coincided with a particular season. These eight scenes were combined and converted to a percent probability map. Locations with a predicted likelihood of having tsetse present between 50% and 90% were designated as tsetse reservoirs, while locations with a predicted likelihood greater than 90% were classified as tsetse refugia.

### Model assessment and validation

*Spatial goodness of fit.*—The spatial goodness of fit (GOF) analysis involved comparing the TED Model percent probability map to 1) the 1996 fly belts map (Muriuki et al. 2005, KETRI 2008), and 2) the Food and Agriculture Organization of the United Nations (FAO)/The International Atomic Energy Agency (IAEA) combined *morsitans*-group 1 km predicted tsetse suitability maps for Kenya (Wint 2001, DeVisser and Messina 2009). The comparison of these maps was quantified through the calculation of a Mapcurves GOF score, which measures the degree of spatial concordance between classes of categorical maps (Hargrove et al. 2006). The Mapcurves GOF analysis produces a standardized value between 0.0 (no spatial agreement between of classes) and

1.0 (perfect alignment of map classes). To facilitate the calculation of a Mapcurves GOF scores both the FAO/IAEA tsetse distribution map and the TED Model percent probability map were reclassified into ten classes of equal 10% probability increments.

*Model sensitivity.*—The sensitivity analysis examined how sensitive the TED Model was to changes in the three climate parameters that were used to identify suitable tsetse habitat (i.e., moisture, maximum temperature, and minimum temperature). Land cover and fly movement rates were excluded from the sensitivity analysis since land cover is a nominal variable and can not be incrementally increased or decreased, and fly movement rates could only be increase by relatively large increments of 250m due to the spatial resolution of the TED Model. To compare the sensitivity of the TED Model to changes in the climate parameters, a sensitivity index was calculated, which compares the percent change in a parameter of interest to the percent change in a model’s state variable, resulting in a normalized dimensionless index value (Lenhart et al. 2002, Millington et al. 2009). The sensitivity index used to explore the TED Model’s sensitivity was the relative sensitivity index (RSI), which compares the change in the standardized state variable between two distinct model runs with varying parameter thresholds (DeVisser 2010) (Eq. 1).

$$RSI = \frac{\Delta Y_{i_1 \& i_2} / Y_D}{\Delta P_{i_1 \& i_2} / P_D}$$

where  $Y$  is the dependant output state variable,  $P$  is the parameter threshold of the input variable being analyzed,  $i_1$  and  $i_2$  are the model runs being compared, and  $D$  are the values associated with the default baseline model. The resulting RSI calculated for each parameter was then classified into one of four categories ranging from insensitive to extremely sensitive as described in Lenhart et al. (2002) (Table 1). A parameter was deemed insensitive if the RSI was between 0.00 and 0.05, implying that a change in the parameter resulted in little to no change in the state variable. Moderate and high sensitivity was assigned to RSI values between 0.05 to 0.20 and 0.20 to 1.00, respectively. RSI values greater than 1.00 imply a proportional change in the state variable that was greater than the proportional change in the parameter, thus indicating extreme

Table 1. Sensitivity classes adapted from Lenhart et al. (2002).

Sensitivity index	Class	Sensitivity
$0.00 \leq SI < 0.05$	I	insensitive
$0.05 \leq SI < 0.20$	II	moderate
$0.20 \leq SI < 1.00$	III	highly
$SI \geq 1.00$	IV	extremely

sensitivity.

The state variable in the TED Model sensitivity analysis was the surface area of the percent probability map above 50%. The NDVI parameter threshold of 0.39 was varied by 0.02 (~5%) to a minimum threshold value of 0.00 and a maximum threshold value of 0.79. The maximum and minimum temperature parameter thresholds of 40°C and 10°C for night LST and 17°C for day LST were varied by 1°C. However, due to the diurnal nature of tsetse activity, minimum temperature has different day and night LST threshold values. Considering that 10°C is a lethal threshold (Terblanche et al. 2008) and 17°C is a mobility threshold (Mellanby 1936, 1939), the standardization of the minimum temperature RSI was performed using only the nighttime parameter threshold.

The two different threshold values of minimum and maximum temperature present another issue since a 1°C change at 10°C represents a 10% change in the parameter threshold, while at 40°C a 1°C change represents a 2.5% change. The influence of this difference on the calculation of the RSI would cause direct comparison of model sensitivity to minimum and maximum temperature to be inappropriate. To avoid this predicament, a 1°C change in both minimum and maximum temperature was standardized to a 4% change, the equivalent of a 1°C change if both default parameter thresholds were set at 25°C (i.e., halfway between the two original threshold values). Thus minimum and maximum temperature RSI values were calculated using Eq. 2:

$$RSI = \frac{\Delta Y_{i_1 \& i_2} / Y_D}{\Delta P_{i_1 \& i_2} \times 0.04}$$

where  $Y$  is the dependant output state variable,  $P$  is the parameter threshold of the input variable being analyzed,  $i_1$  and  $i_2$  are the model runs being compared, and  $Y_D$  is the state variable value associated with the default baseline model.

*Tsetse reservoir field sampling.*—Unfortunately, the use of previously collected fly capture site data (e.g., KETRI 2008) is of limited use in the validation of the TED Model, since very little information is available outside of existing fly belts; specifically the absence of tsetse has not been sampled or recorded. For this reason seven sites were selected for monitoring tsetse presence/absence in potential reservoir locations predicted outside of traditional fly belts. The selection of sites outside of traditional belts was important to test not only the reservoir, but also for the presence of flies in previously unidentified areas.

The sites selected were near the towns of Machakos, Mwingi, Namanga, Meru, Nanyuki, Eldama Ravine, and Kitale. The sampling used the minimal survey method where a survey is carried out once to determine the distribution of tsetse species (Gamba 2009). Random and stratified methods were used in the survey after the most suitable locality accessible within the predicted reservoir was identified. We used the unmodified biconical traps (Challier and Lavoisier 1973) at all the sites. All traps were baited with sachets containing a combination of phenols and acetone, dispensed at 500mg/h from glass bottles with a 2 mm aperture at the top (Gamba 2009). The traps were greased to prevent ants from damaging the captured tsetse. The trapping period in each location was 4 nights and the number of traps used ranged from 2 to 10 per site (Gamba 2009).

## RESULTS

### *Model outputs*

Excluding the one-year initialization period, the TED Model produced 184 binary tsetse distribution maps, one for each 16-day period from 1 January 2002–19 December 09. The cumulative size of the areas predicted to have tsetse present was plotted over time to demonstrate that tsetse distributions fluctuate both at intra-annual and inter-annual temporal resolutions (Fig. 2). The maximum area of infestation (67,378 km<sup>2</sup>) occurred during the 2002 long rains (25 May 2002), while the minimum area of infestation (16,082 km<sup>2</sup>) was predicted at the end of the 2009 cool, dry season (30 September 2009). The fluctuations in tsetse distributions

predicted by the TED Model correspond very well with seasonal weather patterns (Fig. 3). Fly populations expand with the onset of the long rains (roughly the beginning of March), contract at the start of the cool dry season (roughly the beginning of June), expand again with the commencement of the short rains (roughly late October), and contract during the hot dry season.

To assess the overall distributions of tsetse predicted by the TED Model, the individual scenes were summed and divided by 184 (the number of scenes) to produce the tsetse percent probability map (Fig. 4). Due to the use of the fly front in the TED tsetse movement model, the TED Model percent probability map displays the percent likelihood of encountering high tsetse population densities at any time between the beginning of 2002 and the end of 2009. Since the TED Model only identifies areas of higher population densities, in reality one should expect to find tsetse in lower densities outside the predicted TED Model distributions. However, the exact fly population densities and distance from the edge of the predicted tsetse distributions will vary significantly from location to location.

### *Tsetse reservoirs and refugia*

Analysis of the country-wide timing of the tsetse reservoirs and refugia showed that in 6 out of the 8 years, the minimum predicted annual infested area occurred at the end of the cool dry season (i.e., mid- to late-October). The two exceptions were 2006 and 2007, when the smallest predicted annual distribution occurred during the hot dry season (i.e., end of February). The variability in the timing of the country-wide annual minimum predicted tsetse distributions spurred us to examine the temporal and spatial patterns of predicted tsetse expansion and contraction at finer scales.

Two relatively isolated distributions (i.e., a low probability of the predicted tsetse distribution being connected with a neighboring tsetse population) were identified and named Mwingi and Loiya after nearby towns (Fig. 5). The cumulative predicted area of tsetse infestation was plotted over time for both of these isolated distributions (Fig. 6). The Mwingi distribution was predicted to contract during the cool dry season and generally expand during the rest of



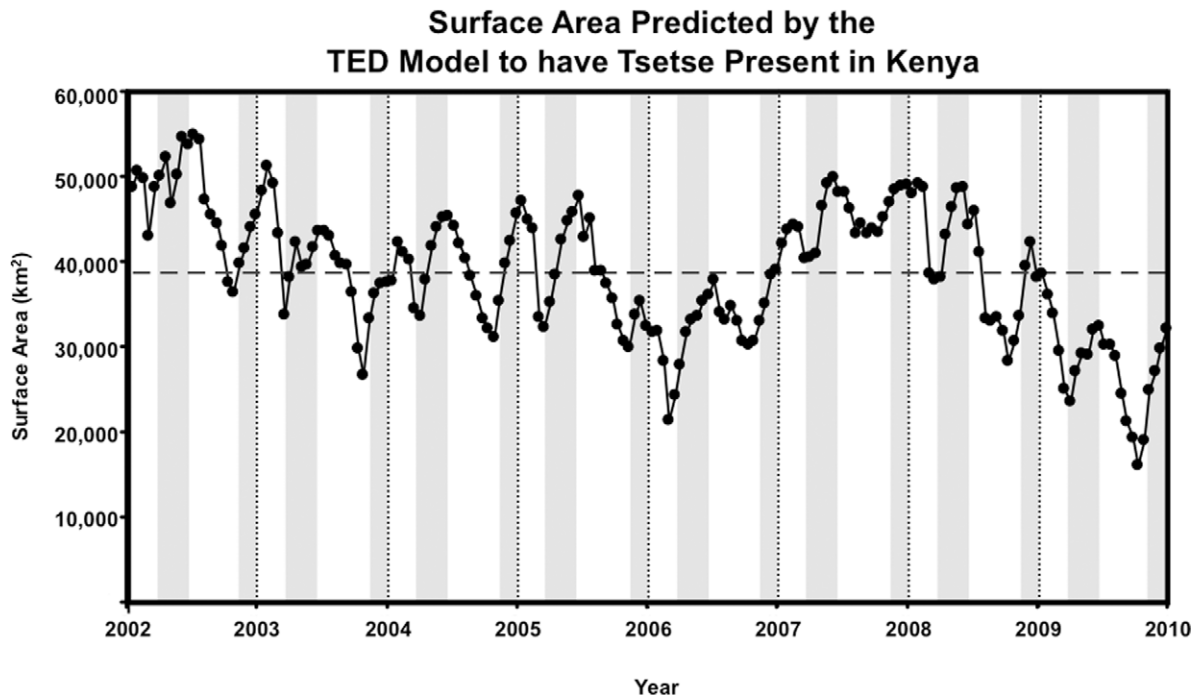


Fig. 2. The surface area predicted to have tsetse present by the TED Model between the beginning of 2002 and the end of 2009. The timing of the long and short rains is denoted in grey, and the mean predicted surface area (i.e., 38,733 km<sup>2</sup>) is denoted with slashed line.

the year. The Loiya distribution predicted expansions during the wet seasons, contractions during the dry seasons, with the annual minimum infested area occurring at the end of the hot dry season.

Using the tsetse reservoir and refugia identification guidelines, the Mwingi distribution had approximately 33.4 km<sup>2</sup> of reservoir habitat and 7.4 km<sup>2</sup> of refugia habitat at the end of the cool dry season (roughly the beginning of October) (Table 2). The Loiya distribution displayed larger tsetse reservoir and refugia than the Mwingi distribution, with 121 km<sup>2</sup> identified as reservoir habitat and 19.3 km<sup>2</sup> of refugia habitat. The Loiya distribution exhibited an establishment date range from the middle of February to the beginning of April.

#### *Model assessment and validation*

*Spatial goodness of fit.*—The spatial GOF analysis comparing the TED Model percent probability map with the 1996 fly belts map resulted in a Mapcurves GOF score of 0.560 (Table 3), with approximately 70% of the TED Model predicted

distributions falling within the boundaries of the fly belts. The comparison between the TED Model and the FAO/IAEA distributions resulted in a Mapcurves GOF score of 0.126. Comparing the FAO/IAEA distribution map with the 1996 fly belts map resulted in a GOF score of 0.650. Approximately 60% of the FAO/IAEA tsetse distributions fell within the boundaries of the fly belts.

*Model sensitivity.*—The sensitivity analysis examined how sensitive the TED Model was to changes in the three climate parameters used to identify suitable tsetse habitat (i.e., moisture, maximum temperature, and minimum temperature). Changes in these climate parameter thresholds can be framed in two ways: 1) tsetse tolerance for a variable changed (i.e., tsetse are more or less sensitive to changes in temperature/moisture), or 2) climate conditions changed (e.g., regional increase or decrease in temperatures/moisture). Here, we assume species physiology is constant, and therefore, the sensitivity analysis is framed as how sensitive predicted tsetse distributions are in lieu of a uniform regional change

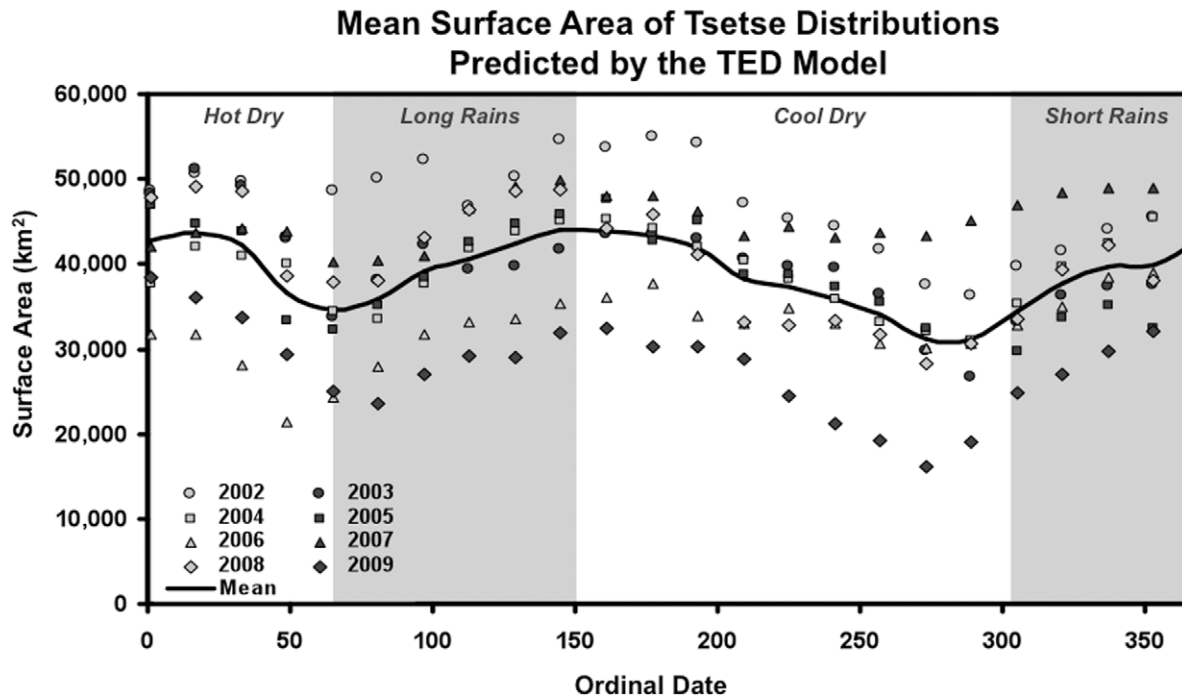


Fig. 3. The intra-annual variability of tsetse distributions predicted by the TED Model, with four seasons denoted to emphasize the seasonal patterns of tsetse expansion and contraction.

in climate conditions.

The results of the sensitivity analysis performed on the maximum temperature variable showed an inverse relationship with predicted tsetse distributions (i.e., an increase in maximum temperature resulted in smaller area tsetse distributions) (Fig. 7). Maximum temperature produced RSI values ranging from 0.00 (class I) to 3.96 (class IV), with the highest RSI values being associated with a decrease in the parameter threshold (i.e., increase of regional maximum temperatures). The TED Model varies from highly sensitive (class III) to moderately sensitive (class II) in response to 1) approximately a 7°C decrease in maximum temperatures when tsetse distributions no longer increase in area; or 2) a 12°C increase in maximum temperatures when the tsetse distribution is reduced to nearly 0 km<sup>2</sup>.

The results of the sensitivity analysis performed on the minimum temperature variable showed a synchronistic relationship with predicted tsetse distributions (i.e., an increase in minimum temperature resulted in larger-area tsetse distributions) (Fig. 7). The minimum temperature variable produced RSI values rang-

ing from 0.13 (class II) to 7.48 (class IV), with the highest RSI values being associated with a decrease in the parameter threshold (i.e., a decrease of regional minimum temperatures). The TED Model shifts from highly sensitive (class III) to moderately sensitive (class II) only after a 20°C increase in minimum temperatures, when tsetse distributions no longer increase in size. But, the model never reaches moderate sensitivity before tsetse distributions are reduced to nearly 0 km<sup>2</sup> at an 8°C decrease in regional minimum temperatures.

The results of the sensitivity analysis performed on moisture showed a synchronous relationship with predicted tsetse distributions (i.e., an increase in moisture resulted in expanded tsetse distributions) (Fig. 7). The moisture sensitivity analysis produced RSI values ranging from 0.00 (class I) to 4.75 (class IV), with the highest RSI values being associated with a decrease in the parameter threshold (i.e., increase of regional available moisture). The TED Model only becomes moderately sensitive (class II) with approximately a 95% decrease or 70% increase in NDVI parameter thresholds, at which point the

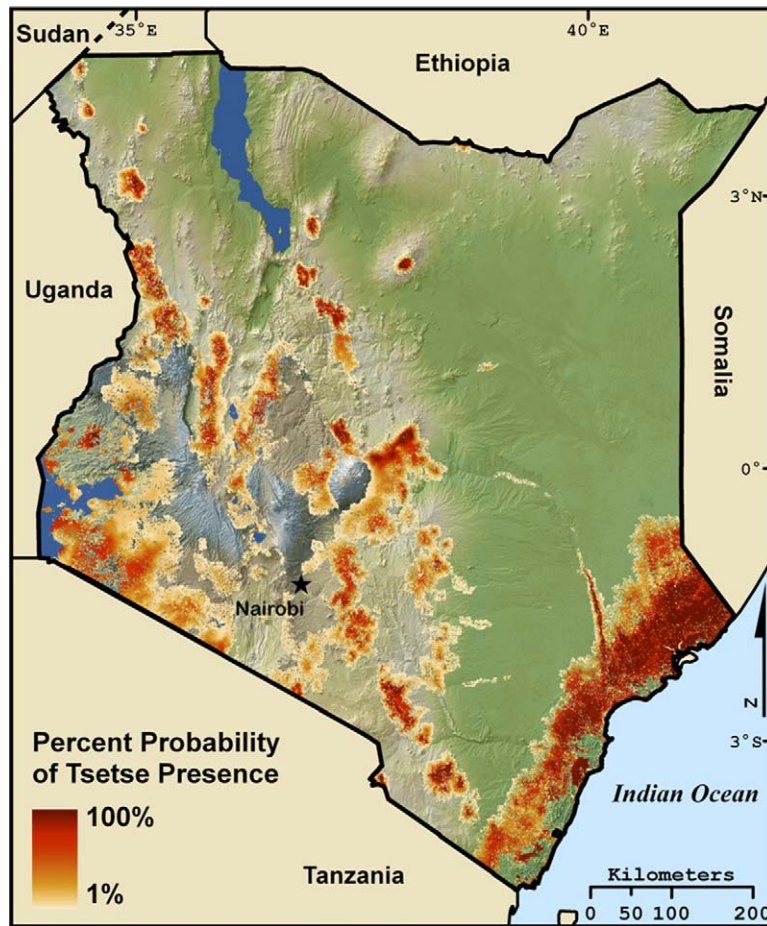


Fig. 4. The TED Model percent probability map overlaid on a physiographic map of Kenya to show the location of predicted tsetse distributions.

predicted tsetse distributions have either reached their maximum distribution or are reduced to nearly 0 km<sup>2</sup>.

*Tsetse reservoir field sampling.*—Our trapping efforts failed at all seven sites. However, in one instance tsetse flew into our field vehicle. Interviews with veterinary service providers and local herders confirmed the recent presence of tsetse at all sites. Trypanosomiasis in cattle was present at all but the Machackos site. In the Mwingi and Namanga sites animals that had been treated with trypanocides within the previous two weeks were shown to the field team.

## DISCUSSION AND CONCLUSION

### *Model assumptions and uncertainty*

Arguably, the largest source of uncertainty in

the TED Model is the spatial resolution of the data used. All the outputs from the TED Model are at a spatial resolution of 250m, however, only the NDVI data are collected at that spatial resolution, while the temperature and LULC data are both a coarser 1km spatial resolution. The underlying assumptions in using remotely sensed data within the TED Model are that conditions are uniform within a pixel, and that all suitable tsetse habitat can be identified using the MODIS products at 250m and 1km resolutions. These assumptions are surely violated when one considers that a patch of a particular plant species (e.g., *Cordia sinensis*) can provide suitable habitat for tsetse and be much smaller than 250m<sup>2</sup>. Thus, conditions within some pixels are not uniform and some suitable habitat is undetectable at this spatial resolution. Hence,

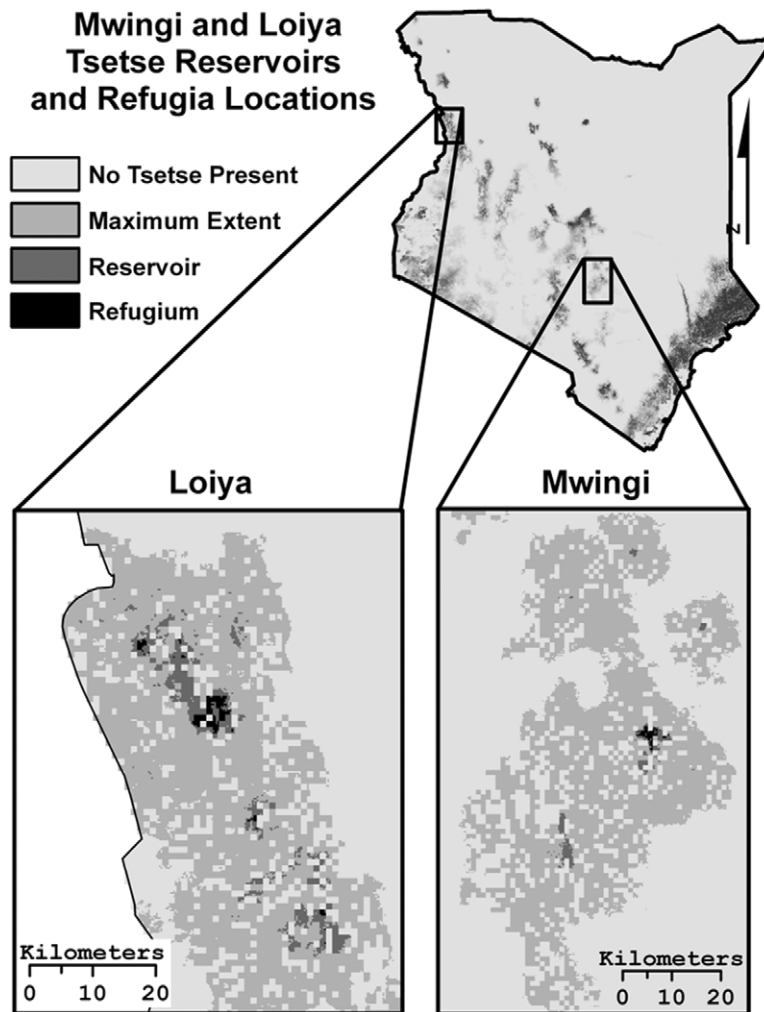


Fig. 5. The Mwingi and Loiya subset locations and predicted tsetse distributions. Light grey indicates no tsetse were predicted; grey indicates the maximum extent that tsetse were predicted to reach between 2002 and the end of 2009; dark grey indicates a tsetse reservoir; black indicates a tsetse refugium.

users of tsetse distributions predicted by the TED Model must understand that they very likely exclude scattered and sparse tsetse populations that rely on patches of suitable habitat smaller than 250m<sup>2</sup>. However, a single *C. sinensis* plant or a very small patch of woody vegetation may not provide enough suitable habitat to sustain a tsetse population over the long-term.

In addition to the TED Model not being able to identify small patches of suitable tsetse habitat, it also does not identify the spatial location of tsetse that move at a rate faster than the fly front rate of expansion. However, the TED Model was not designed to account for individuals or the

maximum possible extent that tsetse could expand during seasonal periods hence the use of the fly front expansion model. The term “fly front” and the associated rate of expansion is based on the previous research of Hargrove (2000), which uses the fly front to predict the linear re-invasion of tsetse into previously controlled regions (e.g., flies re-invading valley from one end to the other), essentially as a “wave” of tsetse. While in the TED Model the fly front expansion out from a tsetse reservoir or refugia may function more as a “ripple” of tsetse emanating out from a source into seasonally suitable habitat. Given that tsetse are k-strategists



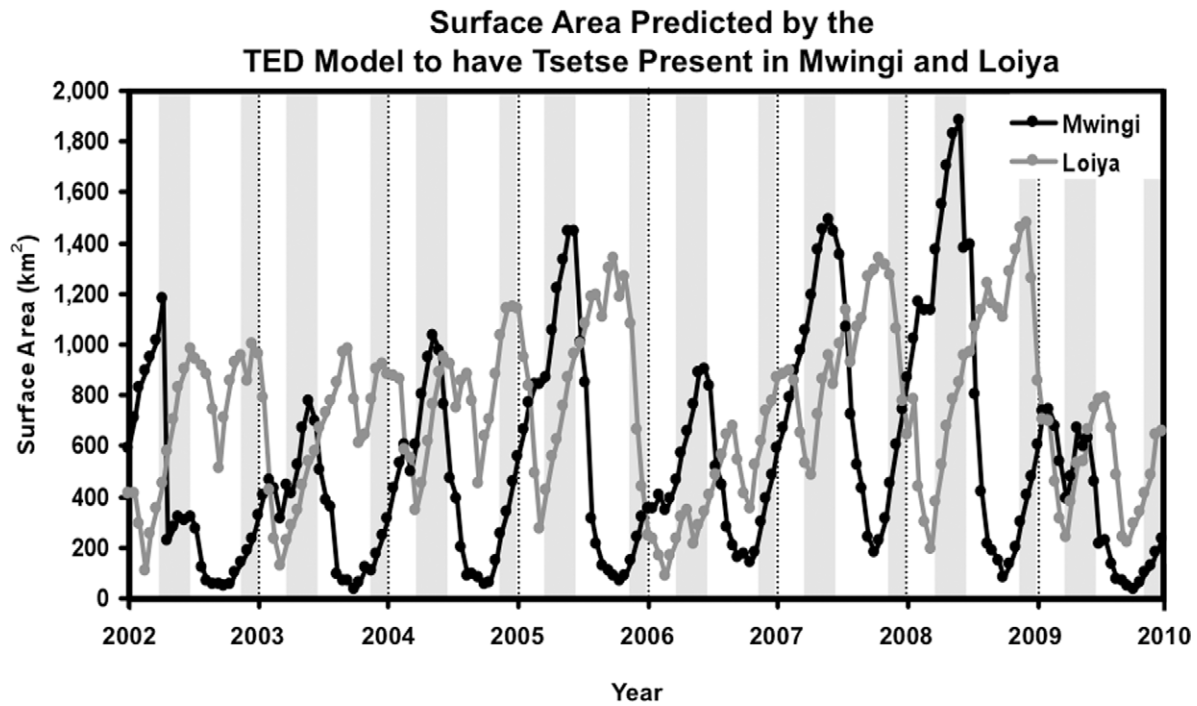


Fig. 6. The surface area of tsetse infestation predicted by the TED Model in the Mwingi and Loiya regions between the beginning of 2002 and the end of 2009. The timing of long and short rains is denoted in grey.

Table 2. The Mwingi and Loiya annual minimum and maximum predicted tsetse distributions.

Year	Mwingi distribution				Loiya distribution			
	Annual minimum		Annual maximum		Annual minimum		Annual maximum	
	Ordinal date	Area (km <sup>2</sup> )	Ordinal date	Area (km <sup>2</sup> )	Ordinal date	Area (km <sup>2</sup> )	Ordinal date	Area (km <sup>2</sup> )
2002	273	43	97	1,176	49	105	353	1,000
2003	273	36	145	774	65	127	257	981
2004	273	52	129	1,030	81	343	353	1,145
2005	289	63	161	1,445	65	273	273	1,335
2006	289	142	161	901	49	88	353	774
2007	273	178	145	1,488	97	482	289	1,340
2008	273	78	145	1,880	65	195	337	1,476
2009	273	31	33	741	81	238	193	787
Reservoir area		33		792		121		803
Refugia area		7		52		19		250
Total		40		844		140		1,053

Table 3. Ground truth comparison GOF scores.

Maps compared	GOF score
TED Model vs. 1996 Fly Belts	0.560
FAO/IAEA vs. 1996 Fly Belts	0.650
TED Model vs. FAO/IAEA	0.126

the wave versus ripple fly front would be associated with different populations densities,

which in turn would affect the expansion rates. However, again the TED Model was not designed to accurately predict tsetse distributions as a whole, rather to identify the spatial location and timing of tsetse reservoirs and refugium.

Another assumption related to fly movement in the TED Model is that tsetse host species are uniformly present throughout Kenya at all times. Since both wild and domestic hosts migrate at

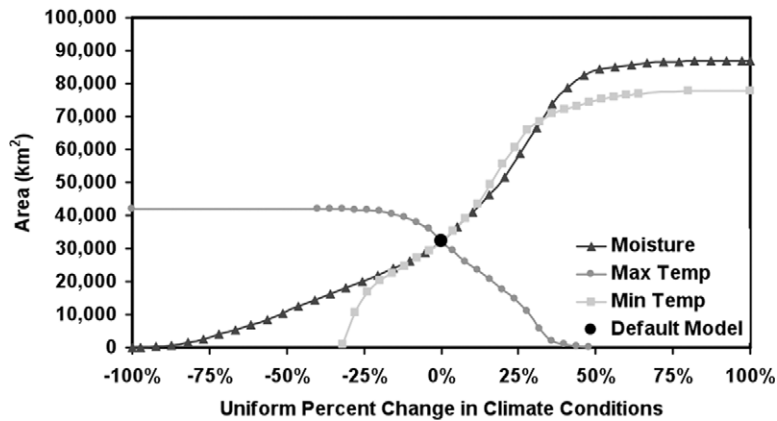


Fig. 7. Combined and standardized parameter threshold values and the corresponding surface area state variable used in the sensitivity analysis.

various time scales for a variety of reasons (Homewood et al. 2001), and tsetse may be forced to follow the host species, this assumption is a source of uncertainty in the predicted tsetse distributions. However, the primary factor in animal migration is the search for food (Eloff 1959), a limited resource in the semi-arid regions of Kenya, especially in the dry seasons. NDVI, our surrogate for moisture, could also be used as a surrogate for forage quality, a major constraint on animal populations.

#### Model assessment and validation

*Spatial goodness of fit.*—The spatial GOF analysis showed that the level of agreement between all three maps is very low and thus asserts that the maps do not agree where tsetse are located. The disagreement between the three maps is most likely attributable to the differences in what each map represents and how each map was constructed (i.e., species distribution model, logistic regression predicting the fundamental niche of tsetse, and fly capture sites/historical distributions). The use of a fly movement model coupled to a fundamental niche model in the TED Model means that only tsetse populations with access to some ecologically suitable habitat year round (e.g., a reservoir) will be predicted (i.e., realized niche). Conversely, the FAO/IAEA map claims to predict the percent likelihood of encountering tsetse in a given location, but more precisely predicts the likelihood of encountering suitable tsetse habitat (i.e., the fundamental niche). Without the incorporation of a fly

movement model, the logistic regression model used to construct the FAO/IAEA map cannot take into account tsetse movement rates. Thus to make the claim to predict the likelihood of encountering tsetse in a given location, the FAO/IAEA model assumes if tsetse habitat is present, then tsetse are present. By making this assumption, the FAO/IAEA map likely over estimates the realized niche of tsetse, essentially producing a product similar to the TED Model's fundamental niche output (Fig. 8).

The 1996 fly belts map, although based on field data, is essentially a polygon drawn around historical tsetse populations and point sampled fly capture sites. Unfortunately this method of mapping tsetse distributions has the unintended effect of presenting tsetse distributions as static in both space and time. Furthermore, the 1996 fly belts map displays the distribution of all eight tsetse species in Kenya, while both the TED Model and FAO/IAEA distribution maps focus on the *morsitans*-group. Although the distributions of the other four tsetse species are either relatively small in size or overlap regions where *Glossina* subgenus *Morsitans* species are found, the addition of the other species may lower the level of agreement.

Another source of disagreement between the TED Model and the other two reference maps is the use of the fly front, which induces the TED Model to only predict locations with high tsetse population densities. A solution to this problem could be to simply increase the fly movement rates, essentially buffering the predicted tsetse

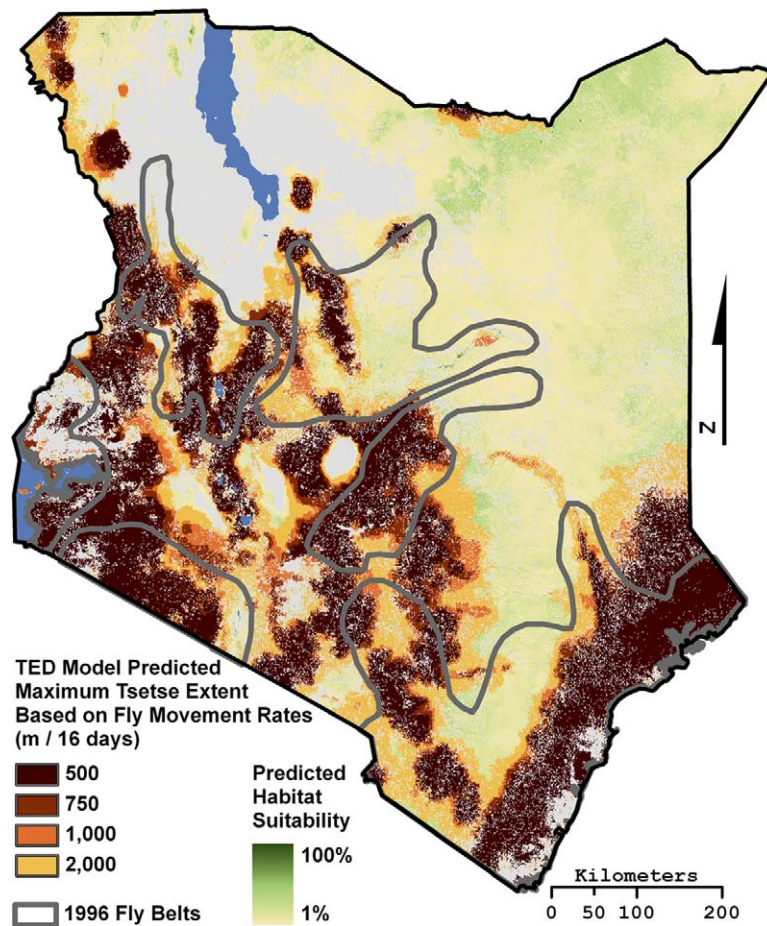


Fig. 8. The maximum extent of tsetse distribution during the 8-year analysis period with the fly movement rate set at 500 m/16 days (i.e., the default value), 750 m/16 days, 1,000 m/16, and 2,000 m/16 days, overlaid with the output from the default TED fundamental niche model and the 1996 fly belts.

distributions (Fig. 8). However, this may lead to an over estimation of tsetse distributions, the exploration of which is beyond the scope of this manuscript.

Given the differences in the TED Model, the FAO/IAEA, and the 1996 fly belt maps, in particular the lack of accounting for fly movement over space and time, a great deal of disagreement between these products should be expected. However, the lack of agreement between the TED Model and the existing reference data might highlight the unsuitability of the existing FAO/IAEA and 1996 fly belts maps for mapping space/time dependent tsetse distributions. Curran et al. (2000) outline two underlying premises to justify the use of remotely sensed data in the modeling of vector borne diseases.

First, the spatial distributions of vector-borne diseases are related to the habitat of the vector (Pavlovskii 1966). Second, remotely sensed data can be used to provide information on land cover/climate and, by association, the habitat of species (Innes and Koch 1998). As a result, remotely sensed data can provide useful information on the spatial distribution of vector-borne diseases (Hay et al. 1997). Our study asserts an additional premise; by using a time-series of remotely sensed data, the user is able to gain information on the temporal nature of vector-borne diseases. Assuming that the remotely sensed data and parameters used in the TED Model are accurate, then the TED Model should correctly predict the spatio-temporal location of tsetse distributions.

*Model sensitivity.*—The sensitivity analyses demonstrated that the tsetse distributions predicted by the TED Model were extremely sensitive to changes in the climate parameters. The sensitivity analyses also explored the impact that each climate variable could have in limiting or expanding the predicted tsetse distributions based on uniform regional changes in climate conditions. Although this scenario of uniform regional changes in climate is unlikely, the general relationships between tsetse and the climate variables that determine habitat suitability should hold true.

Maximum temperature was shown to have the greatest potential to limit tsetse distributions. This is of particular interest given a projected increase of roughly 1.7°C by 2050, and 4°C by 2100 for East Africa by the Intergovernmental Panel of Climate Change's (IPCC) A1B scenarios (Mitchell et al. 2004, Boko et al. 2007, Christensen et al. 2007). If these projections hold true, then a decrease in tsetse populations can be expected. However, this would only occur in localities where the maximum temperatures are at or near 40°C currently, which is mostly in the lowlands below 1,500 meters elevation.

In the highland regions, an increase of minimum temperature by 1.7°C to 4°C could potentially cause an expansion of tsetse into these landscapes. In southern Africa, minimum temperature is considered to be the most influential climate variable limiting tsetse distributions (Leak 1999). Due to Kenya's location on the equator, minimum temperature only affects tsetse distributions in the highland areas around Mount Kenya and the rim of the rift valley. The potential spread of tsetse into higher elevations is of particular concern because the Kenyan highlands are home to the majority of Kenyans, and the livestock in this region are generally highly susceptible to trypanosomiasis.

The sensitivity analysis performed on moisture showed that a uniform increase in regional moisture conditions has the greatest potential to expand predicted tsetse distributions in the TED Model. Current climate change projections call for potentially higher precipitation totals, but more variability in rainfall patterns in East Africa (Christensen et al. 2007). Since moisture was calculated to have the greatest potential to expand tsetse distributions in the sensitivity

analysis, increased precipitation levels could increase the overall area of tsetse infestation. However, increased rainfall during the wet season combined with the higher projected temperatures may not translate into higher available moisture levels during the dry seasons.

*Field sampling.*—The failure of the field sampling was likely due a severe drought in Kenya brought about by the weak long rains of 2008, followed by failed short rains in 2008 and long rains of 2009 (Gettleman 2009, KFSSG 2008, KFSSG 2009a, b). The drought likely restricted tsetse distributions to refugium habitat. Given that the ability of the TED Model to predict tsetse distributions is limited to approximately one month prior to the current date (i.e., the most recent MODIS data), and the site selection took place roughly two months before the field sampling, we unfortunately sampled within the predicted tsetse reservoirs rather than refugia.

In addition to the sampling of reservoirs rather than refugia, the inability of current trapping technology to effectively sample low-density fly populations may have contributed to the lack of trapped flies (Kgori et al. 2006). Normally in the dry season, tsetse population densities are low (Brightwell et al. 1992); during prolonged droughts, tsetse densities are even lower. This severe drought likely reduced fly population densities to such a low level that a long-term intensive monitoring operation covering the whole reservoir area would be needed to conclusively test whether or not tsetse were present (Leak et al. 2008).

Despite the field sampling, the visual observation of flies in a few locations in conjunction with the interviews of local veterinary service providers and local (i.e., non-migratory) herders who confirmed transmission of animal trypanosomiasis in 7 of the 8 sites strongly suggests the presence of tsetse. While the mechanical transmission of trypanosomiasis by non-tsetse insects is a remote possibility, such transmission depends on the type of trypanosomes and specific alternative vectors, and neither is traditionally found in any of our sampling sites (Desquesness and Dia 2003). Regardless of the drought negatively impacting our field sampling endeavors, the TED Model has now incorporated the predicted drought tsetse distributions, which led to the distinction between reservoirs and refugia



and increases the accuracy of future predictions.

#### *Trypanosomiasis, tsetse, and the TED Model*

African trypanosomiasis is a neglected tropical disease spread by the tsetse fly. Most efforts to control trypanosomiasis have focused on tsetse; however, such efforts have relied on fly belt maps to identify where to target tsetse. Fly belts, although useful in delineating where tsetse were historically found, do not account for seasonal variation in tsetse distributions. All other tsetse models predict tsetse distributions at a particular moment in time despite numerous studies that discuss the seasonal expansion and contraction of tsetse populations (e.g., Austen and Hegh 1926, Nash 1933, Bursell 1956, Brightwell et al. 1992, Hargrove 2001, Odulaja et al. 2001, Bett et al. 2008). Since tsetse distributions fluctuate over space and time, a dynamic realized niche/species distribution model that predicts when and where fly reservoirs occur will be useful to control operations for many reasons including: 1) reductions in cost by focusing on smaller areas identified as reservoirs and refugia; 2) improved ability of control efforts to target flies; and 3) operating in small reservoirs/refugia minimizes the environmental impacts associated with control campaigns.

The TED Model tracks both spatial and temporal fluctuations in predicted tsetse distributions in Kenya. A strong seasonal pattern was apparent in the country-wide expansion and contraction of suitable tsetse habitat. By plotting the cumulative predicted tsetse infestation area over time, the timing of constrained tsetse populations was identified. However, due to fluctuations in the ITCZ and the variety of physiographic features and climate regions in Kenya, the timing, duration, and climate conditions that influence the amount of suitable tsetse habitat vary across space making local analyses necessary. For this reason, two subsets of the countrywide data in the form of relatively isolated predicted tsetse distributions were extracted and used to identify tsetse reservoirs and refugia at a finer spatial scale. The results of the Mwingi subset predicted tsetse expansion during the short rains, a slight contraction during the hot dry season, continued expansion during the long rains, and a dramatic contraction in tsetse distributions during the cool dry season. The

predicted slight decrease in tsetse distributions during the hot dry season was surprising, but may be attributable to the local hilly topography and high elevation providing cooler temperatures than the surrounding plains. The TED Model predicted that the Loiya tsetse distributions would generally follow the expansion and contraction patterns of Kenya as a whole, with expansion of tsetse in the wet seasons and contraction during the dry seasons. The annual minimum predicted tsetse distributions in the vicinity of Loiya occurred in the hot dry season, but unlike the Mwingi distributions, the timing of constrained tsetse distributions was more variable.

Regardless of whether the most constrained tsetse distributions were predicted to occur in the hot dry or the cool dry season, the identification of the tsetse reservoirs and refugia habitats demonstrated the value of studying seasonal patterns of tsetse distributions. The maximum annual predicted tsetse distributions occupied 844km<sup>2</sup> in the Mwingi region (~20 times larger than the reservoirs and refugia combined), and 1,053km<sup>2</sup> in the Loiya region (~7.5 times larger). Due to the dramatic difference in area, the cost of implementing control techniques inside the reservoirs and refugia vs. the maximum annual predicted distribution would be greatly reduced. In addition to the advantage of reducing the treatment area and associated costs, tsetse are k-strategists and rely on high survival rates to compensate for low reproductive rates. By reducing the tsetse population that would normally survive a seasonal fluctuation in habitat (e.g., the dry season), the residual population is unable to quickly reproduce enough offspring to allow for normal distribution expansion when suitable habitat does become available (e.g., the wet season).

Furthermore, the ability of the TED Model to predict the location and timing of tsetse reservoir and refugia habitat will improve with each additional year of data. Over time, a distinction between the truly critical reservoir locations and the sporadically suitable habitat will become apparent. Of particular importance is the TED Model's identification of tsetse refugium habitat, which represents area critical to tsetse survival during periods of extreme climatic events. One such extreme event captured by the remotely

sensed data used in the TED Model was the 2009 drought, which for parts of Kenya was the worst drought in living memory (Western 2009). Although drought events are wholly undesirable, they do offer the potential to implement a smaller-scale control campaign inside identified tsetse refugia, with possibly even greater control efficacy than that of a non-drought year.

## ACKNOWLEDGMENTS

This research was supported by The National Institutes of Health, Office of the Director, Roadmap Initiative, and NIGMS: award # RGM084704A.

## LITERATURE CITED

- Afrane, Y. A., G. Zhou, B. W. Lawson, A. K. Githeko, and G. Yan. 2007. Life-table analysis of *Anopheles arabiensis* in western Kenya highlands: Effects of land covers on larval and adult survivorship. *The American Journal of Tropical Medicine and Hygiene* 77:660–666.
- Allsopp, R. 2001. Options for vector control against trypanosomiasis in Africa. *Trends in Parasitology* 17:15–19.
- Austen, E., and E. Hegh. 1922. Tsetse-flies; Their characteristics, distribution and bionomics: with some account of possible methods for their control. The Imperial Bureau of Entomology, London, UK.
- Awange, J. L., L. Ogalo, K. H. Bae, P. Were, P. Omondi, P. Omute, and M. Omullo. 2008. Falling Lake Victoria water levels: Is climate a contributing factor? *Climatic Change* 89:281–297.
- Bett, B., P. Irungu, S. O. Nyamwaro, G. Murilla, P. Kitala, J. Gathuma, T. F. Randolph, and J. McDermott. 2008. Estimation of tsetse challenge and its relationship with trypanosomiasis incidence in cattle kept under pastoral production systems in Kenya. *Veterinary Parasitology* 155:287–298.
- Boko, M., I. Niang, A. Nyong, C. Vogel, A. Githeko, M. Medany, B. Osman-Elasha, R. Tabo, and P. Yanda. 2007. Africa. *Climate Change 2007: Impacts, Adaptation and Vulnerability. Contribution of Working Group II to the Fourth Assessment Report of the Intergovernmental Panel on Climate Change*. Cambridge University Press, Cambridge, UK.
- Bourn, D., R. Reid, D. Rogers, B. Snow, and W. Wint. 2001. Environmental change and the autonomous control of tsetse and trypanosomiasis in Sub-Saharan Africa. Information Press Limited, Oxford, UK.
- Brightwell, R., R. D. Dransfield, and B. G. Williams. 1992. Factors affecting seasonal dispersal of the tsetse flies *Glossina pallidipes* and *G. longipennis* (Diptera: Glossinidae) at Nguruman, south-west Kenya. *Bulletin of Entomological Research* 82:167–182.
- Bursell, E. 1957. The effect of humidity on the activity of tsetse flies. *Journal of Experimental Biology* 34:42–51.
- Bursell, E. 1961. Starvation and desiccation in tsetse flies (*Glossina*). *Entomologia Experimentalis et Applicata* 4:301–310.
- Bursell, E. 1963. Tsetse-fly physiology: a review of recent advances and current aims. *Bulletin of the World Health Organisation* 28:703–709.
- Buxton, P. 1955. The natural history of tsetse flies: an account of the biology of the genus *Glossina* (Diptera). H. K. Lewis and Co. Ltd., London, UK.
- Cecchi, G., R. C. Mattioli, J. Slingenbergh, and S. de La Rocque. 2008. Standardizing land cover mapping for tsetse and trypanosomiasis decision making. Pages 1–97. PAAT Information Service Publications. Food and Agriculture Organisation of the United Nations; IAEA Joint Division, International Atomic Energy Agency, Rome.
- Challier, A., M. Eyraud, A. Lafaye, and Laveissierec. 1997. Amelioraboa due piege biconique pour glossines (Diptera Glossinidae) par l'emploi d'un con inferieur blue cah. *Ser. Entomology Medical Parasitology* 15:283–286.
- Christensen, J. H., B. Hewitson, A. Busuioc, A. Chen, X. Gao, R. Held, R. Jones, R. K. Kolli, W. K. Kwon, R. Laprise, and others. 2007. Regional climate projections, *Climate Change, 2007: The Physical Science Basis. Contribution of Working group I to the Fourth Assessment Report of the Intergovernmental Panel on Climate Change*. University Press, Cambridge.
- Curran, P. J., P. M. Atkinson, E. J. Milton, and G. M. Foody. 2000. Linking remote sensing, land cover and disease. *Advances in Parasitology* 47:37–80.
- Desquesnes, M., and M. L. Dia. 2003. Mechanical transmission of *Trypanosoma congolense* in cattle by the African tabanid *Atylotus agrestis*. *Experimental Parasitology* 105:226–231.
- DeVisser, M. H., and J. P. Messina. 2009. Optimum land cover products for use in a *Glossina morsitans* habitat model of Kenya. *International Journal of Health Geographics* 8:39.
- DeVisser, M. H. 2010. Identifying sensitivity thresholds in environmental models: When does a model become insensitive to change? *in* ASPRS Annual Conference Proceedings. San Diego, CA.
- Eloff, P. 1959. Observations on the migration and habits of the Antelopes of the Kalahari Gemsbok Park-Part I. Koedoe-African Protected Area Conservation and Science 2:1–29.
- Ford, J. 1971. The Role of Trypanosomiasis in African Ecology. Clarendon Press, Oxford, UK.
- Ford, J., and K. Katondo. 1977. Maps of tsetse fly (*Glossina*) distribution in Africa. *Bulletin of Animal*

- Health and Production in Africa 15:187–193.
- Gatebe, C. K., P. D. Tyson, H. Annegarn, S. Piketh, and G. Helas. 1999. A seasonal air transport climatology for Kenya. *Journal of Geophysical Research* 104:14,237–14,244.
- Gettleman, J. 2009. September 8. Lush Land Dries Up, Withering Kenya's Hopes. *The New York Times*.
- Gilbert, M., J. Jenner, D. Pender, D. Rogers, J. Slingenbergh, and W. Wint. 2001. The Programme Against African Trypanosomiasis Information System (PAATIS). Pages 11–24 *in* *World Class Parasites: The African Trypanosomes*. Kluwer Academic Publishers, Boston, Massachusetts, USA.
- Grant, I. F. 2001. Insecticides for tsetse and trypanosomiasis control: is the environmental risk acceptable? *Trends in Parasitology* 17:10–14.
- Guisan, A., and W. Thuiller. 2005. Predicting species distribution: offering more than simple habitat models. *Ecology Letters* 8:993–1009.
- Guisan, A., and N. Zimmermann. 2000. Predictive habitat distribution models in ecology. *Ecological Modelling* 135:147–186.
- Hargrove, J. W. 1980. The effect of ambient temperature on the flight performance of the mature male tsetse fly, *Glossina morsitans*. *Physiological Entomology* 5:397–400.
- 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. 2001. 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. Pages 1–134. *Research Report, Animal Health Programme, Center for Tropical Veterinary Medicine, University of Edinburgh, UK*.
- Hargrove, W. W., F. M. Hoffman, and P. F. Hessburg. 2006. Mapcurves: a quantitative method for comparing categorical maps. *Journal of Geographical Systems* 8:187–208.
- Hay, S. I., M. J. Packer, and D. J. Rogers. 1997. Review article: The impact of remote sensing on the study and control of invertebrate intermediate hosts and vectors for disease. *International Journal of Remote Sensing* 18:2899–2930.
- Homewood, K., E. F. Lambin, E. Coast, A. Kariuki, I. Kikula, J. Kivelia, M. Said, S. Serneels, and M. Thompson. 2001. Long-term changes in Serengeti-Mara wildebeest and land cover: Pastoralism, population, or policies? *Proceedings of the National Academy of Sciences* 98:12544–12549.
- Hotez, P., E. Ottesen, A. Fenwick, and D. Molyneux. 2006. The neglected tropical diseases: the ancient afflictions of stigma and poverty and the prospects for their control and elimination. Pages 23–33 *in* *Advances in Experimental Medicine and Biology*.
- Hotez, P. J., D. H. Molyneux, A. Fenwick, J. Kumarasan, S. E. Sachs, J. D. Sachs, and L. Savioli. 2007. Control of neglected tropical diseases. *The New England Journal of Medicine* 357:1018–1027.
- Hursey, B. S. 2001. The programme against African trypanosomiasis: aims, objectives and achievements. *Trends in Parasitology* 17:2–3.
- Innes, J. L., and B. Koch. 1998. Forest biodiversity and its assessment by remote sensing. *Global Ecology and Biogeography Letters* 7:397–419.
- Jordan, A. 1986. *Trypanosomiasis Control and African Rural Development*. Longman Singapore Publishers Ltd., New York, New York, USA.
- Kearney, M., and W. Porter. 2009. Mechanistic niche modelling: combining physiological and spatial data to predict species' ranges. *Ecology Letters* 12:334–350.
- KETRI. 2008. Tsetse distribution in Kenya showing tsetse belts and conservation areas. Kenya Trypanosomiasis Research Institute (KETRI).
- KFSSG. 2008. Kenya Food Security Steering Group (KFSSG) Kenya Long Rains Assessment Report 2008. Pages 1–33. A collaborative report of the Kenya Food Security Steering Group: Office of the President, Office of the Prime Minister, Ministries of Development of Northern Kenya and other Arid Lands, Agriculture, Livestock Development, Fisheries Development, Water and Irrigation, Public Health and Sanitation, Medical Services, and Education, WFP/VAM, FEWS NET, UNICEF, FAO, OCHA, Oxfam GB, UNDP, World Vision.
- KFSSG. 2009a. Kenya Food Security Steering Group (KFSSG) Kenya Long Rains Assessment Report 2009. Pages 1–44. A collaborative report of the Kenya Food Security Steering Group: Office of the President, Office of the Prime Minister, Ministries of Development of Northern Kenya and other Arid Lands, Agriculture, Livestock Development, Fisheries Development, Water and Irrigation, Public Health and Sanitation, Medical Services, and Education, WFP/VAM, FEWS NET, UNICEF, FAO, OCHA, Oxfam GB, UNDP, World Vision.
- KFSSG. 2009b. Kenya Food Security Steering Group (KFSSG) The 2008/09 Short Rains Assessment Report. Pages 1–47. A collaborative report of the Kenya Food Security Steering Group; (Kenya Office of the President; Ministries of Agriculture, Livestock and Fisheries Development; FEWS Net, FAO, Oxfam GB, UNDP, WFP; and UNICEF).
- Kgori, P. M., S. Modo, and S. J. Torr. 2006. The use of aerial spraying to eliminate tsetse from the Okavango Delta of Botswana. *Acta Tropica* 99:184–199.
- Knight, C. G. 1971. The Ecology of African Sleeping Sickness. *Annals of the Association of American Geographers* 61:23–44.

- Laird, M. 1977. Tsetse the future for biological methods in integrated control. International Development Research Center, Ottawa, Canada.
- Leak, S. G. A. 1999. Tsetse Biology and Ecology. CABI Publishing, New York, New York, USA.
- Leak, S. G. A., D. Ejigu, and M. J. Vreysen. 2008. Collection of entomological baseline data for tsetse area-wide integrated pest management programmes. Food and Agriculture Organization of the United Nations.
- Lenhart, T., K. Eckhardt, N. Fohrer, and H. G. Frede. 2002. Comparison of two different approaches of sensitivity analysis. *Physics and Chemistry of the Earth* 27:645–654.
- Li, Z. 2004. Production of Regional 1 km $\times$  1 km Water Vapor Fields through the Integration of GPS and MODIS Data. Pages 1–7 in . Long Beach, CA, USA.
- Lillesand, T., R. Kiefer, and J. Chipman. 2008. Remote Sensing and Image Interpretation, 6th edition. John Wiley & Sons, Inc, Hoboken, New Jersey, USA.
- Maitima, J. 2008. The Framework and guidelines for assessing environmental and socioeconomic impacts of tsetse fly interventions. International Livestock Research Institute.
- Mellanby, K. 1936. Experimental work with the tsetse-fly, *Glossina palpalis*, in Uganda. *Bulletin of Entomological Research* 27:611–632.
- Mellanby, K. 1939. Low temperature and insect activity. *Proceedings of the Royal Society of London. Series B, Biological Sciences (1934–1990)* 127:473–487.
- Mitchell, T. D., T. R. Carter, P. D. Jones, M. Hulme, and M. New. 2004. A comprehensive set of high-resolution grids of monthly climate for Europe and the globe: the observed record (1901–2000) and 16 scenarios (2001–2100). Pages 1–30. Tyndall Centre for Climate Change Research Working Paper 55.
- Muriuki, G. W., J. Chemuliti, R. Changasi, M. Maichomo, and J. Ndung'u. 2005. The Impact of Changing Landscapes on Tsetse Distribution in the ASALS North of Mt. Kenya. The International Scientific Council for Trypanosomiasis Research and Control.
- Muzari, M. O. 1999. Odour-baited targets as invasion barriers for tsetse flies (Diptera: Glossinidae): a field trial in Zimbabwe. *Bulletin of Entomological Research* 89:73–77.
- Muzari, M. O., and J. W. Hargrove. 2005. Artificial larviposition sites for field collections of the puparia of tsetse flies *Glossina pallidipes* and *G. m. morsitans* (Diptera: Glossinidae). *Bulletin of Entomological Research* 95:221–229.
- Nash, T. A. M. 1933. A statistical analysis of the climatic factors influencing the density of tsetse flies, *Glossina morsitans* Westw. *Journal of Animal Ecology* 2:197–203.
- Nash, T. A. M. 1937. Climate, the vital factor in the ecology of *Glossina*. *Bulletin of Entomological Research* 28:75–127.
- Odulaja, A., J. Baumgärtner, S. Mihok, and I. M. Abu-Zinid. 2001. Spatial and temporal distribution of tsetse fly trap catches at Nguruman, southwest Kenya. *Bulletin of entomological research* 91:213–220.
- Oluwafemi, R. 2009. The impact of African animal trypanosomosis and Tsetse fly on the livelihood and well-being of cattle and their owners in the BICOT study area of Nigeria. *The Internet Journal of Veterinary Medicine* 5.
- Park, S. 2009. Synchronicity between satellite-measured leaf phenology and rainfall regimes in tropical forests. *Photogrammetric Engineering and Remote Sensing* 75:1231–1237.
- Pavlovskii, E. N. 1966. Natural nidity of transmissible diseases, with special reference to the landscape epidemiology of zoonothronoses. University of Illinois Press, Urbana, Illinois, USA.
- Peterson, A., M. Papes, and J. Soberon. 2008. Rethinking receiver operating characteristic analysis applications in ecological niche modeling. *Ecological Modelling* 213:63–72.
- Peterson, A., V. Sánchez-Cordero C. Beard, and J. Ramsey. 2002. Ecologic niche modeling and potential reservoirs for Chagas disease, Mexico. *Emerging Infectious Diseases* 8:662–667.
- Pilson, R. D., and B. M. Pilson. 1967. Behaviour studies of *Glossina morsitans* Westw. in the field. *Bulletin of Entomological Research* 57:227–257.
- Pollock, J. N. 1982a. Training Manual for Tsetse Control Personnel. Vol. 1: Tsetse biology, systematics and distribution, techniques. Food and agricultural Organization of the United Nations, Rome, Italy.
- Pollock, J. N. 1982b. Training Manual for Tsetse Control Personnel. Vol. 2: Ecology and Behaviour of Tsetse. Food and agricultural Organization of the United Nations, Rome, Italy.
- Rio, R., Y. Wu, G. Filardo, and S. Aksoy. 2006. Dynamics of Multiple Symbiont Density Regulation during Host Development: Tsetse Fly and Its Microbial Flora. *Proceedings: Biological Sciences* 273:805–814.
- Rogers, D. 1979. Tsetse Population Dynamics and Distribution: A New Analytical Approach. *The Journal of Animal Ecology* 48:825–849.
- Rogers, D. J., and S. E. Randolph. 1985. Population Ecology of Tsetse. *Annual Reviews in Entomology* 30:197–216.
- Rogers, D. J., and S. E. Randolph. 1986. Distribution and Abundance of Tsetse Flies (*Glossina* Spp.). *Journal of Animal Ecology* 55:1007–1025.
- Rogers, D. J., and S. E. Randolph. 1991. Mortality rates and population density of tsetse flies correlated with satellite imagery. *Nature* 351:739–741.



- Rogers, D. J., and S. E. Randolph. 2002. A response to the aim of eradicating tsetse from Africa. *Trends in Parasitology* 18:534–536.
- Rogers, D. J., and T. P. Robinson. 2004. *The Trypanosomiasis: Chapter 8 - Tsetse Distribution*. CABI Publishing, Cambridge, Massachusetts, USA.
- Rogers, D. J., and B. G. Williams. 1994. *Tsetse distribution in Africa: seeing the wood and the trees*. Blackwell Scientific Publications, Oxford, UK.
- Soberón, J., and A. Peterson. 2005. Interpretation of Models of Fundamental Ecological Niches and Species' Distributional Areas. *Biodiversity Informatics* 2:1–10.
- Swynnerton, C. F. M. 1921. *An Examination of the Tsetse Problem in North Mossurise Portuguese East Africa*. The Imperial Bureau of Entomology.
- Terblanche, J. S., S. Clusella-Trullas, J. A. Deere, and S. L. Chown. 2008. Thermal tolerance in a south-east African population of the tsetse fly *Glossina pallidipes* (Diptera, Glossinidae): Implications for forecasting climate change impacts. *Journal of Insect Physiology* 54:114–127.
- Torr, S. J., and J. W. Hargrove. 1999. Behaviour of tsetse (Diptera: Glossinidae) during the hot season in Zimbabwe: the interaction of micro-climate and reproductive status. *Bulletin of Entomological Research* 89:365–379.
- Vale, G. A., B. S. Hursey, J. W. Hargrove, S. J. Torr, and R. Allsopp. 1984. The use of small plots to study populations of tsetse (Diptera: Glossinidae): Difficulties associated with population dispersal. *Insect Science and Its Application* 5:403–410.
- Vale, G. A., D. F. Lovemore, S. Flint, and G. F. Cockbill. 1988. Odour-baited targets to control tsetse flies, *Glossina* spp. (Diptera: Glossinidae), in Zimbabwe. *Bulletin of Entomological Research* 78:31–49.
- Vale, G. A., and S. J. Torr. 2005. User-friendly models of the costs and efficacy of tsetse control: application to sterilizing and insecticidal techniques. *Medical and Veterinary Entomology* 19:293–305.
- Western, D. 2009. Drought devastating wildlife, cattle, and human lives. Retrieved from (<http://www.africanconservationfund.org/index.php/news/151-drought-devastating-wildlife-cattle-and-human-lives>)
- WHO. 2009. *Neglected Tropical Diseases Frequently Asked Questions & Fact File*. World Health Organization.
- Williams, B., R. Dransfield, and R. Brightwell. 1992a. The control of tsetse flies in relation to fly movement and trapping efficiency. *Journal of Applied Ecology* 29:163–179.
- Williams, B., D. Rogers, G. Staton, B. Ripley, and T. Booth. 1992b. Statistical modeling of georeferenced data: mapping tsetse distributions in Zimbabwe using climate and vegetation data. Pages 267–280 in *Modeling Vector-Borne and Other Parasitic Diseases*. The International Laboratory for Research on Animal Diseases, Nairobi, Kenya.
- Wint, W. 2001. Kilometre resolution tsetse fly distribution maps for Lake Victoria Basin and West Africa. Pages 1–15. Consultants' Report, Food and Agriculture Organisation of the United Nations. IAEA Joint Division, International Atomic Energy Agency, Vienna, Austria.
- Wint, W., and D. Rogers. 2000. Predicted Distribution of Tsetse in Africa. Pages 1–62. Consultants' Report, Food and agricultural Organization of the United Nations, Rome, Italy.
- Yamey, G. 2002. The world's most neglected diseases: Ignored by the pharmaceutical industry and by public-private partnerships. *BMJ* 325:176–177.