

Use of a geographic information system to explore spatial variation in pathogen virulence and the implications for biological control of locusts and grasshoppers

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- Abstract**
- 1 In a previous study, we developed a model to predict the effects of temperature on performance of a fungus-based biopesticide for controlling locusts and grasshoppers. Currently, the model is limited to predicting rate of mortality after a spray application at site-specific locations. The aim of the present study is to enhance the utility of this model by linking it with meteorological station data in a geographic information system (GIS) framework to investigate the spatial variation in the performance of the biopesticide.
 - 2 The model provides maps that define spatial variation in pathogen virulence (measured as LT_{90} for a treated population) across different regions. The model was used to explore the variation in biopesticide performance against four economically important pest species: Moroccan locust *Dociostaurus maroccanus* in Spain; brown locust *Locustana pardalina* in South Africa; red locust *Nomadacris septemfasciata* in Zambia and; Senegalese grasshopper *Oedaleus senegalensis* in Niger.
 - 3 Model outputs for the different species were partially validated against data from field trials. The models provided good estimates of time to 90% mortality for five out of six independent comparisons. There was also good agreement between the spatial model and equivalent output from the site-specific model.
 - 4 Simulations of virulence against *N. septemfasciata* in Zambia indicated very uniform, rapid mortality with LT_{90} throughout the country generally less than 11 days. Pathogen-induced mortality of *O. senegalensis* in Niger was predicted to be slightly slower and more variable with mortality fastest in the southern regions (< 15 days) and slowing to the north of the country (16–20 days). For both *L. pardalina* in South Africa and *D. maroccanus* in Spain, the model revealed highly variable patterns of mortality with LT_{90} ranging from < 15 days in some areas to > 30 days in others.
 - 5 The implications of these different patterns of variability for the development of optimum use strategies for the various species and the basic understanding of the ecology and evolution of insect–pathogen interactions are discussed.

Keywords Body temperature model, *Dociostaurus maroccanus*, GIS, insect–pathogen interaction, *Locustana pardalina*, *Metarhizium anisopliae* var. *acridum*, *Nomadacris septemfasciata*, *Oedaleus senegalensis*, thermoregulation, virulence.

Introduction

A number of studies have demonstrated the importance of temperature and thermal biology in the outcome of host–

parasite/pathogen interactions (Mitchell *et al.*, 2005; Lambrechts *et al.*, 2006; Thomas & Blanford, 2003). Work on the use of fungal pathogens for biocontrol of locusts and grasshoppers, for example, has shown that the ability of a pathogen to kill the host depends crucially on host body temperature and how this fluctuates with external environmental conditions. The speed of kill and overall mortality caused by

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entomopathogenic fungi, such as *Metarhizium anisopliae* var. *acridum* (= *Metarhizium flavoviride* Gams & Rozsypal; Driver *et al.*, 2000) and *Beauveria bassiana* (Balsamo) Vuillemin, vary greatly with changes in environmental temperature and host thermal biology (Inglis *et al.*, 1996, 1997; Blanford & Thomas, 1999a, b, 2000; Arthurs & Thomas, 2000; Elliot *et al.*, 2002; Ouedraogo *et al.*, 2003; Klass *et al.*, 2007). For biocontrol, this means that biopesticide products based on these fungi will achieve excellent control under some conditions whereas, under other conditions, they might be inappropriate for use (Lomer *et al.*, 2001; Thomas & Blanford, 2003; Klass *et al.*, 2007). Therefore, the key to using such biopesticides effectively is to predict how the pathogen will perform across space and time so that this variability can be managed. To this end, we recently developed a model to predict the performance of a *Metarhizium*-based biopesticide against different locusts and grasshoppers under different environmental conditions (Klass *et al.*, 2007). The model uses site-specific environmental temperature data to drive locust body temperature models, which in turn drives a pathogen development model to predict speed of kill for a population infected after a spray application. This model successfully predicts pathogen virulence for a range of targets in specific locations. The aim of the current study is to extend the utility of this model by using meteorological station data in a geographical information system (GIS) to investigate variation of pathogen-performance (virulence) over wider spatial (and temporal) scales.

In general, temperature is collected at meteorological stations that are geographically scattered throughout a region. Numerous models predicting temperature across space (e.g. interpolation techniques predicting temperature at unsampled points between meteorological stations; Collins & Bolstad, 1996; Jarvis & Stuart, 2001a, b) and time (e.g. hourly intervals using a sine-curve method; Parton & Logan, 1981) have been developed. The accuracy of these techniques can be variable and are largely influenced by the data (e.g. clustered vs. scattered points and the accuracy of the data itself), topography of the landscape, temporal scale (hourly vs. daily vs. monthly samples), spatial scale (regional vs. continental) and computing power.

Several studies have compared the effectiveness of different spatial interpolation techniques for predicting temperature (Collins & Bolstad, 1996; Jarvis & Stuart, 2001a, b). Jones & Gladkov (1999) created accurate monthly temperature surfaces using inverse-distance-weighting (IDW) corrected by the lapse rate method at the continental level for Latin America and Africa. These surfaces have subsequently been used in a number of agricultural applications (e.g. guiding and investigating taxonomic and genetic variation of wild plants; Jones *et al.*, 1997; Jones & Gladkov, 1999), and thus form the basis of the method used here.

Collecting hourly ambient temperatures across a range of microhabitats at different field sites can be time-consuming and expensive. Therefore, models have been developed to predict temperatures based on daily minimum and maximum air temperature recorded at meteorological stations (Parton & Logan, 1981; Cesaraccio *et al.*, 2001). Parton & Logan (1981) developed a sine-exponential model that produces

accurate results of hourly temperatures within and between seasons (Wann *et al.*, 1985) and has been extensively used for agricultural crop models (Porter *et al.*, 2000). However, an important consideration when using temperatures recorded at weather stations is that they may not be representative of temperatures of the microhabitat at the field site (Kennedy, 1997; Bryant & Shreeve, 2002). This difference can be attributed to the fact that air temperatures are recorded in protected environments (often Stevenson's screen) at heights of 1–2 m above the ground surface, where temperatures are less variable than those nearer the soil surface (Arya, 1988; Kennedy, 1997). This discrepancy can lead to gross inaccuracies when determining temperatures actually experienced by insects and, thus, the outcome of processes dependent on temperature rate effects. Incorrect predictions may be further accentuated when, like many locusts and grasshoppers, insects thermoregulate, maintaining their body temperatures at temperatures different from those recorded both in the field and at meteorological stations. Hence, our approach is to interpolate between met-station points to generate temperature surfaces that provide a measure of hourly temperature across the landscape, use these estimates of temperature to recalibrate the previously developed body temperature-ambient temperature models for individual locust/grasshopper species, and then substitute these into the pathogen performance model to predict the rate of mortality.

Materials and methods

Overview

We consider the spatial variation in virulence of *M. anisopliae* var. *acridum* against four of the economically important pest species considered in our earlier study (Klass *et al.*, 2007): the brown locust, *Locustana pardalina* (Walker), in South Africa; the Senegalese grasshopper, *Oedaleus senegalensis* (Krauss) in Niger; the red locust, *Nomadacris septemfasciata* (Serville) in Zambia; and the Moroccan locust, *Dociostaurus maroccanus* (Thunberg) in Spain. For each of these, model simulations are run to coincide with previous field trials conducted within each region to explore variation in performance of the biopesticide over space (with the site-specific field trial results providing a reference point for validation of model predictions).

Meteorological station data

Daily minimum and maximum temperature data collected at meteorological stations around the world were obtained from the National Climate Data Center website (<http://www.ncdc.noaa.gov/>). Data points for all locations contained latitude, longitude, daily minimum temperature, daily maximum temperature and mean daily temperature.

All points were quality checked for missing data. Records were removed if both the daily mean and daily minimum, or maximum, temperature data were missing. Meteorological stations were removed from the analysis if less than 7 days of temperature data were recorded during a single month

and/or when 5 consecutive days of temperature data were missing. For days with missing minimum or maximum temperature values, new temperature values were estimated by interpolating between missing days. Meteorological station points were imported directly into a GIS, ArcView 3.2 (ESRI, Redlands, California).

Simulated hourly temperature values

The sine-exponential model proposed by Parton & Logan (1981) assumes that maximum temperature occurs during daylight hours and minimum temperature during the early hours of the morning just before sunrise. Daytime variations of temperature (T_{day}) are described by a truncated sine wave (Eq. 1), whereas night-time temperatures (T_{night}) are determined by an exponential function (Eq. 2):

$$T_{\text{day}} = (T_{\text{max}} - T_{\text{min}}) \sin\left(\frac{\pi m}{Y + 2a}\right) + T_{\text{min}} \quad [1]$$

$$T_{\text{night}} = T_{\text{min}} + (T_{\text{sunset}} - T_{\text{min}}) \exp\left(-\frac{bn}{Z}\right) \quad [2]$$

where T_{max} is daily maximum temperature ($^{\circ}\text{C}$), T_{min} is daily minimum temperature ($^{\circ}\text{C}$), T_{sunset} is the temperature recorded at sunset ($^{\circ}\text{C}$), m is the number of hours after the occurrence of minimum temperature until sunset (h), n is the number of hours after sunset until the time of the minimum temperature (h), Z is the night length (h) and Y is the day length (h). Time of sunrise and sunset vary seasonally and geographically. These were calculated based on latitude, longitude, time zone and date, for each location using astronomical algorithms of Meeus (1998), programmed into Microsoft Excel, version 10 (Microsoft Corp, Redmond, Washington, DC).

Two parameters (where a is the lag coefficient for the maximum temperature and b is the night-time temperature coefficient) control the rate of temperature increase and decrease. An additional parameter, c , determines the lag time of minimum temperature from the time of sunrise.

Sine-curve parameters

The parameters for the sine-curves (a , b and c) vary as a function of height, location, habitat (Reicosky *et al.*, 1989) and day length, and are not the same for each region under investigation. To define appropriate parameters for each region in the current study, sine-curves were fitted to daily minimum and maximum mean ambient temperatures collected at the specific field-trial sites. These maxima and minima were determined from temperature data collected daily using temperature data loggers (Klass *et al.*, 2007). For Niger, the best-fit parameters were $a = 1$, $b = 5$, $c = -0.1$; for Zambia, $a = 1$, $b = 5$, $c = -0.1$; for South Africa, $a = 1$, $b = 1$, $c = -0.1$; and, for Spain, $a = 2.5$, $b = 2.2$, $c = -0.1$. These parameters were then used in combination with daily minimum and maximum meteorological station temperature data to estimate hourly temperature.

Interpolating daily minimum and maximum temperature

Minimum and maximum temperature surfaces were created with a 10-km cell resolution, and an inverse-distance-interpolate (IDW) using the five nearest stations (Eq. 3). Temperature surfaces were standardized for elevation (Digital Elevation Model downloaded from the USGS website; USGS, 1999) using a lapse rate model (Eq. 4).

$$Ta_{\text{met}} = \frac{\sum_{i=1}^n (x_i) \cdot d_{ij}^{-r}}{\sum_{i=1}^n d_{ij}^{-r}} \quad [3]$$

$$Ta_{\text{new}} = Ta_{\text{met}} - (L * \Delta h) \quad [4]$$

Where Ta_{met} is the daily minimum or maximum temperature surface created using IDW, x_i are the station points, x_j are the points where the surface is to be interpolated, d^{-r} is the distance weighting power of 2, L = lapse rate ($6.5^{\circ}\text{C}/1000\text{ m}$), Δh is the difference between the elevation at a location and the nearest meteorological station and Ta_{new} is the corrected daily minimum and maximum temperature surface used to create hourly temperature surfaces.

Recalibration of body temperature models

To overcome differences in temperatures recorded in the field and at the nearest meteorological station, body temperature models for the four study species developed using site-specific temperature data (Klass *et al.*, 2007) were recalibrated to meteorological station data. Ambient temperature was simulated at 1-min intervals based on meteorological station minima and maxima. These simulated temperatures were matched to actual body temperatures taken for the same period and used to derive new body temperature (Tb)-ambient temperature (Ta) models using a sigmoid function (Klass *et al.*, 2007).

Predicting the time taken to achieve 90% mortality after a spray application of *M. anisopliae* var. *acridum*

Predicted locust body temperatures were substituted into the pathogen-performance model of Klass *et al.* (2007). After a spray application, daily pathogen growth was calculated for each grid cell and evaluated for mortality events (a mortality event in this instance refers to the LT_{90} for the treated population and not to an individual locust or grasshopper). Grid cells containing a mortality event were assigned the day number after application, where the first 24 h is considered as day 0. Simulations were run for a total of 30 days, except for *L. pardalina*, which was run for a total of 60 days. Start dates for each simulation were in accordance with start dates of actual field trials (i.e. 10 February 2001 for *N. septemfasciata*, 17 August 1997 for *O. senegalensis*, 25 February 1998 for *L. pardalina*). Model predictions of LT_{90} for *L. pardalina*, *O. senegalensis* and *N. septemfasciata* were compared with the empirical field trial data available for specific locations.

For cases where empirical field trial data were absent, such as *D. maroccanus*, model predictions using the current model (i.e. driven by met-station data) were compared with those made using site-specific environmental data collected from 25 May 2000 (Klass *et al.*, 2007).

Results

Re-calibrated body temperature models

Parameter estimates for the modified *Tb-Ta* models for each of the four species are shown in Table 1. A comparison of body temperatures predicted using met-station data and these modified models, with body temperatures predicted using site-specific temperature data and the original *Tb-Ta* models indicated that the re-calibrated body temperature models adequately captured hourly body temperature fluctuations for each of the four species (pairwise regressions showing slopes in the range 0.859–1.003, intercepts in the range –0.226 to 4.244 and r^2 in the range 0.70–0.90).

Spatial variation in pathogen performance

The GIS model provides mapped outputs showing spatial variation in the expected time to achieve 90% population mortality after a standard biopesticide spray application (Fig. 1A–D). These maps indicated considerable variation in virulence of *M. anisopliae* var. *acridum* between, and often within, each country.

Simulations of virulence against *N. septemfasciata* in Zambia indicated very uniform, rapid mortality with LT_{90} throughout the country generally less than 11 days (Fig. 1A). Comparison of model predictions with concurrent field trial data from a specific site in the Kafue Flats suggests the model provides an accurate assessment of mortality rate (Table 2). Although the GIS output is not shown, additional comparison with data from an earlier trial in the Buzi flood plain in Mozambique (Price *et al.*, 1999) also indicates good alignment between model and field data with an LT_{90} of 9.5 and 9.0 days, respectively (Table 2).

Pathogen-induced mortality of *O. senegalensis* was predicted to be slightly slower and more variable than red locust

(Fig. 1B). Mortality was predicted to occur fastest in the southern regions (< 15 days), and became progressively slower to the North of the country (16–20 days). The predicted LT_{90} at the location of the field trial (the village of Maine-Sarao) was 15 days, which is 6 days less than actually observed (Table 2). Equivalent analysis for a field trial conducted at the same site in the next year (GIS output not shown) revealed a better fit with both a predicted and observed LT_{90} of 15 days (Table 2).

Analysis of *L. pardalina* in South Africa revealed highly variable patterns of mortality. Ninety percent mortality was predicted to occur the fastest (generally < 15 days) in areas near the coast and to the south of the Drakensberg mountains, with a slower rate of mortality (> 30 days) occurring in the central and western regions of the country (Fig. 1C). Throughout the main locust recession areas in the Karoo, mortality was predicted to be generally slow; 21–25 days in the areas near Upington, Marydale and Prieska, 26–29 days near Britstown and > 30 days near Brandvlei and Vanwyksvlei. Specific analysis for the field trial location revealed the model to under estimate speed of kill with a predicted LT_{90} of 30 days compared with an observed LT_{90} of 59 days. Analysis using environmental and mortality data from an earlier trial conducted in the Karoo in 1995 (Price *et al.*, 1997) revealed improved model performance albeit, on this occasion, with an overestimate of time to death (predicted LT_{90} = 25 days, observed LT_{90} = 20 days).

Similar to brown locust, the time taken to achieve 90% mortality against *D. maroccanus* was variable across Spain (Fig. 1D). Mortality was predicted to take as little as 11–15 days in the south near Almeria, along the coast of the Atlantic Ocean, and East of Zaragoza. Mortality estimates north of the Sistema central were predominately between 16 and 20 days whereas, in the central/southern region and parts of the north-east, 90% mortality was predicted to take > 30 days. These latter areas included three of the four locust outbreak regions (i.e. Castuera, Ciudad Real and Zaragoza). At present, we have no reliable empirical mortality data to validate the model. However, the GIS-based model does compare well with predictions from our earlier model using site-specific data (the current model predicting an LT_{90} of 43 days compared with 41 days with the site-specific model; Klass *et al.*, 2007).

Table 1 Estimates for parameters used in the sigmoid body temperature-ambient temperature models for *Locustana pardalina*, *Dociostaurus maroccanus*, *Oedaleus senegalensis* and *Nomadacris septemfasciata*

Species	Local Met-Station Name (No.) Country	Model parameters			
		T_{max} (\pm SE)	T_{infl} (\pm SE)	s (\pm SE)	r^2
<i>Locustana pardalina</i>	Marydale (685270) South Africa	40.662 (0.348)	22.778 (0.216)	–6.964 (0.481)	0.60
<i>Dociostaurus maroccanus</i>	Badajoz (83300) Spain	40.179 (0.234)	19.934 (0.152)	–5.97 (0.238)	0.87
<i>Oedaleus senegalensis</i>	Maine-Sarao (610960) Niger	41.975 (0.773)	29.634 (0.533)	–8.456 (1.174)	0.56
<i>Nomadacris septemfasciata</i>	Lusaka (676650) Zambia	37.355 (0.449)	26.604 (0.798)	–3.952 (0.510)	0.63

The body temperature models are modified from the original models of Klass *et al.* (2007) and are based on simulated ambient temperatures derived from meteorological station data. Further details are given in the main text (for development of original models, see Klass *et al.*, 2007).

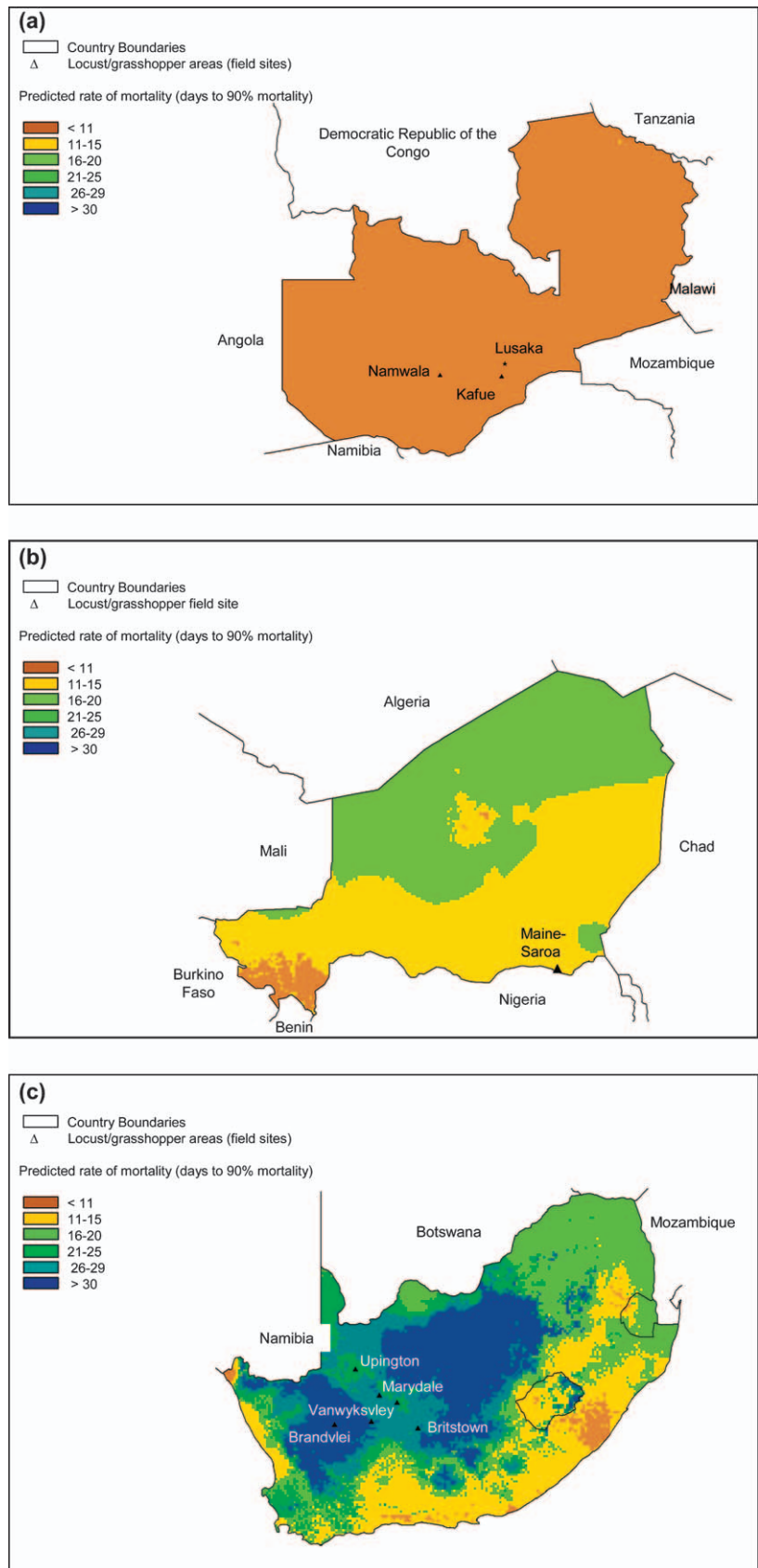


Figure 1 Continued.

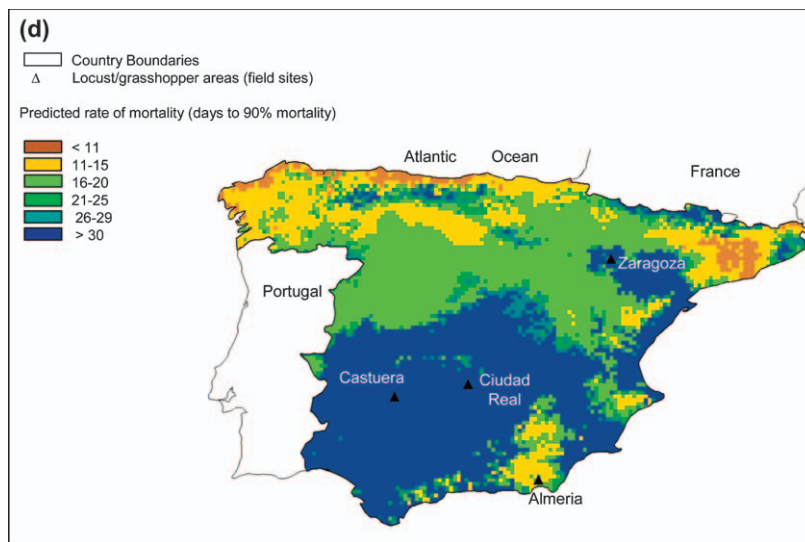


Figure 1 Mapped outputs illustrating the time taken to achieve 90% population mortality after a spray application of the fungal pathogen *Metarhizium anisopliae* var. *acridum* against (A) *Nomadacris septemfasciata* in Zambia: simulation run for 20 days starting on 10 February, 2001; (B) *Oedaleus senegalensis* in Niger: simulation run for 30 days starting on 17 August 1996; (C) *Locustana pardalina* in South Africa: simulation run for 60 days starting on 25 February 1998; and; (D) *Dociostaurus maroccanus* in Spain: simulation run for 40 days starting on 25 May 2000.

Discussion

The aim of the current study was to develop a modelling tool to help explore the variability in performance of *M. anisopliae* var. *acridum* for control of locusts and grasshoppers. By extending our previous site-specific model to use readily available meteorological station data within a GIS framework, we were able to evaluate variation in pathogen performance at a regional scale for a range of economically important locust and grasshopper species.

Model predictions for the time taken to achieve 90% mortality were found to be close to observed values for five of the six cases where field data are available. The exception was one field trial against *L. pardalina* during 1998 where the model predicted an LT_{90} of 30 days compared with the observed LT_{90} of 59 days. This is a substantial error that, based

on the biology that underpins the model, is likely to derive from an underestimate of body temperature extremes experienced by the locusts. That is, the biological model that describes pathogen development *in vivo* includes two delay terms that restrict pathogen growth to zero when locust body temperature is maintained at either very high level or very low levels for periods in excess of 3 h (Klass *et al.*, 2007). Failure to invoke these delays will tend to lead to large underestimates in mortality rate so it appears likely that the simulated temperature surfaces and adjusted body temperature model for *L. pardalina* are failing to adequately capture the extremes of body temperature experienced in field (at least for the year in question; note that the model worked well for *L. pardalina* for data from a previous trial). Errors associated with daily minimum and maximum temperature surfaces could be attributed to several factors, such as the accuracy

Table 2 GIS model predictions for LT_{90} after a spray application of *Metarhizium anisopliae* var. *acridum* compared with mortality observed in field trials for specific sites

Species and year	Days for 90% mortality		Difference (observed – model)	Source of field mortality data
	Observed	Model		
<i>Oedaleus senegalensis</i>				
1996	21	16	–5	Langewald <i>et al.</i> (1999)
1997	15	15	0	Langewald <i>et al.</i> (1999)
<i>Locustana pardalina</i>				
1995	20	25	5	Price <i>et al.</i> (1997)
1998	59	30	–29	Arthurs & Thomas (2000)
<i>Nomadacris septemfasciata</i>				
1997	9	9.5	0.5	Price <i>et al.</i> (1999)
2001	10	10	0	Elliot and Thomas (unpublished) and unpublished DFID report.
<i>Dociostaurus maroccanus</i> ^a				
2000	41	43	2	Based on model predictions using site-specific field data (Klass, <i>et al.</i> , 2007)

^aNote the data for *D. maroccanus* represent a comparison between the GIS model and the site-specific field temperature model presented in Klass *et al.* (2007) because no field mortality data area available).

of the raw data, missing temperature records and the result of interpolating between sparsely distributed station networks. Such errors may further be accentuated in environments with high temperature fluctuation and/or regions that have variable topography (i.e. due to changes in inversion and lapse rates (Collins & Bolstad, 1996)). In our study, these factors apply most clearly to South Africa. In regions where temperature is more stable and topography is similar, interpolating between a sparsely distributed network of stations may be less problematic (as appears to be the case for Niger and Zambia).

Although the availability of reliable data and/or outputs in some regions is a limitation (and suggests the need for further work to better characterize the model as well as conducting more extensive validation), we believe the model still has potential for identifying where and when the biopesticide could be used effectively and hence, for assisting in development of optimum use strategies. In the first instance, there are numerous examples where GIS models based on climate data, which are at the same or at a coarser temporal and spatial scale than used here, have been used effectively to inform management decisions; for example, to inform malaria control (Craig *et al.*, 1999; Martin *et al.*, 2002), predict geographical distribution of non-indigenous pests (Baker *et al.*, 2000) and identify risks to human and animal health from parasites (Sutherst, 2001), and identify conservation hotspots (Peterson *et al.*, 1999, 2002)). In addition, as argued in Klass *et al.* (2007), from a locust control perspective, even relatively coarse mortality predictions with a resolution of 10 days would be very valuable in defining control strategies. In this regard, the outputs for species such as red locust indicate the pathogen should provide effective control irrespective of location and locust age (i.e. 90% mortality in 10 days would provide effective control even for fledgling locusts). For the Senegalese grasshopper, there is slightly more spatial variation with slower mortality further north into the Sahel. The slower the speed of kill, the earlier the nymphs need to be targeted to prevent reproduction and dispersal of mature adults. Nonetheless, with LT_{90} of < 20 days, it appears that the pathogen could be deployed without major restrictions. For brown locust and Moroccan locust, however, the model suggests large spatial variation in performance with some areas showing relatively rapid speed of kill, but others with 90% mortality delayed beyond 30 days. Even with the questions over the accuracy of the model for brown locust, an LT_{90} > 30 days would generally be considered too slow for effective control, unless the very youngest locust nymphs could be targeted. As such, the model points to major limitations to utilizing the pathogen for these species (at least for the periods investigated) and the need for much more considered use strategies than routine spraying.

The spatial model represents a very useful extension of the site-specific model developed previously (Klass *et al.*, 2007). Our current analyses, however, are still limited in that they consider only snapshots in time. How the spatial patterns alter across the course of the season and between years is an important question and one that identifies a very useful application for the model. That is, by collating environmental data over a number of seasons it would be possible to develop maps that define 'average expected efficacy' for particular

months across a region. This would enable us to identify, on average, where and when it would be appropriate to use the biopesticide and to consider, for example, whether 'good years' for locusts coincide with 'good years' for the pathogen. For systems such as brown locust in South Africa, such analyses could reveal increased opportunities for utilizing the biopesticide than are suggested in the current investigation. Nonetheless, restrictions will undoubtedly remain but we would argue that it is better to optimize the use of the biopesticide and employ it when we know it will work, rather than attempt to overuse it and risk control failures.

Finally, beyond the potential practical utility of the model, the outputs provide interesting insights into more fundamental aspects of the ecology and evolution of insect–pathogen interactions. The present study provides a graphic representation of how virulence can vary dramatically across even small spatial scales (and this probably likely apply for temporal scales also). Given the importance of virulence, it follows that temperature must impact on host–pathogen dynamics, generating either quantitatively or qualitatively different dynamics across time and space for the same coupled insect–pathogen combination (Blanford & Thomas, 1999a, b; Thomas & Blanford, 2003). Similarly, with temperature altering virulence and resistance, this must create shifting patterns of coevolutionary selection pressure over time and/or space. This means the net effect of selection at the population level is likely to be very different from that predicted under one set of conditions (Thomas & Blanford, 2003; Mitchell *et al.*, 2005). That virulence can be so context dependent is rarely considered in studies of disease dynamics or the coevolution of resistance and virulence (Thomas & Blanford, 2003).

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