FORUM

Mathematical Modeling, Spatial Complexity, and Critical Decisions in Tsetse Control

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ABSTRACT The tsetse fly complex (*Glossina* spp.) is widely recognized as a key contributor to the African continent's continuing struggle to emerge from deep economic, social, and political problems. Vector control, the backbone of intensive efforts to remove the human and livestock trypanosomosis problem, has been typified by spectacular successes and failures. There is widespread agreement that integrated vector control, combined with direct disease treatment and prevention, has to play a major role in alleviating the tsetse burden in Africa. Mathematical and computer-based simulation models have been extensively used to try to understand how best to manage these control efforts. Such models in ecology have been helpful in giving broad generalizations about population dynamics and control. Unfortunately, in many ways they have inadequately addressed key aspects of the fly's biology and ecology, particularly the spatio-temporal variability of its habitats. These too must factor in any control efforts. Mathematical models have inherent limitations that must be considered in their use for control programs. In this review, we consider some of the controversies being debated within the field of ecology and evolution about the use of mathematical models and critically review several models that have been influential in structuring tsetse control efforts. We also make recommendations on the appropriate role that mathematical and simulation models should play when used for these purposes. Management programs are often vulnerable to naively using these models inappropriately. The questions raised in this review will apply broadly to many conservation and area-wide pest control programs with an ecological component relying on mathematical and computer simulation models to inform their decisions.

KEY WORDS simulation modeling, insect control, Africa, livestock disease, Glossinidae

To set the stage on how modeling has been and can be used in tsetse control, a brief outline of the controversies in this area is useful. The tsetse fly complex (*Glossina* spp.) is widely recognized as a key contributor to the African continent's continuing struggle to emerge from deep economic, social, and political problems. It has been christened "The Poverty Fly" (Leak 1998) and "Africa's Bane" by T. Nash (Nash 1969), because these flies strike both human health, as a vector of human trypanosomoses (sleeping sickness); and food and agriculture through the transmission of animal trypanosomoses (nagana) to livestock, which are used as a source of protein and fertilizer, and also as agricultural traction and transport in Africa. There is no doubt that the sustainable removal of the tsetse and trypanosomosis problem would generate substantial direct benefits and numerous rural development opportunities.

During the last century, humans have fought numerous battles against these flies, and in some instances these intensive control efforts have resulted in spectacular successes: for example, the sustainable removal of *Glossina pallidipes* Austin from Zulu Land, South Africa (Du Toit 1954), and of *Glossina austeni* Newstead from the Island of Unguja, Zanzibar (Vreysen et al. 2000). *Glossina morsitans submorsitans* Newstead and *Glossina tachinoides* Westwood were also removed from 200,000 km^2 in Nigeria (Spielberger et al. 1977), *Glossina morsitans centralis* Newstead from the Okavango Delta, Botswana (Kgori et al. 2006), but little data are available to ascertain the sustainability of these campaigns. Whereas the results can be easily maintained for savannah species that are sensitive to human encroachment, riverine species are much more resilient and *Glossina tachinoides* probably reinvaded part of the cleared areas in Nigeria (Van den Bossche et al. 2010). Moreover, some interventions also have resulted in unfortunate failures (De La Rocque et al. 2001, Hargrove 2003), which are often not reported as such but are rather attributed to reinvasions of the cleared areas after institutional, policy, and economic changes that altered program objectives, strategies, and tactics (Doran 2000, Allsopp 2001, Van den Bossche and Doran 2001). Thus, it is estimated that to date, <0.3% of the total

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tsetse infested area has been cleared after control efforts. Many authors have thus argued for a shift to an autonomous control of tsetse, based on affordable techniques like restricted insecticide treatment of cattle, especially when tsetse target populations are not isolated (Bourn et al. 2000, 2005; Bouyer et al. 2009a, 2011).

There is widespread agreement that vector control remains theoretically the most desirable way of managing the disease trypanosomosis (Leak 1998). Some even argue that a trypanosomosis-free environment can only be created by the removal of major tsetse flies (Jordan 2001). This is especially relevant since the development of a vaccine to protect livestock against trypanosomosis has failed to date, resistance of the parasite against available drugs is increasing and no new trypanocidal drugs have been developed for decades (Geerts et al. 2001). In a review 'Tsetse and Trypanosome Research and Development Since 1980′ on the impact of funding in this area, Mehlitz et al. (1998) concluded that commendable quality research had resulted in the development of a range of powerful control tactics, but their impact has been hampered by sustainability problems; a view shared by Leak (1998). How tsetse control is to be best accomplished has remained controversial to date: one camp promoting a localized, farmer-based and -financed approach (Brightwell et al. 2001, Molyneux 2001, Kabayo 2002, Rogers and Randolph 2002) and another, arguing for area-wide integrated pest management (AW-IPM) that targets all individuals of a pest population even those inhabiting areas not of interest to the farmer (Feldmann 2004, Alemu et al. 2007, Green et al. 2007, Vreysen et al. 2007). The removal of tsetse and trypanosomosis problem in a sustainable manner on a large scale would have a significant impact on the livelihoods of some 260 million Africans, mostly living in heavily indebted poor countries (Budd 1999), but there is no consensus on how to do this or even whether this is feasible.

While there have been limited economic analyses of tsetse control in general (Brandl 1986, Barrett 1997, Vale and Torr 2005, Baumgärtner et al. 2008), they have rarely adequately addressed aspects of control in the context of AW-IPM, that is, integrating medium and long-term environmental impacts. The toolbox of methods presently available is large, including sequential aerial spraying of insecticides at ultra-low volume (SAT), traps and targets (impregnated or not with insecticides) (ITs), epicutaneous treatment of cattle using insecticide (ITC), and the Sterile Insect Technique (SIT) (Bouyer et al. 2010). Most of the economic models have made generic conclusions about these various techniques whereas species-level specificities have been neglected and environmental factors have only been partially considered (Petney 1997, Reid et al. 2000, Grant 2001, Eisler et al. 2003). Much more work in this area is needed, given the ecological sensitivity of many of the very different environments found across the tsetse range and the possible influence of environmental change on the properties of the different control techniques (Terblanche et al. 2008, Van den Bossche et al. 2010).

Another area of concern in tsetse control programs is in SIT in which male tsetse are reared, sterilized, and released into the wild, where it is hoped they will mate with wild females and thereby reduce the probability of viable matings. Several recent assessments have argued for SIT to be removed from the arsenal of tsetse control (Brightwell et al. 2001, Molyneux 2001, Rogers and Randolph 2002, Torr et al. 2005), whereas others stress that it is the only technique that can deal effectively with the last remnants of a suppressed population because of its inverse density dependence (Feldmann and Hendrichs 1999, Hendrichs et al. 2005).

Most of these assessments have relied upon a small cadre of mathematical models (Vale and Torr 2005), which, while useful, do not warrant the weight apportioned to them in making widespread management decisions (Enserink 2007). Such models in ecology have been helpful in giving broad generalizations about population dynamics and control, and theoretical models were often used to compare the different methods available to find the best way to tackle the tsetse problem. However, in many ways they have poorly addressed key aspects of the biology and ecology of the economically important tsetse species and have inadequately considered the complex milieu of ecological factors within which the various tsetse flies are embedded. These models too must factor in an integration of control efforts, and not just play different control tactics against each other. In this review, some of the controversies that are being debated within the field of ecology and evolution about the use of mathematical models are reviewed vis-à-vis a few models that have been used to compare available tsetse control techniques. The paper also shows that various arguments in favor or against different tsetse control techniques or strategic approaches are inadequate in light of these model weaknesses. A part of what we hope to accomplish with this paper is to establish the information, models, and statistical perspectives to support better adaptive management in tsetse control efforts.

Models in Ecology

From its beginning, modeling has played a vital role in the development of ecology as a science. Most early models were unstructured population models that predominantly tracked overall population number and simple population dynamics (Hastings 2005). The widely used models where criticized by Hall (1988) as often being applied inappropriately because the models were too simple to capture much of the complex biological reality. Despite often being fit to data, these fits were generally over parameterized, hence, did not seem to be an adequate take on population behavior in any real ecological system. In the ensuing years there has been much debate about how mathematical models are to be used in ecology to structure theory and on even whether there are any ecological laws at all (Cooper 2003, Lockwood 2008).

The problem is exacerbated because models often try to balance competing interests. This has been captured in what has come to be known as Levins' desiderata (Levins 1966), the tri-fold characterization of models as being constrained by generality, precision, and realism. Because these three goals of models are often incompatible, modelers must make choices about which of these goals is the most important for the intended use of the model.

Ecological processes in a spatial context have been the sine qua non element in most ecological systems for a number of years. In a highly influential paper, Levin (1992) argued that spatial processes were essential in characterizing most ecosystems and the imbedded interactions of constituent organisms. In addition, the importance of developing spatial models and using discrete state spaces that tracked local processes was recognized as providing essential information in modeling efforts (Durrett and Levin 1994). This is essentially a bottom up approach to modeling. Rather than focusing on population level processes such as are used in structured population modeling at the level of population dynamics and behavior, unstructured modeling focuses on bottom up modeling and allows individual behavior and local dynamics to structure the model. De Roos and Persson (2005) have argued that this paradigm prevails in ecological modeling:

> "The insights gained from the population-level models are therefore likely to apply only to those populations in which either within-population variability is low (individuals are identical) or ecological interactions and their consequences are relatively independent of the characteristics and traits of the individuals involved. Both these conditions are generally not the rule but the exception in ecological systems."

These kinds of models make sense especially from the perspective that there are no laws in ecology. If most of the patterns that we see are a result of aggregations of individual-based organism behaviors structuring higher level ecological and population dynamics then this type of modeling offers singular advantage in capturing the complex nature of ecological interactions. This is true when typical ecological systems are extremely complex (Mitchell 1998) and this complexity is thought to matter in how biological patterns unfold and structure explanations for this complexity from the individual up (Grimm and Railsback 2005).

Computer Simulation

Early simulations in ecology, however, suffered from the kinds of misunderstandings that are common to the beginning development of a new technique. Because early computer simulations were easy to construct, the first few generations of simulation models were hastily done, inadequately tested, and used inappropriately. This colored the perception of more mainstream modelers about the usefulness of simulation, believing that the weaknesses of these models were an insurmountable problem inherent in simulation and one unlikely to be overcome. Essentially, they argued that the 'baby should be thrown out with the bath' and simulation dismissed as a useful tool (e.g., see Pilkey and Pilkey–Jarvis 2007).

However, the science of simulation has matured, and a consensus is growing on how these models can productively be used and interpreted. This includes open access and archiving of computer code, adequate testing of the model, and explicit information on model assumptions and algorithms. Despite this, poor models that do not meet these criteria are still being published today.

Computer simulations are likely to play a more and more important role in modeling these kinds of systems as they are well positioned to handle the kind of genuine complexity found in ecological systems. While simple analytic models such as differential equation-type modeling will always have their place for providing insight and general heuristics and possibilities in ecological systems, they do not capture one of their key features, namely, complexity (Peck 2004). This is not just true in ecology. For example, in astrophysics, philosopher of science, Peter Humphreys has argued that the age of analytic models is over (Humphreys 2004). Sorting out how to use these types of models is an on-going debate in ecology (Peck 2008).

One aspect of modeling that needs to be addressed here is William Wimsatt's ideas on 'robustness.' His perspective is summed up nicely in the title of one of his papers, 'False models as a means to truer theories' (Wimsatt 2007). In this paper, he explores the concept of 'robustness' in modeling. He argues that all models are representational abstractions that always fall short of capturing aspects of the systems they are designed to represent. Robustness explores whether different models, which formally represent the same system, come to the same conclusions, see the same patterns and behavior, and make similar predictions. When models converge in the results that they suggest, the story that the model is telling is more likely to be capturing real aspects of the system.

Tsetse Models: A Brief History

Early mathematical models used in exploring questions of tsetse biology and population dynamics drew on the available ecological literature. For example, Rogers et al. (1984) estimate mortality rates for *Glossina palpalis palpalis* (Robineau-Desvoidy) using an exponential decay function of the form:

$$N_t = N_0 e^{-mt}$$

Where m is the mortality rate (estimated from trapping data in Ivory Coast). In a companion paper (Rogers and Randolph 1984b) a survival model from Maynard–Smith and Slatkin (1973) was used to calculate the degree of density dependence in the same trapping series:

$$P_s = \frac{1}{[1 + (aN)^b]}$$

Where P_s is the surviving proportion of a population of size N, and where a is a scaling constant and b gives the strength of density dependence. These models are simple and straightforward applications of simple analytical models of aspects of tsetse data. In a third paper (Rogers and Randolph 1984a) was developed based on these two models in which the authors argue for an overall strategy for using such models in influencing management decisions. In the conclusion of this paper the authors argue:

> "Our understanding of the natural dynamics of the target species, tested by the development of simple mathematical models for it, helps us to identify possible pest management strategies and the choice between them is made by applying cost-benefit analytical techniques, the aim being to achieve the greatest reduction for the smallest cost" pp. 422–423.

This was a significant advancement on the way that tsetse management programs had been designed and implemented in the past. The approach provided a theoretical structure by which one could use biological information, models, and economic considerations to put together a more scientifically based program for tsetse control. This was an important step forward in recognizing the gamut of considerations that should be taken when designing and implementing a tsetse control program. Such methods would become very influential in selecting control strategies and structuring control programs into the future.

However, there was a danger lurking in this strategy that comes from modeling techniques' inherent weakness and which needs to be acknowledged and considered when such management options are being discussed. Certain models can be used to great benefit but they often give the appearance of having more depth of insight than is warranted. This is because mathematical models are sometimes not completely understood by managers and field biologists who assume that a mathematical model, because of its appearance of scientific respectability and sophistication, alone credential the arguments used to marshal particular courses of action. Hall's critique (Hall 1988) of early models becomes relevant here.

In the ensuing decades, tsetse models were developed by a variety of researchers, each with a different focus on aspects of tsetse control (Barclay 2005). Most of these have been deterministic or stochastic analytic models. One of the leading tsetse researchers using mathematical modeling is John Hargrove (Hargrove 1981, 1988, 1990, 1993, 1994, 2000, 2001, 2003, 2005; Hargrove et al. 2003, 2011b; Barclay and Hargrove 2005) who developed a suite of biologically realistic models based on stochastic birth-death theory, and age-structured transition matrices. These models form the backbone of tsetse modeling since Roger et al.'s basic work and have been used to compare management techniques to combat tsetse fly populations and provide guidance on how best to use limited resources in establishing monitoring and suppression programs.

Other models that deserve special attention include these by Gouteux and his collaborators (Jarry et al. 1996, 1999; Gouteux and Jarry 1998; Gouteux et al. 2001; Artzrouni and Gouteux 2003, 2006), who have used a variety of analytic models to explore tsetse population dynamics. Yu used birth-death stochastic models to follow the spread of trypanosome carrying tsetse flies (Yu et al. 1995, 1996). Williams et al. used diffusion equations to capture the movement of tsetse (Williams et al. 1992, Williams 1995). Rogers and Bouyer as well for fuscipes and palpalis respectively (Rogers 1977, Bouyer et al. 2007a).

All of these models were designed to be useful to biologists and program managers involved in tsetse control and were published in top-tier entomological journals. The focus of their attention to a biological audience is apparent in that none of the above mentioned models were published in theoretical or mathematical journals.

A more in-depth analysis shows that some generalizations of these models are appropriate, although extrapolation from one tsetse species to others with very different biologies is inappropriate. All of the models are analytic models with a variety of simplifying assumptions that limit the amount of biology that can be captured, and most of the models do not take into account spatial dynamics of the flies, which can be very different depending on the species. Those that do, are simple diffusion-reaction models.

Attempts to capture more biological complexity have turned to the use of simulation models. Muller et al. (2004) use an agent-based contact model to explore the spread of tsetse-transmitted human African Trypanosomosis. The model is an excellent example of how simulation can be used to capture details of biological complexity that are impossible for simple analytic models.

Models work best when incorporated into a program of 'adaptive management.' Adaptive management is a valuable way of trying to recognize that complex systems require a different perspective in using information for their management. In complex systems, uncertainty levels are high and their management will need real-time adjustments during the course of managing desirable outcomes. Rather than explicitly doing probability assessments and then choosing the best management option from among the set of possibilities in a once-and-for-all fashion. It uses scenario analysis to look at possible outcomes and focuses on the management options that will allow interventions for possible contingencies that may emerge. It is a much more interactive approach to management that relies on ongoing monitoring, modeling, and data gathering. As Sandra Mitchell describes it,

> "For the purposes of this discussion the most important thing to notice about adaptive management is that it modifies the predict-and-act model to be an interactive process of predict, act, establish metrics of successful action, gather data about consequences, predict again, establish met-

> rics of successful action, act, gather data about the consequences, predict anew . Adaptive management is a dynamic, iterative, feedback-rich strategy for decision making that matches the dynamic, feedback-dependent reality of complex systems (Mitchell 2003)."

Simulation models can be very useful for adaptive management of tsetse fly. However they should be used with care. Grimm et al. (2006) lays out appropriate criteria for using and publishing agent-based models, and the process he advocates work nicely for the steps necessary for any complex simulation model. This process is known as ODD (Overview, Design concepts, and Details). Grimm et al. suggests that in every paper using agent-based model these steps should be a part of the explication process. In publishing these models, the first step in describing the modeling effort is to formally give an overview of the model including its purpose, variables, and process description of the model. We would add to this, that all theoretical assumptions of the model should be detailed—including any overarching assumptions for the model in its entirety and the assumptions used in the individual submodels that made up the complete modeling effort.

Next the design concepts used in the model including what the model was and was not designed to achieve. Often the purpose of the model is explained, but the limits of the inferences targeted are not. This should be an explicit part of the model description to avoid problems with it being inappropriately used for purposes for which it was not intended.

Lastly in the ODD framework, details should be given, including initializations, input data, and clear descriptions of all submodels. This should include the equations used to model each compartment or process with in the simulation. This protocol provides a good framework from which to evaluate the adequacy of model descriptions in the literature.

Case study: Using Simulation Models to Advise Tsetse Control Programs

Looking at the case of models designed to explore the relative efficiency of different control techniques to advise policy makers, we find that too often they are inappropriately designed and/or described to be useful in making decisions about tsetse control.

Two models that were subsequently used to argue for and against SIT demonstrate how models can be misapplied to management cases and illustrate why simulation models need to be carefully used in a context of adaptive management when making decisions in tsetse control. This means in particular that all modeling results should be held as tentative and used in an adaptive sense. The models should be designed from the beginning to be updated as more information is gathered during an intervention and used such that there is a back and forth between on-going data collection and reassessing the model in light of this data collection.

Several recent critiques have drawn heavily on certain models to argue for or against the use of the SIT as a valid and efficient tsetse control tactic. Because funding for tsetse fly is limited, turf wars have arisen that praise the use of SIT or disparage it. Those that praise it point to its successes such as those outlined in the introduction. They point out that SIT may be the only way to clean up isolated populations or populations that have only those flies remaining that are not attracted to targets or baits. They also point to successful field operations (Politzar and Cuisance 1984; Oladunmade et al. 1985, 1990; Vreysen et al. 2000). Those who see SIT as unnecessary, for example, Molyneux (2001) argue against SIT as a continent-wide eradication strategy and allow these arguments spill over into a general dismissal of SIT as a component of integrated area-wide control. Likewise, Rogers and Randolph, in an opinion piece (Rogers and Randolph 2002) argue against tsetse eradication from Africa, and go on to claim that SIT is not an effective choice.

Both groups then turn to inadequate models to make their respective points about using SIT. For example, Vale and Torr (2005) created a compartmental deterministic model of tsetse movement and economics to predict the cost and effectiveness of different control strategies, namely SIT and insecticide-treated cattle. However, the model suffers from some important weaknesses: 1) the published model contains few details on the assumptions used to structure the model; 2) there is little information on how the model was tested and parameterized; and 3) doubt about whether and/or how sensitivity and uncertainty analyses were performed. While the excel spread sheets in which the model was implemented are available, it is difficult to dissect the code to reconstruct the flow control, or get a description of the equations of the model which are described by, "The numbers displayed in each cell were determined by a formula behind the cell," which are implemented in individual entries into a spreadsheet and nowhere provided in a typical analytic form. Therefore, the model seems to have several shortfalls as a finished product and is reminiscent of the reasons that models where so severely criticized in the early days of ecological simulation as discussed above.

Likewise, a model developed by Barkley and Vreysen (2011) is used to "facilitate decision making during the planning and implementation of operational area-wide IPM programs against tsetse," by comparing four control measures, for example, aerial spraying of non-residual insecticides, traps and targets, insecticide-treated livestock (ITL) and the sterile insect technique (Hargrove et al. 2011a) rightly argue that there were biological problems with the model principally the time steps used were not reflective of tsetse fly ecology and the way movement was modeled was flawed. Part of what allowed this assessment was that Barclay was more complete in describing the submodel dynamics and the equations used which are absent in the Vale et al. paper critiqued above. In addition, Barclay and Vrayson include a sensitivity analysis that allows for a more complete assessment of the model's adequacy. However, interestingly, Hargrove et al. argue that the Barclay model conflicts with Hargrove's nonspatial models, which are also inappropriate to the task of comparing output with spatial models. However, Barclay and Vreysen do not include an uncertainty analysis, neither is there enough information to properly evaluate the complete set of assumptions used in the model, nor is the computer code available to reproduce the model. Ironically, we are left with inappropriate models being used to criticize inappropriate models, which leave one with the feeling that windmills are being used to tilt windmills.

There are several problems in both models used as arguments for and against SIT. First, all of their arguments rest on simulations that have been inadequately described and tested. For example, Shaw et al. (2007) recently even suggest using the Torr et al. model for management and investment decisions in Uganda on tsetse control tactics, and this is especially troubling given the current state of this model. When critical policy strategies are set and important decision making takes place based on inadequately tested and evaluated models no one wins.

Second, complexity is important for understanding the ecology of these systems. For example, in Hargrove et al. (2011)'s response to the Barclay/Vreysen model, Hargrove (2005) is brought to bear in marshalling their arguments that both the Barclay/Vreysen's model and thus SIT, can be dismissed, they do not seem to recognize that the Hargrove (2005) referenced model is ecologically simple and lacks the spatial complexity needed to adequately understand the effect of metapopulation dynamics and habitat fragmentation on these extinction probabilities. Peck (Peck 2012) has shown that when standard extinction probabilities, as derived by Hargrove (2005), are estimated in a metapopulation context, it completely changes those probabilities because of rescue effects created by movement among the habitat patches. This is especially important for riverine species in West Africa. Population genetics studies have demonstrated the impact of habitat fragmentation on population dynamics resulting in significant structuring of the tsetse populations (Solano et al. 2000, Bouyer et al. 2009b).

The simple models used in making arguments for or against SIT in what are clearly spatially complex environments, are inadequate (Guerrini et al. 2008). To properly assess how best to manage tsetse it will require new models that not only take into account economic issues, but which take into account metapopulation theory, landscape ecology, evolutionarily stable strategy, insights from invasion and conservation biology, source-sink dynamics, and other insights gained from the ecological sciences on population regulation and control. Furthermore, the recommendations derived from such models might vary for different tsetse species (namely because of their dispersal pattern and feeding behavior) or in different environments (according to their fragmentation level). Individual based models may be especially promising for these explorations (Muller et al. 2004, Grimm and Railsback 2005).

We conclude that indeed, not only these models, but also many models used in exploring tsetse control are vulnerable to the criticisms that have been targeted in the mainstream ecological literature discussed above and have not dealt extensively with the realities of biological complexity. The models are also not robust in the Wimsatt sense of the word, in that all of the models have been developed by a handful of researchers and there have been few overlapping models, which would allow for a sense of how well the findings of these models hold up when viewed from a variety of modeling perspectives. This is not a criticism of the general use of models that, in are often well done, properly analyzed, and useful to the extent that their weaknesses are recognized. However, it is this last point that underlies the largest problem with the models discussed, as they have been widely used as the final word in understanding tsetse population dynamics and have carried a disproportional, maybe even inappropriate weight in management decisions with respect to tsetse control. As Rogers articulated years ago, we do agree that models have a place in making management decisions, but the way some of these models have been used recently is inappropriate and misapplied.

We argue strongly that before such simulation models are used, the ODD proposed by Grimm and Railsback (2006) and recently updated and reassessed (Grimm et al. 2010) for agent based models, be used rigorously in all computer simulation models. These should become standard practices before simulations models are accepted into the literature and used by stakeholders, particularly in the context of vector management and control tactics and regarding investment options. These practices are already required by most ecological journals and ecological modeling and theory journals.

In addition, tsetse modelers would do well to follow the protocols proposed by Schmolke et al. (2010) who recently proposed that models used in support of management decisions follow a standard format in documenting the modeling effort: transparent and comprehensive ecological modeling (TRACE). In the TRACE protocol three levels of information are made explicit in reporting the use of models: 1) model Development, including model design, model description, parameterization and calibration; 2) model Testing and Analysis, including verification, sensitivity analysis and validation; and 3) model Application, explicitly the results of the model and how that model will be used in management decisions including uncertainty analysis, and recommendations for management based on the above.

In addition, the following criteria should be considered (Peck 2004).

A. All computer code-based models should have a well-documented programming code that is transparent to competent reviewers and provided for all formal reviews of papers containing simulation models.

B. Careful explanation should be made available of how all of the equations are used in the model, relationships among the equations clarified, and flow diagrams of the flow of state variables provided to make understanding the model's construction explicit.

C. A table of all biological, statistical, societal, economic, and relational assumptions should be explicitly made and justification provided from the literature to give an explanation for the assumptions used or the effect of the assumptions in the model. In addition, details on where the model is discrete, where continuous, the role of stochastic elements in the model, and the spatial assumptions should be made clear.

D. The parameter values used in the model should be provided and should be tested with properly constructed sensitivity analyses (e.g., see Storer et al. 2003). These tests should be detailed in the paper itself or provided in supplemental material or in detailed appendices.

E. The modelers should make a clear assessment of how the model can be used, to which biological systems it should apply, where its weaknesses lie, and provide cautions on where the model should and should not provide insight and information.

F. Details on how the model was tested against the biological system it is designed to represent, or how it could be so tested, should be provided.

Unfortunately, these criteria, broadly recognized in ecological reporting and practice, have played little role in the tsetse literature. Finally, this analysis shows the urgent need for better models allowing integrating important ecological characteristics of tsetse that have been insufficiently (-) or not (o) considered in the present models and that might have important impacts on their conclusions, namely:

- Differences in dispersal capacities between groups (mainly in one dimension for riverine species and two for the savannah and forest groups) or even within (Koné et al. 2011) (-),
- Differences in feeding behaviors between groups, namely opportunistic host selection associated to learning in the palpalis group (Bouyer et al. 2007b) (o),
- Habitat fragmentation and metapopulation structure (Peck 2012) (o),
- Aggregated distribution patterns of tsetse, leading to spatio-temporal heterogeneity of the contact between ITs or ITC and tsetse whereas sterile flies released by air are able to aggregate in the same sites preferred by wild flies (Vreysen et al. 2011) (o),
- Density-dependant mortality (Rogers and Randolph 1984b) (-),
- Density-dependant dispersal, because of feeding competition on the host (Torr and Mangwiro 2000), leading to lower alimentary dispersal with decreasing tsetse densities, associated to lower efficiency of ITs and ITC (o),
- Heterogeneous efficiency of SAT because of variations in the tree cover and thus, insecticide penetration, especially in the case of riverine species (Bouyer et al. 2005) (o).

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