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UE: GMBE40D – Internship M2 BEE

MSc Ecology Biodiversity
Evolutionary Biology and Ecology
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Internship report

Modeling the impact of meteorological and environmental factors on the population dynamics of the vectors of Rift Valley fever in Northern Botswana.

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Jury:
Internship defense: the 13th and 14th June 2013

Mignot (Director), M. Navas (AgroM representative), S. Hättenschwiller, E. Douzery and T. Lenormand

ACKNOWLEDGMENTS

Thank you very much to everyone having brought support to this study, thanks for your help, your presence and your care.

*I'm particularly grateful to my supervisors: **Dr. Ferran Jori** and **Dr. Annelise Tran**. I really appreciated your proofreading and your advices. Ferran, thank you for organising this very interesting three month internship in South Africa, for introducing me to the local scientific environment and for your unconditional availability and enthusiasm. Annelise, thanks a lot for your time and your patience, your e-mails and for the constant clearness of your explanations and also for our useful discussions.*

*I thank the **University of Pretoria**, the **CIRAD** and the **Maison de la Télédetection** to have hosted me for this internship.*

*I am so grateful to **Dr. Power Tshikae** from the University of Pretoria and **M. Alan Kemp** from the National Institute for Communicable Diseases of South Africa for the laborious identification work, the future virological studies, and for sharing your entomological knowledge with me.*

*Thank you to **M. Patrick Kgori** from the National Veterinary services and **to Mrs. Keitumetse Gladys Mangate** from the National Veterinary Laboratory for the trapping and preservation of mosquito samples.*

*Thank you to **Dr. Catherine Sole** from the Mammal Research Institute for your help with the entomological publications so hard to find.*

*Thank you to **M. Poitr Wolski** from the Okavango Research Institute and to **the Maun Weather station** for your help on accessing climatic data and your advices about the inputs on the complex hydrological system of the Delta.*

*And of course, I thank warmly **Charlotte, Daniel, Kablan, Gary, Rob, Noémie, Riri, Sophie, Caro, Amar, Naïma, Agathe, Anna, Marinette, Carotte, Ju** and all the others for your support, discussion, proofreading, travel, diner, etc, in one word: for your time.*

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MSc Evolutionary Biology and Ecology Internship report

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INTRODUCTION

Mosquitoes are a major source of nuisance throughout the world, and due to the abundance of pathogens transmitted by their bite they pose a direct health threat to many hot blood species (Linthicum *et al.* 2007). Indeed, many pathogens responsible for important diseases, such as malaria, dengue, yellow fever or filariasis, are transmitted by infected mosquito vectors. Prevention and control of these diseases, which significantly affect the health of animals and/or human, induce a very heavy economic impact in the societies where they are present, and particularly in developing countries of tropical and sub-tropical areas.

Rift Valley fever, an acute disease

Rift Valley fever (RVF) is precisely one of such diseases considered as a significant global threat to both humans and animals. The pathogen responsible for this disease is the RVF virus (RVFV), an arbovirus belonging to the genus *Phlebovirus*, family *Bunyaviridae*. Transmitted to vertebrates by mosquitoes or by direct contact with viraemic animal products, the virus causes epizootics and associated human epidemics throughout Africa (Daubney *et al.* 1931). In ruminant livestock, especially sheep and cattle, the disease is characterized by high abortion and mortality rates (100% in neonatal animals and from 10% to 20% among adult animals). Human infections are characterized by a severe influenza-like syndrome, although some patients can develop complications such as encephalitis (less than 1% of patients), ocular disease/retinis (0.5-2%) or fatal hemorrhagic fever (less than 1%) (WHO 2010). Because of its potential to cause severe disease in both animals and humans, RVFV is considered as a major zoonotic threat and a potential bioterrorism weapon.

Since the first description of RVFV in 1931 during an investigation into an epidemic among sheep in the Rift Valley of Kenya, the geographical distribution of RVF has been steadily expanding (Bird *et al.* 2009; Chevalier 2013). Historically confined to the African continent until 2000, RVF spread to the Arabian Peninsula at the beginning of the century (Ahmad 2000) and more recently, into several islands of the Indian Ocean (Carroll *et al.* 2011). As RVF is a mosquito-borne disease, the distribution of the disease, in space and time, is closely associated to the geographical distribution and dynamics of RVFV vectors and thus to climatic and landscape features. As a matter of fact, different studies have shown that *i)* the sudden availability of water in the environment, for example, allows infected *Aedes* eggs, which were dormant for several months, to hatch and cause the pullulation of RVF vectors, and *ii)* outbreaks generally occur in the mid- to late summer months with widespread and heavy rainfalls, when vector abundance has peaked (Davies *et al.* 1985; Digoutte & Peters 1989; Wilson 1994; Linthicum *et al.* 1999; Swanepoel & Paweska 2011).

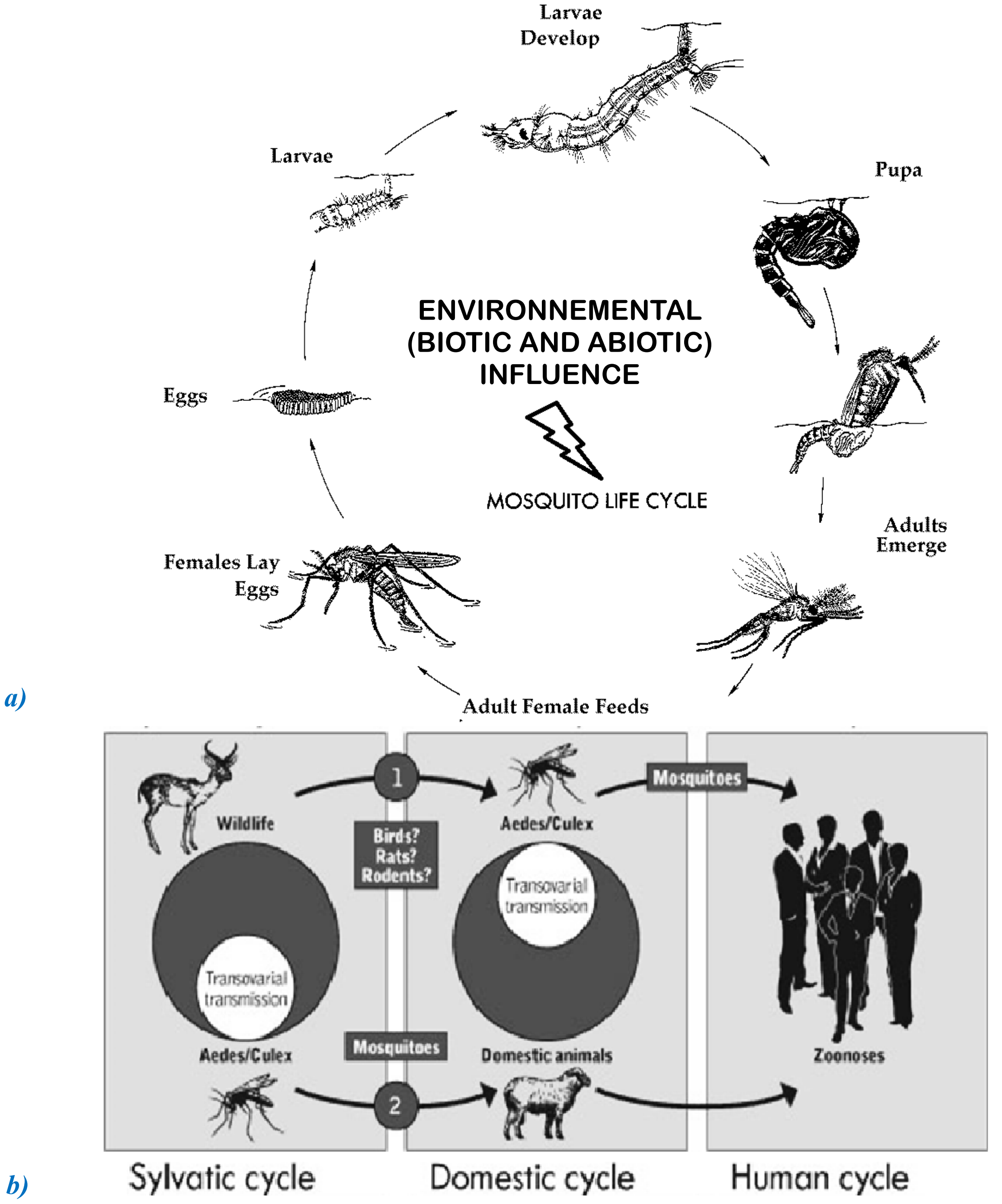

Figure 1. *a)* Mosquito life cycle; and *b)* conceptual model of Rift Valley fever virus transmission (source: B. Mondet (IRD), IRAD, FAO website)

Water presence and temperature, important drivers of RVF dynamics

Vector-borne diseases are among the most sensitive diseases to environmental changes as both the ecology of vectors and the development rate of pathogens within them are highly dependent on environmental conditions. For example, mosquitoes require specific environmental conditions to develop and survive, such as water presence to lay the eggs, optimal temperature for aquatic stage development, limited wind for the adult behaviour (seeking-host or seeking-breeding site), or specific vegetation for some species (Clements 1992). Thus, meteorological variations influence vector population dynamics and consequently vector-borne disease dynamics.

A well-known relationship is the one existing between the mosquito life cycle and water availability (Davies *et al.* 1985; Fontenille *et al.* 1998): rainfall volumes can influence the number of available mosquito breeding sites[1], resulting in a variation on the number of vectors and therefore more or less intense virus transmission and circulation (Figure 1). Likewise, the presence of a waterway can increase the flooded surface and consequently the number of mosquito breeding habitats. Thus, excessive flooding allowing massive hatching and a tremendous increase in the number of vectors, may result in an outbreak (Davies *et al.* 1985; Zeller *et al.* 1997; Woods *et al.* 2002). Nevertheless, other environmental factors, such as temperature or host density are also suspected to be important in the vector dynamics (Brubaker & Turell 1998; Reisen *et al.* 2006; Shaman *et al.* 2006; Loncaric & Hackenberger 2013).

Consequently, understanding the disease dynamics requires a reasonable knowledge on both the conditions leading to an outbreak and the possible causes of the persistence of RVFV during the inter-epidemic periods which involve vector ecology, meteorological and environmental parameters (biotic and abiotic). Indeed, many biotic and abiotic processes may affect death and birth rates, and produce effects on vector size population though alteration of growth and development. Vector population size is regulated by both *i)* density dependent processes and *ii)* density independent processes. The former regulate the population size to an equilibrium density[2]. The later, having no feedback of density of the population on the processes affecting it, can cause drastic change in the abundance (Juliano 2007). Computer models represent valuable tools for predicting increases in mosquito abundances and thus possible disease outbreaks because they are able to include both kinds of processes to describe the population size variation over time. Indeed, the development of analytical tools allows to understand a variety of processes of mosquitoes and diseases dynamics, such as the effect of

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[1] Location with all required conditions for the oviposition and the aquatic stages development.

[2] At the equilibrium density, the population growth is 0. This population present density dependent regulation affecting size and growth rate to stay at stable equilibrium level.

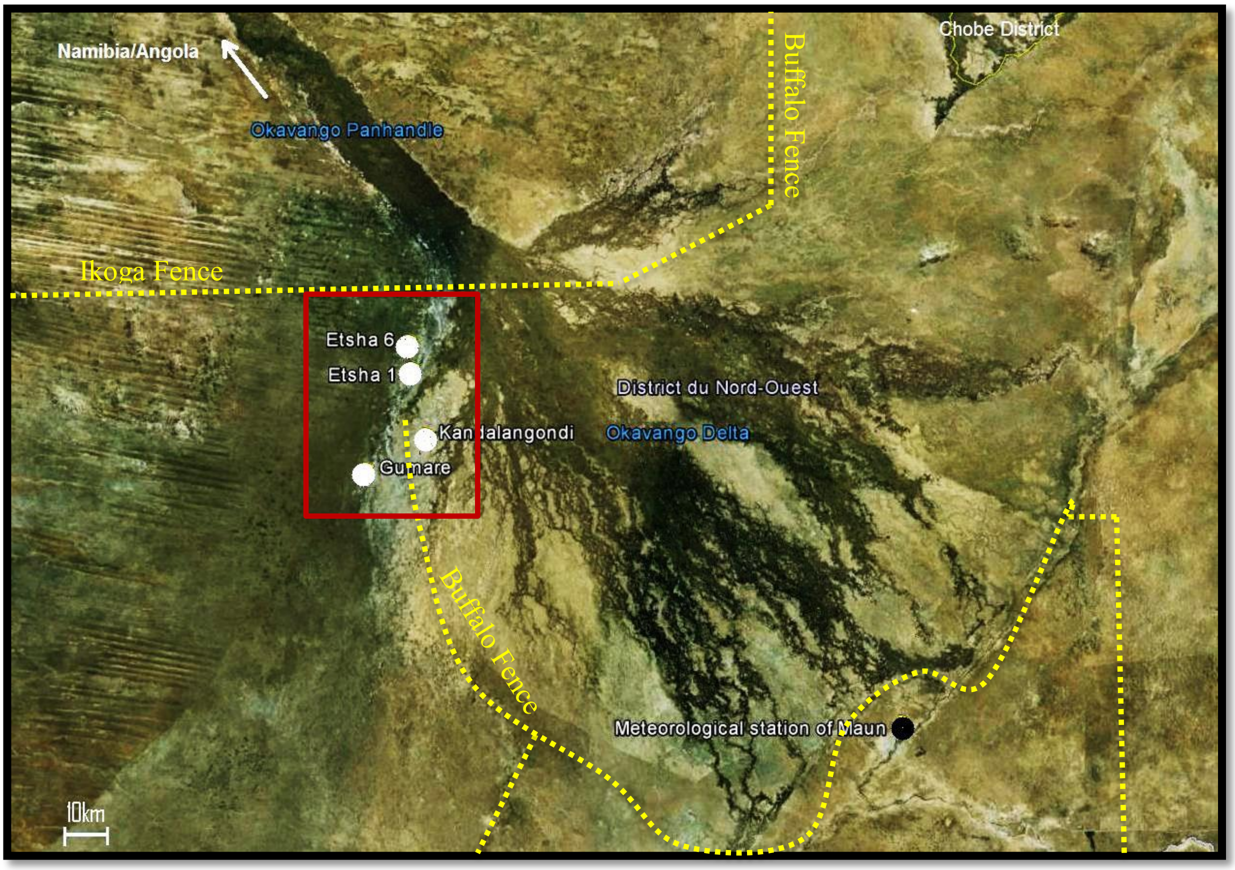

Figure 2. Map of the study area - the Okavango Delta.
The trapping sites are represented by white points and the meteorological station by the black point. Fences separating domestic animals and wildlife are in yellow.
The study area is represented by a red rectangle.

environment, transport, competition, etc. Métras *et al.* (2011) recently reviewed different modelling tools used to evaluate RVF risk emergence in animals and their contribution to the improvement of surveillance and control strategies. According to their opinion, the combined use of climatic models and epidemiological mathematical models to predict RVFV emergence and spread and to test the impact of different interventions strategies, would allow to improve outbreak monitoring and control.

Okavango Delta, a hazardous environment for RVFV transmission in Botswana

The Okavango Delta system provides large surfaces of available water all year round (Wolski *et al.* 2005). In addition, the tropical temperatures and the availability of abundant animal hosts (domestic and wild) provide a perfectly suitable environment for mosquito development.

While substantial RVF outbreaks have occurred in neighbouring countries (South Africa, Namibia, Zambia) in a variable temporal cycle ranging between 7 and 11 years (Manore & Beechler 2013), no outbreaks of RVF have ever been reported in Northern Botswana. However, some cases of abortion in livestock and hemorrhagic fever in humans, compatible with clinical cases of RVF, were suspected 25 years ago in Chobe District, Northern Botswana (Tessier *et al.* 1987) (Figure 2). Moreover, the interface between wildlife in National Parks and livestock farming areas in the Ngamiland district of northern Botswana may increase host availability and therefore arbovirus circulation. Indeed, wildlife-livestock interactions could involve pathogen transfer and consequently potential invasion of pathogens from distinct ecological habitats. Consequently, the evolution of Transfrontier Conservation Areas (TFCA) in which wildlife is able to move freely is of great concern for the neighbouring countries such as Botswana and Angola (Mendelson *et al.* 2010).

To test the hypothesis of silent RVFV circulation in this region, a serological survey was performed in different human (154 villagers) and animal (23 cattle, 4 buffalos, 2 zebra, 1 impala, 1 tsessebe and 1 warthog) populations in December 1984, after a heavy rain episode. Results showed that 27 % of tested humans presented antibodies against RVFV, although none antibodies were detected in domestic or wild animals. To complete this picture, a serological study was undertaken in April 2010 by the Department of Veterinary Services of Botswana, in collaboration with the Emergency Center for Transboundary Animal Diseases from the Food and Agriculture Organization (FAO) and the Centre de coopération Internationale en Recherche Agronomique pour le Développement (CIRAD), in order to evaluate RVF occurrence at this livestock–wildlife interface. On the Western border of the Delta, 500 cattle from 10 different diptanks were sampled and tested at the Onderstepoort Veterinary Institute in South Africa, with an i-ELISA test for the detection of RVFV

Table 1 Seroprevalences of IgG detected in the 5 different diptanks located on the Western boundary of the Okavango Delta.

	N° positives	Observed Diptank Prevalence
GUMARE	6	12%
DANEGA	8	16%
KANDALANGONDI	11	22%
ETSHA 1	37	74%
ETHSA 6	15	30%
TOTAL	**78**	**16%**

antibodies (IgG). Results revealed an overall 16% seropositivity for IgG antibodies to RVFV, with substantial differences depending on the diptanks (Table 1). Thus, despite no outbreak were reported in the region, there is clear serological evidence that RVFV circulates among local human and animal hosts.

These observations provide evidence that an RVF inter-epidemic circulation exists in the Okavango Delta of Botswana with mild or subclinical manifestation in animals and possibly humans, as described in other regions in Africa (Fafetine *et al.* 2013). These findings illustrate that the epidemiology of RVF is not yet well understood, and that the reasons for the emergence of RVF outbreaks remain unclear. Under these circumstances, carrying out efficient and timely control measures remains a challenge. Studies on RVF are relatively abundant, including risk factor studies, spatial techniques, dynamics transmission models or risk assessment (Métras *et al.* 2011). In these modelling studies, the mosquito vectors are often considered, but generally their density over time is not taken into account. Modelling mosquito population dynamics could be an efficient tool to better understand the relationship between RVF transmission and environmental components over time.

The present study focuses precisely on both modeling and analysis of the relationship between environmental factors (rainfall, temperature and rise in the water level) and the abundance of the main vector of RVF sampled in the western border of the Okavango Delta, *Culex pipiens pipiens* (*Cx. pipiens*). A climate driven abundance model of mosquito populations previously developed by Cailly *et al.* (2012) has been used to understand the *Cx. pipiens* dynamics, which allowed us to test the model genericity and to test the hypothesis that according to the constant water availability around the Okavango Delta, rainfall is not sufficient to predict the mosquitoes population dynamics in this area. Entomological collections of adult stages of mosquitoes captured in four different sites during a year cycle between 2011 and 2012 were used for model validation. A sensitivity analysis described by Saltelli *et al.* (2000) was instrumental in specifying the influence of different inputs in the vector dynamics and to define the behaviour of the model.

This report is structured around two main research questions: *i)* Is the model developed by Cailly *et al.* (2012) for European mosquito populations applicable to any mosquito populations and in any environments? *ii)* What is the influence of the climatic and environmental factors on the main mosquito vector of RVF (*Cx. pipiens)* in the livestock-wildlife interface in the Okavango Delta?

MATERIAL AND METHODS

A continued-time and stage structured model designed by Cailly *et al.* (2012) has been adapted in order to simulate the population dynamics of main RVF vectors in north-western region of the Okavango Delta. The model runs for a seven-year period (2005-2012), and only females are modelled. In this section, we present the study area, the environmental and meteorological data, the mosquito collection and the model building.

Study area

The Okavango River basin, shared by Botswana, Angola and Namibia, is a unique wetland environment that supports a fragile and extremely complex ecosystem and one of the largest, most pristine, best protected and well known aquatic ecosystems on the African continent. With the floodwaters of both the Cuito and the Cubango rivers that rise in the well-watered Angolan highlands and through Namibia, 'disappearing' into the sands of the Kalahari Desert and the 'thirsty' atmosphere above the Okavango Delta, the whole Okavango system is endoreic[3] in nature.

The Delta, located in semi-arid NW Botswana, is an interface between wetland and dryland and a rich reservoir of nutrients. The quality, volume and timing of water flow entering the Delta are determined in the catchment areas in Angola and the passage of the Okavango River through Namibia. Indeed, the hydrological system is dominated by annual flood from the Okavango River. These flood events are primarily caused by a first flood wave arriving from the higher rainfall happening in the northern catchment which lies entirely in the Angolan part of the Okavango river basin. During these events, depending on the size of the flood, the extent of the inundated area increases between 5000 km^2 and 6000-12000 km^2 (Wolski *et al.* 2005). In addition, between October and April, the Delta area is exposed to highly seasonal rainfall ranging between 1300 mm/y in parts of the catchment furthest to the north-west and, steadily declining as the river moves southward, 450 mm in the lowest reaches of the Delta. In the most northern areas, rainfall is concentrated in two peaks, one in November-December and the other in February-March. As a consequence, there are often two peak periods of flow in the Delta. There is a 600 km distance from the headwaters of the Okavango River and the low topographic gradient of the alluvial fan (1:3500), causing a delay of the annual flood in the system. As a result, the flooding in the distal part of the Delta occurs only during the late dry season (August-October) (Wolski *et al.* 2005). The frequency of annual floods and flood duration are the principal drivers of the ecosystem (Milzow *et al.* 2009; Wolski *et al.* 2012). Globally close to 2100 mm/y, potential evaporation is also lower in

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[3] Endoreic: areas with terminal lakes and an interior drainage basin)

the upper catchment and therefore, rain is more effective in supplying the moisture needed for crops and pastures than downstream.

As a result of flooding, nutrient resources accumulate progressively over a long time in the Delta's sediment and those of adjacent areas flooded by much larger lakes. Indeed, each flood brings more of these chemical constituents of life. Nutrients blown by wind are trapped in the water, and faecal matters from animals attracted to the water and its associated floodplain pastures likewise, enrich the Delta. The key point is that the rich nutrient supplies take a very long time to accumulate here, in contrast with the fresh supplies of water which arrive to re-flood the Delta year after year.

Few people live permanently in the area of the inner Delta and the remote areas of western and northern Ngamiland (district located in around the Delta in western-northern Botswana). Most of the existing settlements are very small, with a high proportion of the population clustered in a handful of larger villages and in the district capital of Maun. In total, the 13 largest villages together with the town of Maun are home to about 84,800 people, representing the 58 % of Ngamiland's province. Most land is used for three purposes: communal farming, private ranching, and wildlife conservation and tourism. The conditions are poorly suited to agriculture and ranching because soils have low fertility, rainfall varies too much to produce good yields from such rain-fed crops as maize, cassava (manioc), sorghum and pearl millet, pastures cannot support large numbers of livestock, and livestock diseases and crop pest limit production. Yet, the Delta is extremely rich in biodiversity, which favours tourism activities. About 1300 species of flowering plants have been identified there. The animal diversity is also very important, and particularly in the dryland that surround the Delta with crocodiles, elephant, birds, etc. Large herbivorous mammals are very abundant as a result of sediments and forage being rich in nutrients. In terms of livestock, cattle and goats are generally the most abundant stock, with smaller numbers of sheep and donkeys (Mendelson *et al.* 2010). Most stocks are held on communal or tribal land, and the great majority of animals are kept south of the buffalo veterinary fence erected to limit the spread of disease between wildlife and livestock as well as to control infection between domestic animals when outbreaks occur. Our study area is precisely located on this fence, at the western border of the Delta between 22°08' and 22°18' east, and 19°07' and 19°26' south (Figure 2).

Meteorological and environmental data

To model the population dynamics of mosquitoes in the Okavango Delta, we assumed that their dynamics are mainly driven by temperature and water presence. Therefore, the model requires daily rainfall, temperature and flooding extent data as input.

Rainfall & Temperature

The hydrological Okavango system is very complex. In Botswana, the year is divided into two seasons: summer (October to March) and winter (April to September). During summer, a low-pressure system develops over the region, drawing in air from the surrounding land and oceans. Most rainfall occurs during summer downpours between December and March. Otherwise, during winter, low pressure areas move northward and the influx of high-pressure leads to stable dry condition. The lack of cloud cover in winter can lead to ground frosts, which may influence mosquito life cycle.

Climatic data (rainfall and temperature) have been recorded by the department of Meteorological Services of Botswana at Maun airport located at the Delta's southern fringes. Maun Airport is the closest meteorological station to the study area (Figure 2) and records daily climatic data since 1921. Correlation tests, based on Pearson's product moment correlation coefficient, were computed in order to check if data from Maun were applicable to our study area using rainfall estimates from satellite Tropical Measuring Mission (TRMM), downloaded from NASA's Goddard Earth Sciences Data and Information Services Center from 2005 to 2012 (Huffman & Bolvin 2013).

Mapping flooding extent

Usually, flooding dynamics follow the rain dynamic, but the vast size of the system and the scattering of the water at the Delta scale make this relation very complicated. Indeed, the northern catchment spans an area of about 400 kilometres from east to west and 500 kilometres from north to south, and is divided into two sub-catchments. Flows down the Cubango sub-basin are rapid, peaking at the end of the summer rains, while the slower flows down the Cuito only reach its confluence with the Cubango/Okavango two or three months later. The Okavango River rises in the uplands of central Angola and drains an area of over 140 000 m² before terminating in an inland alluvial fan, the iconic Okavango Delta located in Botswana (Mendelson *et al.* 2010).

To assess to the hydrological dynamics, we cannot use water level data from hydrological stations because those are not representative from our study area. In fact, they are located too far and therefore in a totally different distributary, and the existing hydrological model able to predict the flooding of the Okavango Delta (Wolski *et al.* 2006) does not reach the resolution needed (P. Wolski personal communication). Therefore, following advices from Dr. P. Wolski of the Okavango Research Institute, we decided to use inundation extents measures from satellite imagery. Indeed, it seems to be the most prominent tool for evaluating the flood extent because of its easy data acquisition and the development of robust image processing techniques for gauging the flood map (Senthilnath *et al.* 2013).

Box 1 Imagery processing protocol

Moderate Resolution Imaging Spectroradiometer (MODIS) satellite images were acquired from Land Process Distributed Active Archive Center (https://lpdaac.usgs.gov/). MODIS Terra 8-day composite images of surface reflectance estimates at 500 m spatial resolution (product MOD09A1) covering the Okavango Delta were collected between 2005 and 2012. Preprocessing steps consist in masking the low quality pixels and the pixels covered by clouds using the surface reflectance quality file, and performing a linear temporal interpolation of the masked pixels using the Time Series Generator (TiSeG) freeware (Colditz *et al.* 2008). Temporal series of water indices were then computed from the reflectance values of the cleaned images according to the following equation: MNDWI= (G-SWIR)/G+SWIR), with G: Reflectance in green wavelength; SWIR: reflectance in short wave infrared range. A threshold was then applied on MNDWI images to delineate free water (MNDWI threshold value=-0.4).

Image processing was performed using ENVI IDL software 4.8 (Exelis, Boulder, C0, USA). GIS analyses were performed using ArcGIS 10.1 + Spatial analyst extension (ESRI, Redlands, CA).

Box 2. Trapping protocol

Trapping episodes took place from the sunset (between 15:30 and 18:00) to the next sunrise (6:00 to 8:00). The traps consisted of a rectangular “tent” of fine voile spread over 4 aluminium corner poles and have dimensions of 2 m long X 1.5 m wide X 1.6 m high (schema). The trapping method is based on the attraction of mosquitoes to carbon dioxide. Dry ice was used as a source of carbon dioxide to bait mosquitoes just before sunset in order to collect the mainly crepuscular/nocturnal vector species (Magnarelli 1975). Four traps were set every evening in every location. The netting was rolled up to approx. 15 cm from the ground to allow mosquito entry and left overnight. To maximize the trap effort, the tent traps were cleared of mosquitoes just before sunrise, by entering the trap, rolling the sides down to ground level and collecting the mosquitoes with a mechanical aspirator. Mosquitoes are transferred to small cages for transport to the base station, where they are killed by freezing for 20 minutes at minus 20 degrees Celsius, sorted according to genus and stored in 1.8 ml cryotubes in lots of up to 200 per tube. The sorted mosquitoes are then frozen at minus 20 degrees C or lower for preservation and transported to the laboratory for identification to species and for virological testing.

Several methods are used in radar and optical remote sensing to delineate water bodies and map flooded areas. The Modified Normalized Difference Water Index (MNDWI) is particularly suited to the detection of free water (Xu 2006).

The proportion of flooded areas was computed around each trapping location (Etsha1, Etsha6, Gumare, Kandalangondi) within a 2 km radius, around the study area and for the whole Delta, using Geographic Information System (GIS) functionalities, following the method detailed in Box.1.

Entomological data

Biology of mosquitoes

Mosquitoes are holometabolous insects, which means that they undergo complete metamorphosis. Their life cycle, which follows a seasonality cycle, consists of four different developmental stages: egg, larva, pupa, which are aquatic stages, and a terrestrial adult stage (Figure 1a). Indeed, to promote the survival during unfavourable period (e.g. winter, or dry season), mosquito cycle include a diapause event. According to the species, the diapause can concern either the adult stage, such as for *Culex* or *Anopheles* species (Clements 1992), or the egg stage, like for *Aedes* species. A few days after oviposition (or after a diapause event for *Aedes* species), larvae hatch from the eggs and start their development in the water. Several days later, depending on environmental conditions, food abundance and species, larvae turn into pupae which do not feed anymore. After approximately two days, adult mosquitoes emerge from the pupae (Clements 1992). Male and female adults mate rapidly after emerging from the last aquatic stage. The lifespan of males usually is shorter than for females. Mating occurs only once in male’s lifetime. After fertilization, females disperse to seek a host, possibly resulting in long-distance movements and a risk of host defence response. After a blood meal, females mostly remain in a sheltered place during the few days needed for the eggs to mature. They ingress and egress from resting sites, resulting in local and less risky movements. Then, females seek for an oviposition site, which may result, one more time, in long-distance and risky movements. Depending on the species, different oviposition sites may be used, from aquatic environments to humid places.

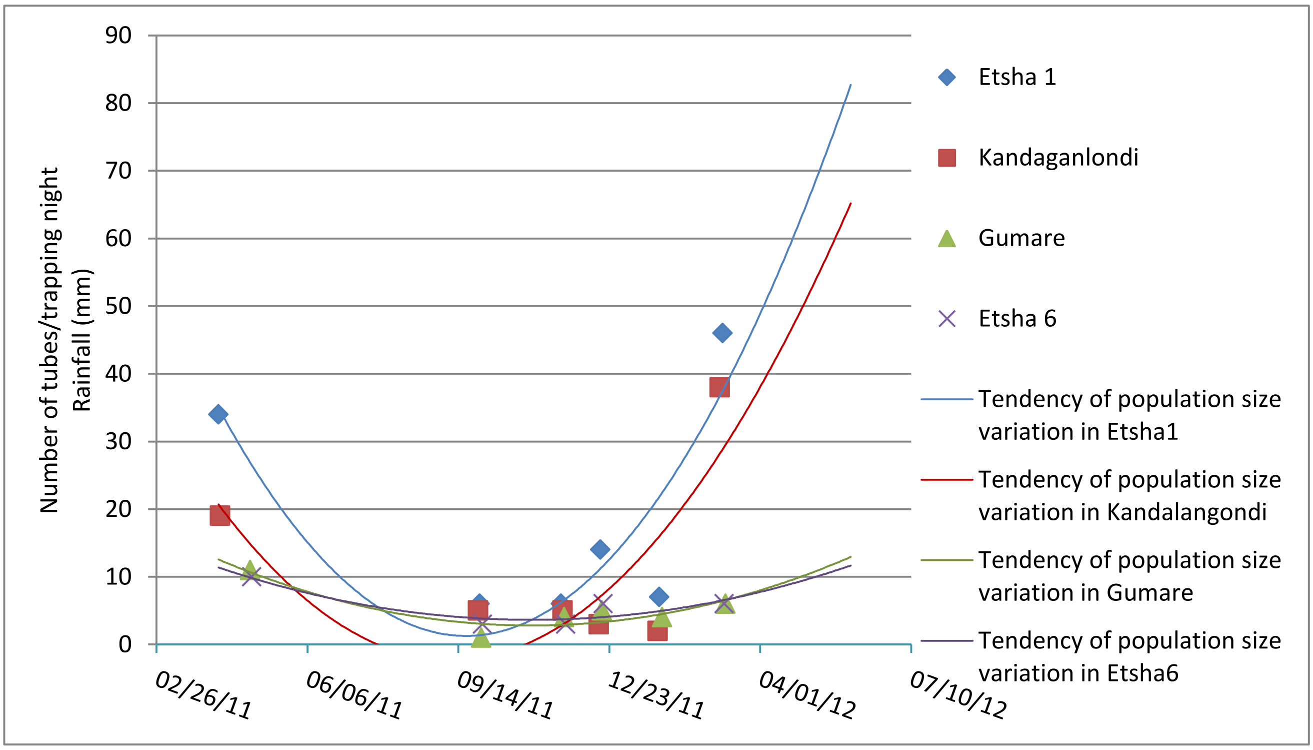
Mosquito females usually pass through several gonotrophic cycles, whose number depends on environmental factors. Each gonotrophic cycle consists of host seeking, blood feeding, and oviposition. As poikilotherms, mosquitoes are unable to regulate their body temperature (Jetten & Takken 1994), in this way temperature is one of the most important abiotic factors affecting the complete mosquito life cycle development, growth, and survival of immature mosquitoes (Clements, 1992), and blood digestion rates, ovary development, and gonotrophic cycle duration in adult females (Eldridge 1968; Madder *et al.* 1983).

Table 2 *a)* Trapping summary for the four sites with the date of each trapping episode and the number of tubes collected (Nb).
HR: heavy rainfall prevented the trapping session.
***b)* Related graphic illustrating the tendency of abundance variation over time form April 2011 to March 2012.**

a)

SITE	ETSHA 1		KANDALANGONDI		GUMARE		ETHSA 6	
	DATE	Nb	DATE	Nb	DATE	Nb	DATE	Nb
	08/04/2011	34	09/04/2011	19	29/04/2011	11	03/04/2011	10
	28/09/2011	6	27/09/2011	5	30/09/2011	1	29/09/2011	3
	22/11/2011	6	21/11/2011	5	24/11/2011	4	21/11/2011	3
	17/12/2011	14	16/12/2011	3	19/12/2011	5	18/12/2011	6
	25/01/2012	7	24/01/2012	2	27/01/2012	4	26/01/2012	HR
	07/03/2012	46	05/03/2012	38	08/03/2012	6	08/03/2012	6
TOTAL		**113**		**72**		**31**		**28**

b)



Sampling

The preliminary survey undertook in April 2010 enabled to identify four diptanks with higher seroprevalence rates of RVF. Those diptanks correspond to Ethsa 1, Ethsa 6, Kandalangondi and Gumare (Figure 2). Thus, a sampling campaign of mosquitoes was carried out in the premises four small scale cattle farmers from the area, in close proximity to the crushpens where RVF antibodies were detected. Trapping and preservation of mosquito samples were done by M. Patrick Kgori from the National Veterinary services and by Mrs. Keitumetse Gladys Mangate from the National Veterinary Laboratory.

The sampling extended from April 2011 to March 2012 and followed the method explained in Box 2. During this period, 22 trapping operations were undertaken (6 in each location, Table 2). Due to limited funds and human resources, a daily trapping was not feasible. Most of the trapping were performed during the rainy season (from October to April, considered as favorable season to mosquito development) and very little trapping activity (only one) was undertaken during the dry cold season (between May and September during unfavorable season).

The identifications have been performed by P. Tshikae of the University of Pretoria and Alan Kemp of the National Institute for Communicable Diseases of South Africa. *Culicinae* mosquitoes were identified according to the keys and descriptions of Jupp (1996) and (Edwards 1941). To test the presence of RVFV in mosquitoes, mosquito pools were processed to obtain a supernatants fluid as described by Jupp *et al.* (2000) which was inoculated in infant mice (NHLS Animal Ethics Clearance Certificate No. 124/11), and those mice were tested by RT-PCR. At the time of writing this report, some mosquitoes have not yet been identified, principally *Anopheles*, but entire contents from 67 tubes are still unknown (33 from Kandalangondi collected the 05/03/2012 and 34 from Etsha1 collected the 07/03/2012). The whole trapping of April 2011 has been analysed in order to have an idea of the species present. After this first population screening, we decided to focus the identification effort on the main family: *Culicinae*[4], and we reduced the identification to 5 tubes by trapping night for the largest sites with the largest number of mosquitoes.

Modeling mosquito population dynamics

The model used has been recently developed and described by Cailly *et al.* (2012). Simulation and plotting were performed using Scilab (version 5.4.1), a free and open-source software for numerical computation and graphics (Scilab Entreprises 2012).

Model design

The model takes into account the entire mosquito's life cycle (Figure 3). It is *i)*

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[4] Sub-family of mosquitoes including genera *Culex, Aedes* and *Orthopodomia*

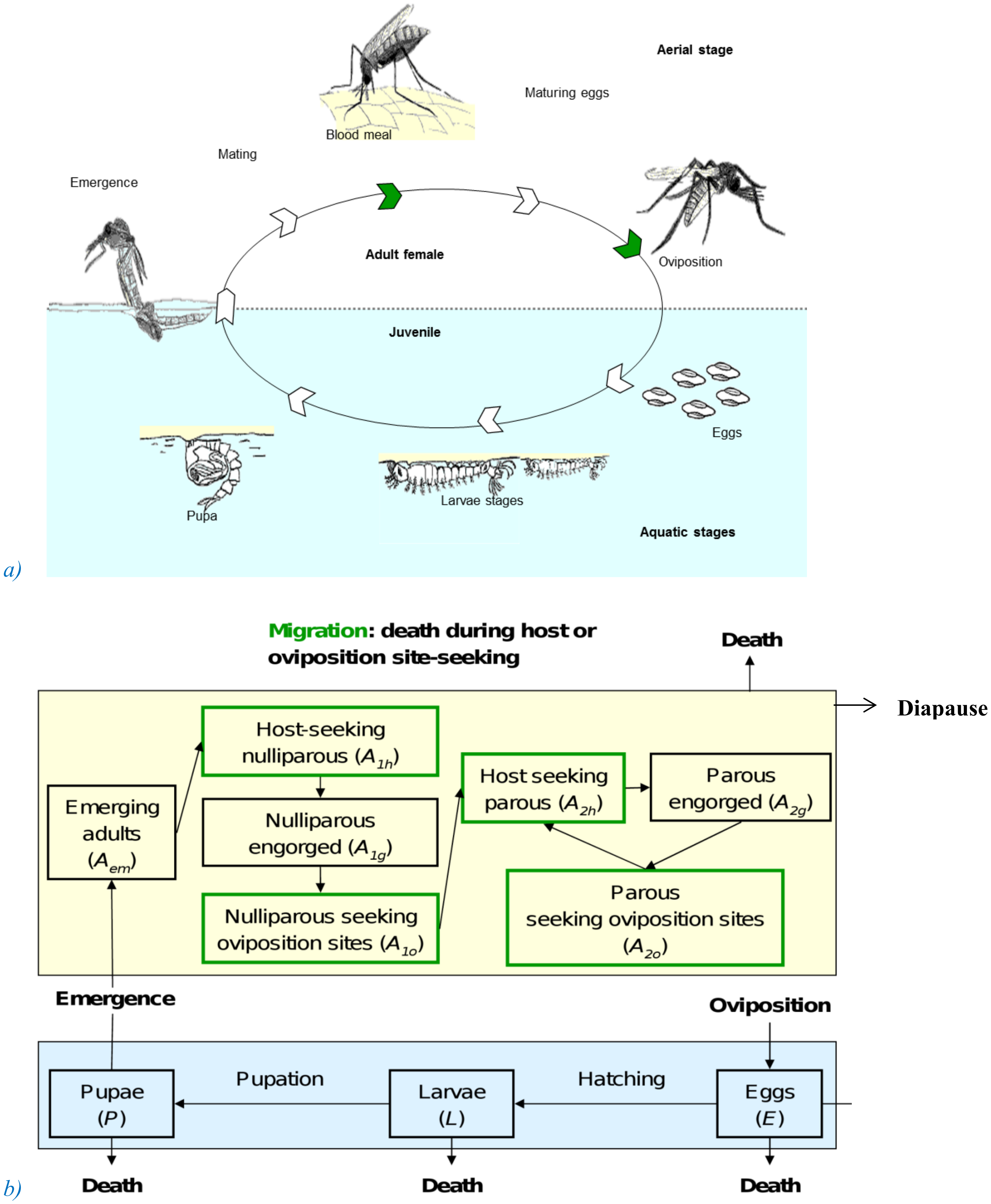

Figure 3 *a)* Mosquito life cycle associated to *b)* the representation of the 10 different stages considered in the model and the events processing at each stage.
(Cailly *et al.* 2012)

mechanistic, i.e. uses an a-priori mathematical description of all processes of mosquito population dynamics; *ii*) deterministic, i.e. represents the average behaviour of the population – such an approach is well adapted for large populations such as those formed by mosquitoes; *iii)* environment-driven; mosquitoes are highly dependent on environmental conditions, such as water presence and temperature; and *iv)* explicitly takes diapause processes into account (favorable and unfavorable season during which processes are different) and therefore it can be run through several consecutive years, the dynamics in year $n + 1$ explicitly depending on the dynamics in year n and on survival rates during the unfavorable seasons.

Ten different stages are considered: 3 aquatic stages (E, eggs; L, larvae; P, pupae), 1 emerging adult stage (A_{em}), 3 nulliparous [5] stages (A_{1h}, A_{1g}, A_{1o}), and 3 parous stages (A_{2h}, A_{2g}, A_{2o}) (Figure 3b). Adults are subdivided regarding their behaviour during the gonotrophic cycle (h, host-seeking; g, transition from engorged to gravid; o, oviposition site seeking). Individual transitions between stages are due to different events such as egg mortality and hatching, larvae mortality, pupation (moult of larvae to pupae), pupa mortality, adult emergence, adult mortality, adult engorgement, egg maturing or oviposition (Figure 3b). Density-dependent mortality is assumed at the larval and egg stages (Clements 1992; Alto *et al.* 2012). The success of adult emergence is considered dependent and negatively correlated to pupae density (Jetten & Takken 1994). Because they do not feed on blood (and therefore cannot be involved in pathogen transmission), adult males are not explicitly considered and are excluded from future computations at emergence by implementing the sex-ratio in the equation defining the transition from pupae to emerging adults.

To take into account the environmental influence and the seasonality of mosquito life cycle, the model is based on two systems of ordinary differential equations (ODE), one for the favourable period, during which mosquitoes are active, and one for the unfavourable period, during which, according to the temperature level and the length of the day, diapause occurs. For *Culex* and *Anopheles* species, for which nulliparous adults are those surviving during the diapause, the ODE systems is detailed in Box 3.

Adaptation of the mosquito population model to the main species of Okavango Delta

When the main species present in our study area were identified, we defined the model parameters using literature and expert opinion. Systematic literature reviews were performed in PubMed, ISI Web of Knowledge and at the library of the University of Pretoria, in order to define the values of model parameters for the most abundant species, using words related to the life cycle of mosquitoes, the name of the species and region in southern Africa. For the same purpose, we contacted various entomologist (A. Kemp, P. Tshikae, S. Niassy, D.

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[5] Nulliparous females are females that never have oviposited/layed.

Box 3. Ordinary differential equation systems

$$\begin{cases} \dot{E} = \gamma_{Ao}\left(\beta_1 A_{1o} + \beta_2 A_{2o}\right) - \left(\mu_E + f_E\right)E \\ \dot{L} = f_E E - \left[m_L\left(1 + L/k_L\right) + f_L\right]L \\ \dot{P} = f_L L - \left[m_P + f_P\right]P \\ \dot{A}_{em} = f_P P \sigma \exp\left[-\mu_{em}\left(1 + P/k_P\right)\right] - \left[z * m_A + (1-z) * \mu_A + z * \gamma_{Aem}\right]A_{em} \\ \dot{A}_{1h} = z * \gamma_{Aem} A_{em} - \left(m_A + m_r + \gamma_{Ah}\right)A_{1h} \\ \dot{A}_{1g} = \gamma_{Ah} A_{1h} - \left(m_A + f_{Ag}\right)A_{1g} \\ \dot{A}_{1o} = f_{Ag} A_{1g} - \left(m_A + m_r + \gamma_{Ao}\right)A_{1o} \\ \dot{A}_{2h} = \gamma_{Ao}\left(A_{1o} + A_{2o}\right) - \left(m_A + m_r + \gamma_{Ah}\right)A_{2h} \\ \dot{A}_{2g} = \gamma_{Ah} A_{2h} - \left(m_A + f_{Ag}\right)A_{2g} \\ \dot{A}_{2o} = f_{Ag} A_{2g} - \left(m_A + m_r + \gamma_{Ao}\right)A_{2o} \end{cases} \quad , with \ z = \begin{cases} 0 & during\ diapause \\ 1 & otherwise \end{cases}$$

Model parameters are in Greek letters. They are constant. For stage *X*, γX is the transition rate to the next stage, βX the egg laying rate and μX the mortality rate. Finally, σ is the sex-ratio at the emergence, and only the female proportion of emerging pupae that survives to emergence is considered in the stage “emerging adults”.

Model functions are in Latin letters. They depend on parameters and are climate-driven functions (*i.e.* functions involving temperature, flooding extent and precipitation varying over time). For stage *X*, *fX* is the transition function to the next stage, *mX* the mortality function and *kX* the environment carrying capacity which limits also the population growth due to density-dependent. The density-dependent survival rate is expressed as a probability. We also assumed an additional adult mortality rate related to the seeking behavior, *mr*, which is applied only on adult stages involving risky movements. This rate includes mortality related to host seeking and oviposition site seeking behaviors.

Poumou) working in the sub-saharan Africa and organized three meetings to discuss the parameters' values.

In order to take into account the specificities of Okavango Delta, the model functions were adapted from Cailly *et al.* (2012) either by functions already described in the literature or by functions built from hypotheses about known ecological features. These functions are specific to the main *Culicinae* species trapped during the mosquito sampling activities.

We then tested and compared 4 different possible scenarios: Is the population dynamics describable by taking temperature as the unique input *(Scenario 1)*? Is the description better if we considered rainfall (*Scenario 2)* or flooding extents *(Scenario 3)* as a second input? Or is the combined use of three environmental factors required to model the mosquito population dynamics in this study area where we don't know many about the breeding site evolution *(Scenario 4)*? In order to test these different *scenarii*, functions were modified according to the hypothesis tested (rainfall influence and/or flooding influence).

Initial conditions and model outputs

Each run was initiated during the unfavorable season, when mosquito numbers are supposed to be the lowest. According to the seasonality of our study area, this date corresponds with the 1^{st} of July. Thus, the model was parameterised with an initial population of 10^7 emerging adults for *Culex* species.

The model gave us the simulated daily abundance at each stage. Then we determined 5 aggregated outputs: *1)* the abundance peak of female by year; *2)* the date of the abundance peak by year; *3)* the mean date of emergence by year; *4)* the parity rate, which is the proportion of parous females by day; and *5)* the attack rate, which represents the proportion of host-seeking females by day. The abundance peak and date of emergence enabled us to characterize the mosquito dynamics while the parity rate provided us with an idea about the proportion of mosquitoes having already taken a first blood meal, therefore potentially infected, and the attack rate allowed accessing to the proportion of females in search of a blood meal.

Model validation.

To validate the model, we compared the model outputs of simulated host-seeking adult abundance ($A_{1h}+A_{2h}$) for the years 2011-2012 with the field data. The degree of association between observed and simulated data at the time of trapping was assessed for each collection site and globally by calculating the Bravais–Pearson correlation coefficient. Tests for correlation were computed using R (version 2.15.1; R Development Core Team 2011), a free open-source software for statistical computing and graphics.

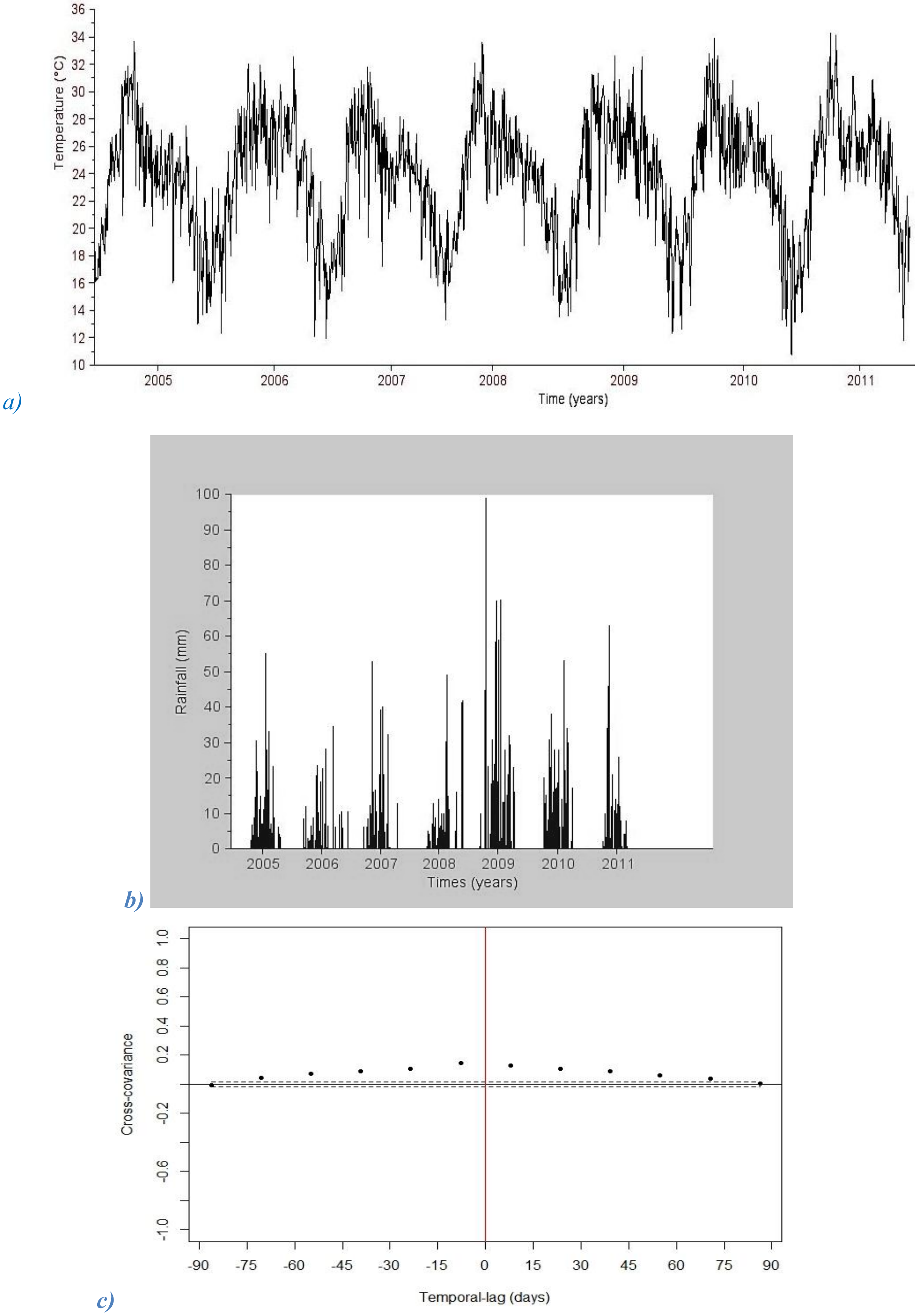


Figure 4 *a)* Daily mean temperature over time (°C); *b)* Daily rainfall over time (mm); *c)* Results of the crossed covariance analysis between rainfall estimate at Maun and on the study area

Sensitivity analysis. We used the ANOVA-based global sensitivity analysis described by Saltelli *et al.,* (2000), to assess the dependence of the model to the different factors, but also to understand the behaviour of the model. System dynamics models are generally insensitive to many parameters changes and the structure of the system, rather than the parameter values, has the higher impact on the behaviour of the model. Thus, the method tests the influence of the inputs variation on the aggregated outputs normally distributed. This analysis enables *i)* to determine the key parameters involved in the biological dynamic system, and *ii)* to adjust the functions together with the model.

The ANOVA is a parametric analysis of variance that reduces the requirements and defines the best predicting model with the lower number of parameters, while these last parameters are the most sensitive. Simulation and plotting were computed using R (version 2.15.1; R Development Core Team 2011). Simulations enabled to estimate the contribution of each single parameter to the variance because it is not feasible to calculate the impact of parameters interactions for a complex model in practice due to computational limitations.

The minimum variance criterion was defined in order to achieve 90% of the variance. Thus, only the main factors or interactions accounting for these 90% of the output variance were retained in the model. These contributions were computed as the ratio of sum of squares related to the factor or the interaction on the total sum of squares of the model for output.

RESULTS

Meteorological and environmental data

Rainfall and temperature

Annual average temperatures vary between 22.9°C in 2006 and 24.4°C in 2010 and 2012, and daily temperatures vary between 10°C and 34°C (Figure 4a). The total number of days by year with precipitation of rain varies between 43 and 80 and the daily precipitations vary between 0 and 99.6 mm (Figure 4b).

Comparison between rainfall estimates from TRMM satellites did not showed a temporal discrepancy between rainfall in Maun and in our study area, but these two rainfall regimes appear very different (Figure 4c), moreover rainfall in Maun estimated from TRMM imagery and measured at the meteorological station are very different. Therefore, we decided to use precipitation measures from the station of Maun.

Mapping flooding extent

According to the scale used, the flooding dynamics recorded is more or less strong. Indeed, at the site scale the proportion of flooding area is null during the most part the winter months whereas at the scale of the Okavango, even during the winter months when the

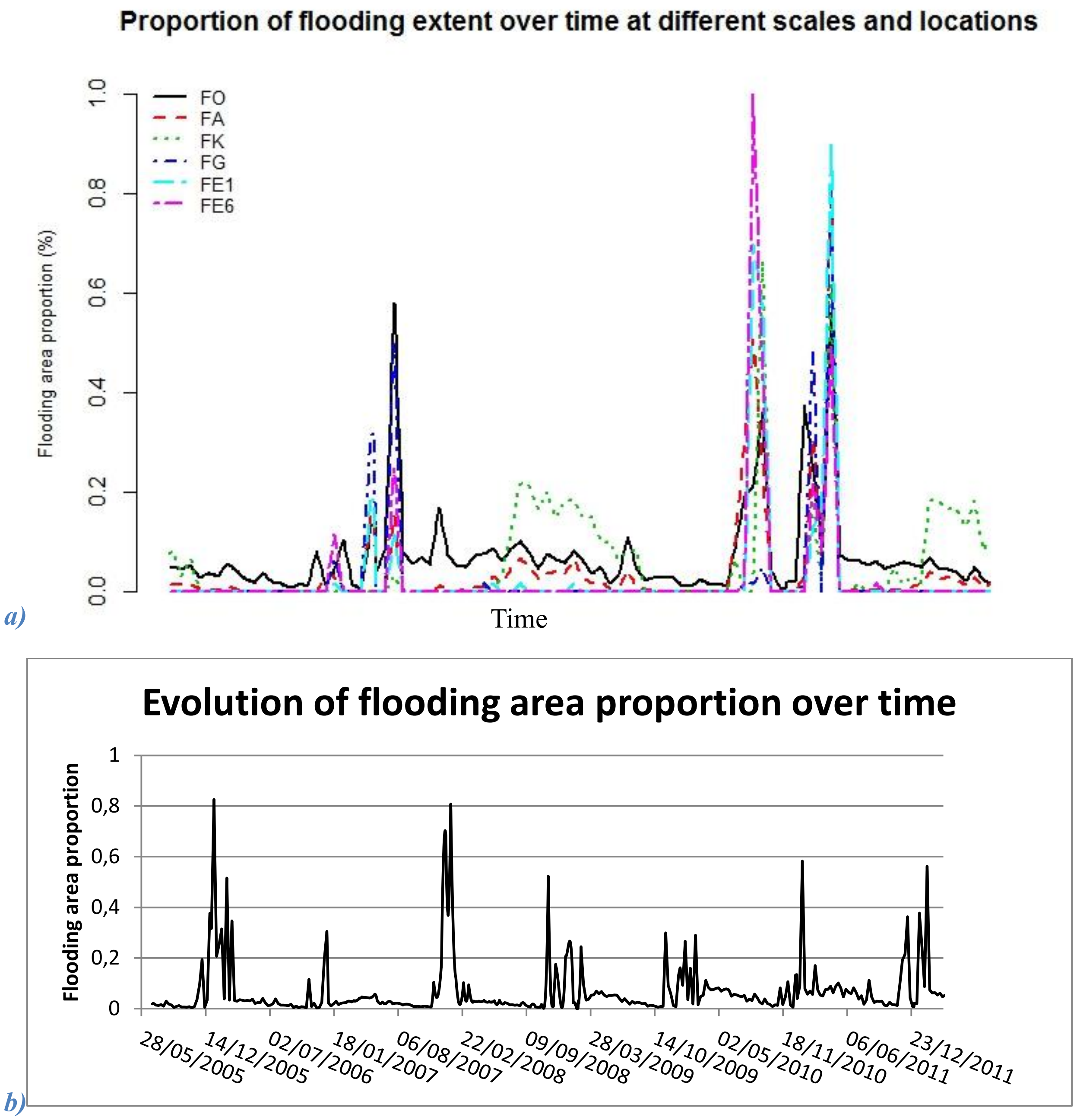


Figure 5 ***a)*** **Variation over time (from July 2010 to July 2012) of proportion of flooding area estimated at different scales: Okavango Delta (FO), Study area (FA), and for each site: Kandalangondi (FK), Gumare (FG), Etsha1 (FE1) and Etsha6 (FE6).** ***b)*** **Evolution on flooding at the scale of the entire Okavango Delta from 2005 to 2012.**

flooding proportion is lower than in summer, some water extents are still reported (Figure 5a). At the scale of the entire Delta, the proportion of flooding area presents a strong seasonal variation, reaching 80 % of the total surface between the summer months of December and February, and less than 1% during winter (Figure 5b).

Sampling

The number of tubes containing mosquitoes specimens collected during each trapping night illustrates the global mosquito dynamics (Table 2), with very low trapping results between September and December. According to the temperature, we assumed that the population decreases from the end of June, and increases again at the end of September.

Our trapping records presented two different types of population dynamics. Indeed, while the trapping from Kandalangondi and Etsha1 showed a distinct abundance variation over time, those from Gumare and Etsha6 presented a limited variation.

At the time of writing this report, 19,283 mosquitoes from 39 different species were identified (Table 4). The three main species representing respectively 48%, 27% and 6% of the total number of identified mosquitoes, are *Culex (Culex) pipiens* (*Cx. Pipiens*) with 9,162 individual, *Mansonia (Mansoniodes) uniformis* with 5,138 specimens and *Mansonia (Mansonioides) africana* with 1,105 individual. All these species are able to transmit the RVFV (Prehaud & Bouloy 1997; Modou 2012). It should be noticed that a very low number of *Aedes* was detected (4 species including 87 individuals) mostly represented by *A. mcintoshi* and *A. unidentatus*.

While *Cx. pipiens* mean abundance distribution over time is relatively well marked with 3806 mosquitoes caught by site in April 2010, 4 in September 2011, 6 in November 2011, 388 in December 2011, 122 in January 2012 and 4836 in mars 2012, the two other species remain relatively constant during the whole trapping period (Figure 6). Therefore, we decided to perform the model only on *Cx. pipiens*. Moreover, the main arthropod vectors of RVF are mosquitoes from the genera *Aedes* and *Culex* (Métras *et al.* 2011).

Definition of the parameters and functions of the model for *Cx. pipiens*

⇨ Model parameters

Cx. pipiens is widely distributed in the world (Europa, Africa, Asia, America and Australia) except in extremely cold areas and very variable morphologically and biologically in different geographical region (Barr 1967; Vinogradova 2000; Linthicum *et al.* 2007). Hence, defining ecological parameters of this species in our very local area turns out to be arduous. We have been able to assess to 20 parameters (Table 5).

⇨ Model functions

Table 4 Summary of identifications.
The two main species appear in bold and the main species in red. *Aedes* genus in grey.

Species	**Total**	**%**
***Aedes (aed.) argenteopunctatus* ♀**	**1**	**0%**
***Aedes (Diceromyia) adersi* ♀**	**42**	**0%**
***Aedes (Neomelaniconion) mcintoshi* ♀**	**45**	**0%**
***Aedes (Neomelaniconion) unidentatus* ♀**	**3**	**0%**
Aedes spp. unidentifiable	**1**	**0%**
Anopheles (Anopheles) caliginosus ♀	5	0%
Anopheles (Anopheles) implexus ♀	3	0%
Anopheles (Anopheles) tenebrosus ♀	19	0%
Anopheles (Anopheles) ziemanni namibiensis ♀	8	0%
Anopheles (Cellia) arabiensis (gambiae complex) ♀	7	0%
Anopheles (Cellia) argenteolobatus ♀	74	0%
Anopheles (Cellia) distinctus (Newstead & Carter, 1911) ♀	1	0%
Anopheles (Cellia) pharoensis ♀	185	1%
Anopheles (Cellia) pretoriensis ♀	3	0%
Anopheles (Cellia) squamosus cydippus ♀	298	1%
Anopheles spp. unidentifiable ♀	836	4%
Coquillettidia (Coquillettidia) flavocincta ♀	1	0%
Coquillettidia (Coquillettidia) fuscopennata ♀	265	1%
Coquillettidia (Coquillettidia) microannulata ♀	10	0%
Culex (Culex) neavei ♀	230	1%
Culex (Culex) pipiens	**11773**	**54%**
Culex (Culex) poicilipes ♀	85	0%
Culex (Culex) quinquefasciatus ♀	5	0%
Culex (Culex) striatipes ♀	1	0%
Culex (Culex) univittatus ♀	54	0%
Culex spp. unidentifiable ♀	1680	8%
Culex (Eumelanomyia) horridus	25	0%
Mansonia (Mansonioides) africana	**1106**	**5%**
Mansonia (Mansonioides) uniformis	**5053**	**23%**
Coquillettidia (Coquillettidia) chrysosoma ♀	3	0%
Anopheles (Cellia) kingi??? ♀	1	0%
Anopheles tchekedii ♀	1	0%
Anopheles theileri ♀	6	0%
Anopheles (Cellia) garnhami	0	0%
Aedeomyia africana	1	0%
Aedeomyia furfurea	1	0%
Chironomidae	28	0%
Culicoides spp.	5	0%
Musca spp.	6	0%
Simulium spp.	8	0%
Apidae	4	0%
Tupilidae	2	0%
TOTAL	21,885	100%

Cx. pipiens females lay their eggs only upon standing water, and the latter are not drying resistant. In cool temperate areas, *C. pipiens* hibernate as nulliparous, inseminated females that enter a facultative reproductive diapause (Mitchell 1983). The adult diapause in females is induced by shorter day length and the low temperature experienced during larval and pupal development (Spielman 2001). Following Cailly *et al.* (2012), we assumed that transitions between successive stages (f_X) are all temperature-driven for the aquatic stages, whereas only the duration of egg maturation (transition from engorged to gravid, f_{Ag}) is climate-driven in adults (Jetten and Takken, 1994). Moreover, we assumed that the egg mortality is not related to the temperature, while other mortalities are (Jetten and Takken, 1994). However, we integrated a relationship between adult mortality related to seeking behavior (m_r) and the climate, considering that m_r is inversely correlated with the water availability. We also considered that water availability impacts the environment's carrying capacity of aquatic stages (k_L and k_P), increasing the number of breeding sites available for *Culex pipiens*.

Thus, we defined the functions presented in Table 6.

These functions take into account daily temperature (T) and different rates of water presence (w) including either 8 days cumulated rainfall in millimetres divided by 100 (*scenario 2*), or the flooding area proportion (*scenario 3*), or the mean of both (*scenario 4*).

Model parameters are constant and described in Table 4.

We also defined the beginning of the favourable period as a sequence of 5 consecutive days with a mean temperature above or equal to 21°C and the ends after the last sequence of four consecutive days in the year with mean temperature above or equal to 18°C.

Simulation and validation

Simulations were computed for a seven-year period (2005-2012) for *Cx. pipiens*, but the validation test was only performed during the two last years (2011-2012). It needs to be emphasized that considering the low number of trapping sessions, the validation of the temporal dynamics of *Cx pipiens,* couldn't be completely achieve but the model is still informative about the seasonal dynamics and different influences on this dynamic.

Scenario n°1 Temperature, single-handedly, has a significant effect on mosquito dynamics. Simulations under the hypothesis of temperature as the only driver of the mosquito dynamics provide the best correlated prediction with the global mosquito population dynamics (when trappings from the four sites are aggregated). The Pearson-Bravais coefficient (r) is 0.89, thus the coefficient of determination (r^2) is 0.79 (Table 7, Figure 7). This statistic provides a measure of the model ability to replicate the field data, as a proportion of field data explained by the model.

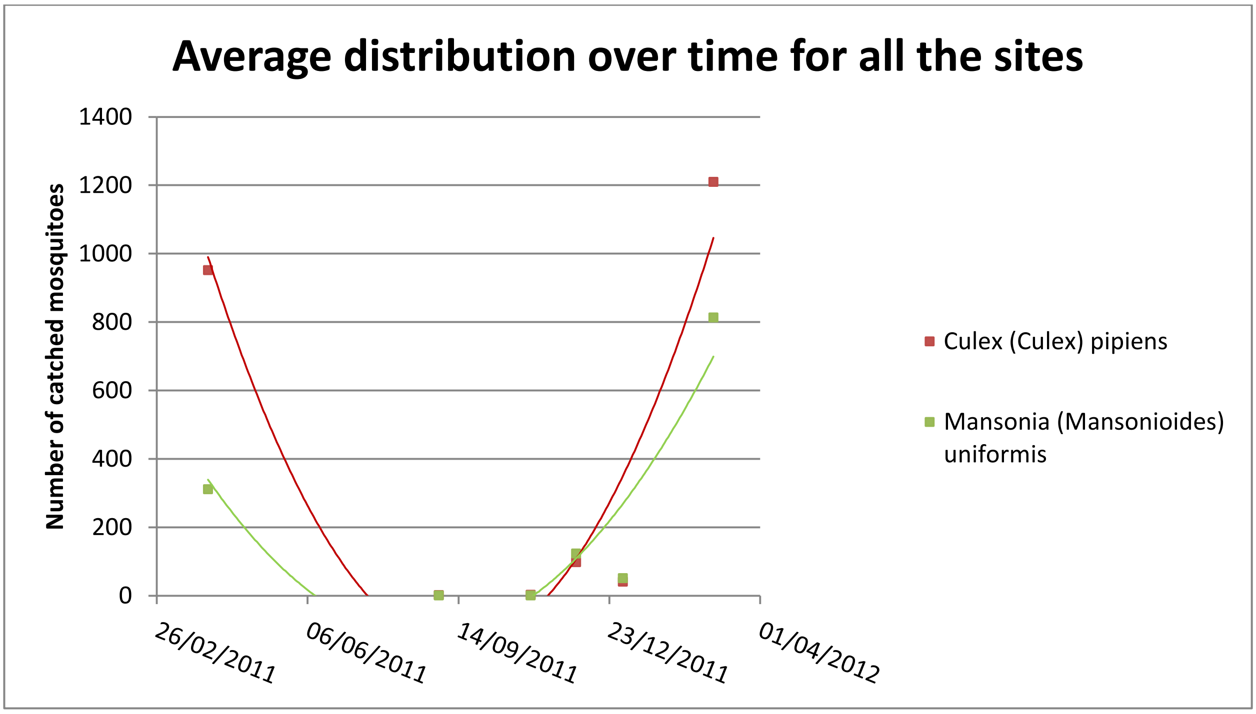


Figure 6 On the four sites average distributions of the two main species over time.

The tests of comparison applied to each site separately showed a better correlation for both site with most abundant trapping records: Etsha 1 ($r^2=0.76$) and Kandalangondi ($r^2=0.61$), but the model failed to predict the dynamic of *Cx. pipiens* with accuracy in the two remaining sites with low mosquito abundances: Gumare ($r^2=0.11$) and Etsha 6 ($r^2=0.19$) (Table 7).

Scenario n°2 Both temperature and rainfall are involved in mosquito dynamics. Inversely, simulations using rainfall estimation from satellite imagery as a second driver of the mosquito dynamics in addition to temperature are lightly the less correlated with the mean mosquito population dynamics on the four sites. The Pearson-Bravais coefficient is 0.63, thus the coefficient of determination is 0.40 (Table 7, Figure 7).

The Pearson's test applied to each site separately showed the lowest correlation for the two sites with most abundant trapping records: Etsha1 ($r^2=0.27$) and Kandalangondi ($r^2=26$), although the two other sites were better fitted, this scenario provides the best correlation for Gumare ($r^2=69$) and Etsha6 ($r^2=86$) (Table 7).

However, when we used rainfall measures from the meteorological station of Maun, even if the model produced closer prediction to the global dynamics ($r^2=0.80$), it seems answer differently according to the four site. Indeed, we found that the simulated values were better correlated with the trapping results from Etsha1 (37%) and Kandalangondi (33%), while, prediction for Gumare and Etsha6 gave lower correlations, with respectively 36% and 44% of correlation (Table 7).

Scenario n°3 Both temperature and flooding surface proportion are involved in mosquito dynamics. Simulations using flooding area proportion estimated in the Okavango Delta (see identification of the suitable scale [Delta, smallest area including the 4 sites, site-scale] for the estimation in Box 4.) as the second driver of the mosquito dynamics, in addition to temperature, can be quite well fitted to the field data or, inversely, very far from the field records according to the dataset of field data that we compared. Indeed, while the model always failed to predict the abundance evolution appearing in the data from Gumare and Etsha6 (r^2 are respectively 6% and 12%), the simulated values are correlated to the field data from Etsha1 and Kandalangondi at respectively 79% and 67%. Pearson's coefficient between predicted values and global field data gave a high correlation value ($r^2=0.81$) (Table 7, Figure 7).

Scenario n°4 All three elements, temperature, rainfall and flooding, are required to explain

Table 5 Description of the different parameters used in the model.
"To our best knowledge": estimation from others species or areas
"Personal communication": estimation from specialists

Parameter	Definition	Value	Reference
β_1	Number of eggs laid by ovipositing nulliparous females (per female)	225	Marshall and Staley, 1935 Al-Doghairi *et al.* 2004
β_2	Number of eggs laid by ovipositing parous females (per female)	114.33	MacGregor 1932 Mattingly *et al.* 1951 Jobling, 2009 Galal, 2010 Pratt and Moore, 1993
κ_{Lmin} κ_{Lmax}	Standard environment carrying capacity for larvae (larvae ha^{-1})	$8x10^6$ $1x10^8$	To our best knowledge
κ_{Pmin} κ_{Pmax}	Standard environment carrying capacity for pupae (pupae ha^{-1})	$8x10^6$ $1x10^7$	To our best knowledge
σ	Sex-ratio at the emergence	0.5	Alto *et al.* 2012
μ_E	Egg mortality rate (day^{-1})	0.004	Al-Doghairi *et al.* 2004 Galal, 2010
μ_L	Minimum larva mortality rate (day^{-1})	0.026	Al-Doghairi *et al,* 2004 Vasuki, 1990
μ_P	Minimum pupa mortality rate (day^{-1})	0.074	Vasuki, 1990
μ_{em}	Mortality rate during adult emergence (day^{-1})	0.218	Zequi and Lopes, 2012
μ_A	Minimum adult mortality rate (day^{-1})	0.1	Zequi and Lopes, 2012
μ_{rmin} μ_{rmax}	Adult mortality rate related to seeking behavior (day^{-1})	0.18 0.59	Lutambi *et al,* 2013
T_E	Minimal temperature needed for egg development (°C)	18	Personal communication
TDD_E	Total number of degree-day necessary for egg development (°C)	70	To our best knowledge
γ_{Aem}	Development rate of emerging adults (day^{-1})	0.25	To our best knowledge
γ_{Ah}	Transition rate from host-seeking to engorged adults (day^{-1})	0.88	Faraj *et al.* 2006
γ_{Ao}	Transition rate from engorged adult to oviposition site-seeking adults (day^{-1})	0.25	Faraj *et al.* 2006 Subra, 1972
T_{Ag}	Minimal temperature needed for egg maturation (°C)	18	Personal communication
TDD_{Ag}	Total number of degree-days necessary for egg maturation (°C)	105	To our best knowledge

mosquito dynamics. The last scenario involved flooding area proportion on the Okavango Delta, rainfall and temperature as three significant drivers of the mosquito dynamics. When we used rainfall estimation from satellite, Pearson's coefficient between predicted values and global field data is 0.80 (r^2=0.64) (Table 7, Figure 7).

Considering each site separately, the correlation between predictions and field data were not very significant: Etsha1 (r^2=0.46), Kandalangondi (r^2=0.39), Gumare (r^2=0.50) and Etsha6 (r^2=0.64) (Table 7).

However, the best correlation was obtained when we used rainfall records from the meteorological station of Maun and our field data from Etsha1 (r^2=48). Pearson's test applied independently to the field data from the three other site computed less significant coefficients of determination with respectively r^2=39%, r^2=25% and r^2=34% for Kandalangondi, Gumare and Etsha6 (Table 7).

Sensitivity analysis

A first sensitivity analysis has been computed during the model adaptation for the scenario 2 (before adding the variation in seeking adult mortality related to the water presence, before using flooding extents and before defining the favourable period extent in function of the temperature). This sensitivity analysis identifies *a)* the end of the unfavourable period, *b)* the sex ratio at the emergence and *c)* the adult mortality rate related to seeking behaviour as the three most sensitive parameters to the outputs of the model (Figure 8). Computations for the identification of the key parameters contributing to aggregated outputs variance for the scenario providing the highest correlation coefficients (scenario 1) identified *a)* the gravid adult development rate, *b)* the adult mortality rates, *c)* the sex-ratio at the emergence and *d)* the end of the unfavourable period as the four most sensitive parameters to the aggregated outputs of the model: the abundance peak value, the parity rate and the attack rate (Figure 9).

DISCUSSION

Trapping results

Our sampling presents a strong spatial variability. Indeed, while an important number of mosquitoes (>21,800) were collected in the locations of Etsha1 and Kandalangondi, a lower number of mosquitoes (<1,500) were trapped in Etsha6 and Gumare. This important difference could be due *i)* to a lower equilibrium density of the *Cx. pipiens* populations in Gumare and Etsha6 compared to Kandalangondi and Etsha1 (spatial variability), or inversely *ii)* to the fact that the equilibrium density is not yet reached. This second hypothesis is improbable because no substantial ecological disturbance has been reported in the Delta in the

Table 6 Description of the different functions used in the model.
With T: the daily temperature (°C); and
w: rates of water presence including either 8 days cumulated rainfall (mm) divided by 100 or the flooding area proportion, or the mean of both (%).

Description	**Function**
Egg hatching function (rate of egg reaching the following stage)	$f_E(t) = (T(t) - T_E) / TDD_E$
Larvae development function (rate of larvae turning in pupae)	$f_L(t) = (\rho_1 * (\exp[\rho_2(T(t) - 10)] - \exp[\rho_2(35 - 10) - ((35 - T(t)) / \rho_3)])) / 4$
Pupae development function (rate of pupae emerging)	$f_P(t) = \rho_1 * (\exp[\rho_2(T(t) - 10)] - \exp[\rho_2(35 - 10) - ((35 - T(t)) / \rho_3)])$
Rate of adults becoming gravid	$f_{Ag}(t) = (T(t) - T_{Ag}) / TDD_{Ag}$
Larvae mortality rate	$m_L(t) = \exp(-T(t)/2) + \mu_L$
Pupae mortality rate	$m_P(t) = \exp(-T(t)/2) + \mu_P$
Daily adult mortality rate	$m_A(t) = \delta 1 + \delta 2 * T(t) + \delta 3 * (T(t)^2)$
Additional adult mortality rate related to the seeking behavior	$m_r(t) = \mu_{r\max} - w(t) * (\mu_{r\max} - \mu_{r\min})$
Daily environment carrying capacity for larvae	$k_L(t) = \kappa_{L\min} + w(t) * (\kappa_{L\max} - \kappa_{L\min})$
Daily environment carrying capacity for pupae	$k_P(t) = \kappa_{P\min} + w(t) * (\kappa_{P\max} - \kappa_{P\min})$

recent years, and the ecological balance in the mosquito population in this area should have been already established. However, the stable equilibrium density level depends on different parameters. In our case, the differences in mosquito density could be due to the distance between the trapping sites and the edge from the Delta. Indeed, Kandalangondi and Etsha1 being closer to the Delta (Figure 2), they could benefit from a higher or more constant water availability than Gumare and Etsha6 (Figure 5a). This stagnant water availability being essential for the laying of *Cx. pipiens,* this parameter could contribute to explain the lower numbers of that species trapped in Gumare and Etsha6 compared to the two other trapping sites involving effects of density dependence at different levels (Figure 10). Another possible explanation could be that Gumare and Etsha6 provide more habitats favourable to mosquito predators (Onyeka 1983; Lounibos *et al.* 1997). Therefore, they could concentrate a higher density of mosquito predators which, according to the extensions from Lotka-Volterra competition models (Gotelli 1995), could involve stronger predation or competition pressures. This last point could be induced by others biological interactions that may act in a density dependant manner, such as parasitism, intraspecific resource competition, intraspecific interference and other social interactions (Juliano 2007).

Another important observation relative to the trapping results is the overabundance of *Cx. pipiens* (>11,700) compared to the other species, and especially, compared to the minimal number of *Aedes* (<100) detected. Indeed, *Aedes* is known like the main reservoir and the primary vector of RVF, moreover its development involves flooding and even if the environment did not exactly correspond to the initial ecological niche, the genre of *Aedes* is known for its high capacity of adaptability (Urbanski *et al.* 2010, 2012) common in invasive species. Thus, we would have expected a higher presence of *Aedes* specimens in our catches. The overabundance of *Cx. pipiens* and almost absence of *Aedes* can involve different processes. As above-mentioned, these populations can be regulated differently, for example *Aedes*'s breeding sites could be exposed to competition with other species or victims of specialised predators or pathogens. But, according to its status of invasive species, we have to suggest a potential sampling effect. Considering that the trapping method has been proven efficient to catch *Aedes* in other locations (Alan Kemp personal communication), the lack of field data relative to the winter months between April and September, when temperature is relatively low, could have hidden a higher presence of some species such as *Aedes*. Indeed, it's known that some species are influenced by different factors and can increase during certain periods taking advantage of the absence of competition. Otherwise, *Aedes* species hatch only one every 14 days, and a single capture per month would have failed to capture at the points in time where there were more abundant. Finally, another explanation could be that

Table 7 Pearson's coefficient of determination (r^2) between simulated values from each scenarii and field data.

Simulation using rainfall estimation from satellite imagery

Scenario	Percentage of correlation using the aggregated field data	Percentage of correlation using the field data by site			
		Etsha1	Kandalangondi	Gumare	Etsha6
1	79	76	61	11	19
2	40	27	26	69	86
3	81	79	67	6	12
4	64	46	39	50	64

Simulation of scenarii 2 and 4 using rainfall records from the meteorological station of Maun

Scenario	Percentage of correlation using the aggregated field data	Percentage of correlation using the field data by site			
		Etsha1	Kandalangondi	Gumare	Etsha6
2	80	37	33	36	44
4	85	48	39	25	34

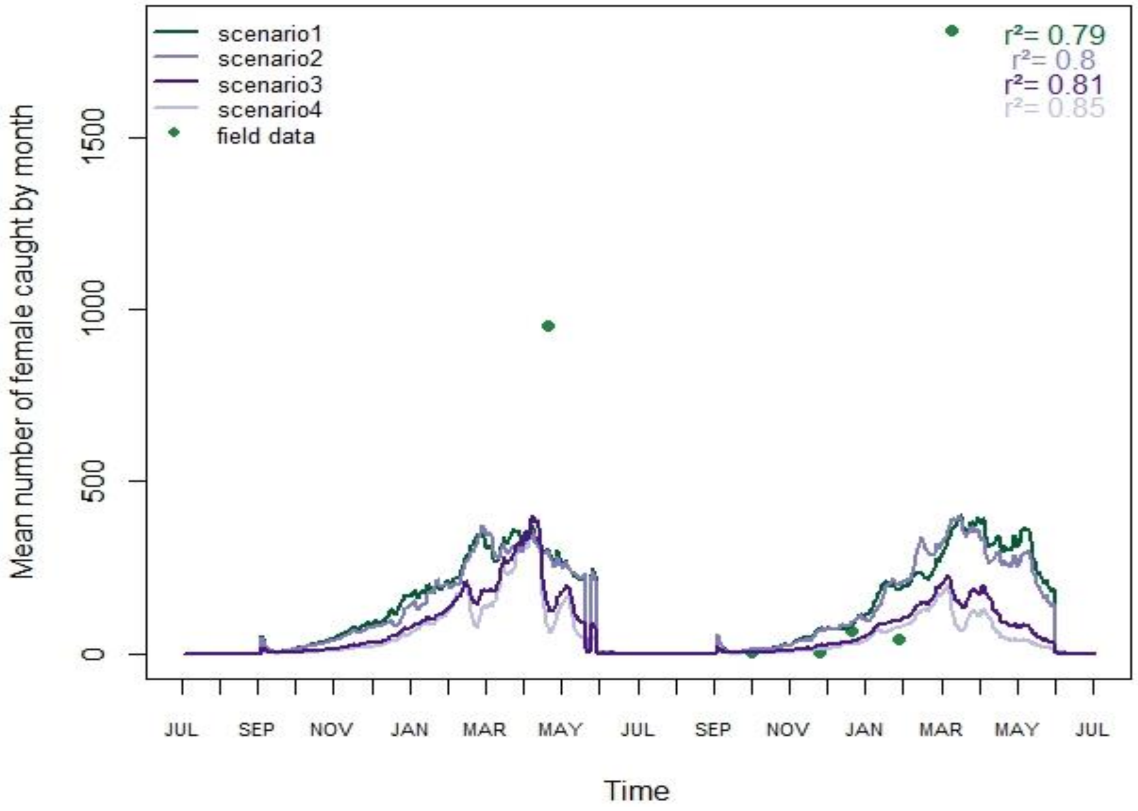


Figure 7 Comparison of the different values predicted under each scenario Green points represent the mean number of *Cx pipiens* caught by trapping activity

the habitat of the Delta, with permanent water all year round is too high in humidity and consequently not favorable to *Aedes* species which prefer hatching in dry environments, their life cycle including an event of desiccation of the eggs. However, if the quasi-absence of *Aedes* specimens is confirmed, it can explain the absence of outbreaks reported in this area. Indeed, *Aedes spp*. are able to transmit RVFV vertically/transovarially, thus they are responsible for the maintenance of the virus during the interepidemic period in infected eggs (Manore & Beechler 2013). Therefore, a low presence of *Aedes* could be a possible explanation for the absence of observed or reported outbreaks in this region.

Model adaptability

As far as we know, it's the first time that the population dynamics of *Cx. pipiens* in a semi-arid environment, have been modelled using a mechanistic approach. The model, driven by three environmental variables – temperature, rainfall and flooding extents –, predicted quite accurately the entomological field data qualitative variation of host-seeking adults over one year period, for the trapping areas where catches were more consistent (Etsha1 and Kandalangondi).

Results from the model suggest that the underlying assumption on the main drivers of mosquito dynamics in this region (i.e., a significant influence of both rainfall and flooding on *Culex,* to the constant water availability) seems correct for two sites (Gumare and Etsha6, the most distant sites from the edge from the Delta) and incorrect for the two others. Indeed, the best fitted estimated values have been produced using the scenarii 1 and 3 involving temperature and flooding extents for Etsha1 and Kandalangondi, and using the scenarii 2 and 4 involving temperature, rainfall and flooding extents for Gumare and Etsha6. However, a complementary sampling over several years and more frequently is required to evaluate the real capacity of the model in predicting the dynamics of *Cx. pipiens* populations of following years using only those three inputs and therefore confirm the importance of these environmental factors. Nevertheless, despite the low number of catching episodes, the fairly good prediction on the mosquito dynamics in Kandalangondi and Etsha1 produced by the model with only the above mentioned environmental inputs, is promising.

Mosquito population dynamics is driven by environmental conditions (Ahumada *et al.* 2004; Schaeffer *et al.* 2008). Predicting mosquito abundances would be helpful in order to focus on nuisance or vector-borne disease control programs. The relationship between meteorological parameters and mosquito densities could be established by statistical (Shone et al., 2006), mechanistic like in the present study (Shaman *et al.* 2002; Schaeffer *et al.* 2008; Cailly *et al.* 2012) or mixed (Bicout & Sabatier 2004) approaches. It is already very

Box 4. Identification of the suitable scale for the estimation of the flooding surface proportion

The correlation tests indicated an absence of correlation between the entomological field data from one site and the predicted value obtained from the flooding area proportion computed at the scale of this site. The best correlation was observed when using the scale of the entire Okavango Delta (Table below).

Pearson's coefficient of determination (r^2) between values simulated by *scenarii* involving flooding measured at different scale and field data.

Simulation using rainfall estimation from satellite imagery

Scenario	Scale used for the flooding proportion acquisition	Percentage of correlation using the aggregated field data	Percentage of correlation using the field data by site			
			Etsha1	Kandalangondi	Gumare	Etsha6
3	Okavango Delta	81	79	67	6	12
3	Study Area	75	76	70	3	9
3	Site		88	82	5	4
4	Okavango Delta	64	46	39	50	64
4	Study Area	65	46	39	51	64
4	Site		46	39	51	64

Simulation of scenarii 2 and 4 using rainfall records from the meteorological station of Maun

Scenario	Scale used for the flooding proportion acquisition	Percentage of correlation using the aggregated field data	Percentage of correlation using the field data by site			
			Etsha1	Kandalangondi	Gumare	Etsha6
4	Okavango Delta	85	48	39	25	34
4	Study Area	85	49	40	23	32
4	Site		49	41	23	31

interesting to see that the population dynamics of *Cx. pipiens* can be easily reproduced from a simple model using only meteorological and environmental data (temperature, rainfall and flooding extents) as inputs.

The model used in this study has actually been implemented so far, in three different and very diverse ecological contexts: *i)* In the French Camargue region to analyse *Anopheles*, *Culex* and *Aedes* mosquito population dynamics in a temperate wetland (Ezanno *et al.* 2012; Cailly *et al.* 2012); *ii)* in the French coastal region of Cote d'Azur to study *Aedes* mosquito population dynamics in an urban area (Tran *et al.* 2013); and *iii)* in this case, to describe *Cx. pipiens* population dynamics in a semi-arid environment at the interface between a wetland and a dryland. The model was able to simulate the seasonal variations in mosquito abundance for European and African mosquito species in three different types of environment related to three different types of environmental influences.

As mentioned earlier, modelling is a valuable tool to understand biological systems. It enables to predict and evaluate evolution of different *scenarii*. In some circumstances, it is also useful to identify some knowledge gaps. In our case, the model, built from theoretical and experimental knowledge, informed us about the effective relationships between *Cx. pipiens'*s life cycle and the environmental variations in the Okavango Delta.

Environmental variables influence *Cx. pipiens* population dynamics

Both, permanent water due to the Delta presence and seasonal regime of rainfall, influence the population dynamics of *Cx. pipiens*. We made the hypotheses that these factors influence *i)* the environmental carrying capacity for both larvae and pupae, and *ii)* the adult mortality rate related to seeking behaviour. Indeed, in the case of *Cx. pipiens* females which lay their eggs in standing water, such as the edge of the Delta or the puddle on the ground formed by rainfall, the adult mortality rate related to oviposition site seeking behaviour should be inversely correlated to the water availability. According to the sites with most abundant trapping records (Etsha1 and Kandalangondi), our model seems to confirm these hypotheses and suggests that due to the Delta presence, the abundance variation of *Cx. pipiens* is mostly lead by temperature and not by the variation in water availability over time. Nevertheless, *i)* according to the comparison between scenario 1 (r^2=76% for Etsha1 and r^2=61% for Kandalangondi) and scenario 3 (r^2=79% for Etsha1 and r^2=67% for Kandalangondi), the model did not allow to reject the effect of the regime of flooding, and *ii)* according to the results provide comparing predicted values to the field data from Gumare and Etsha6, the water variations could locally have an important impact on the abundance variation of the mosquito populations.

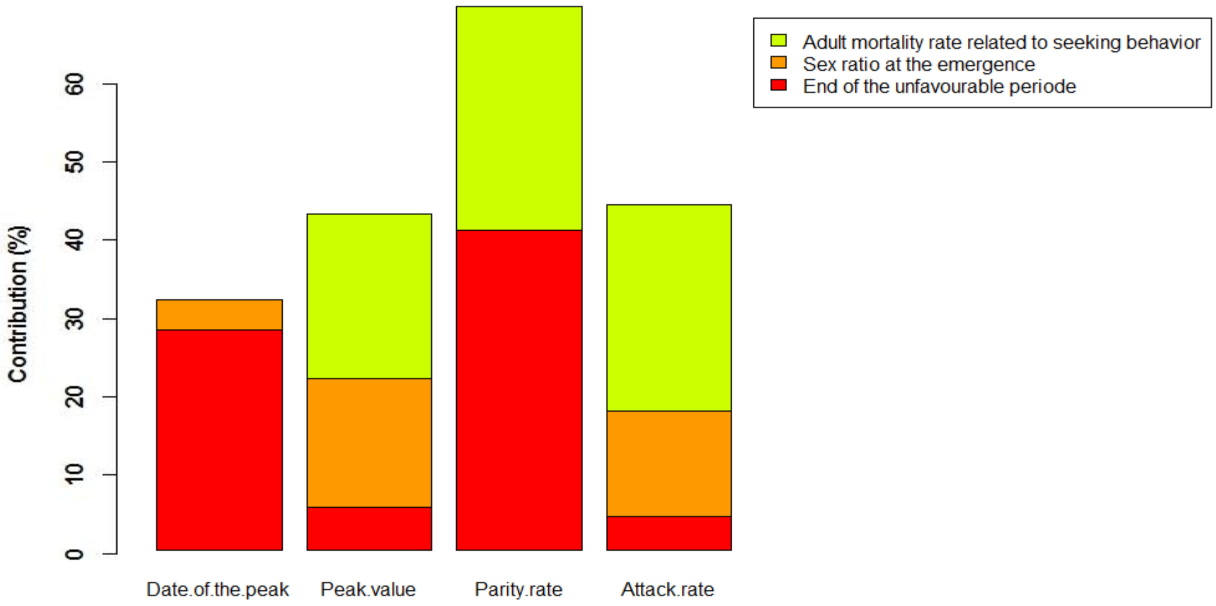


Figure 8 Key parameters contributing to aggregated outputs' variance under the *scenario 2* (preliminary results obtained before modifying the seeking adult mortality function related to the water presence).

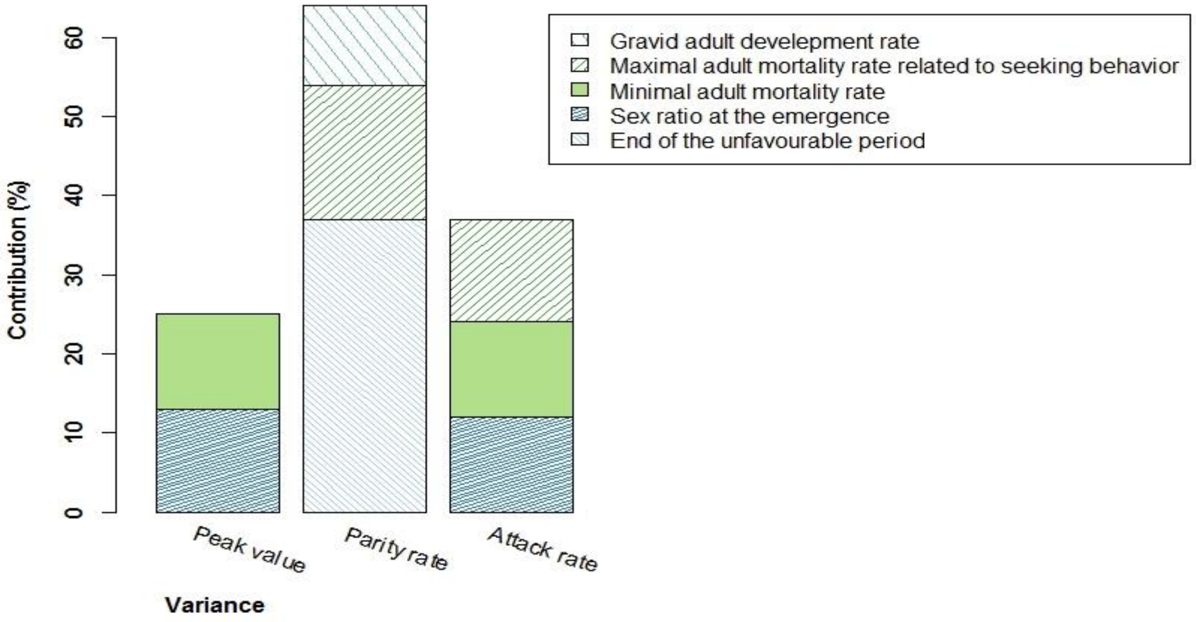
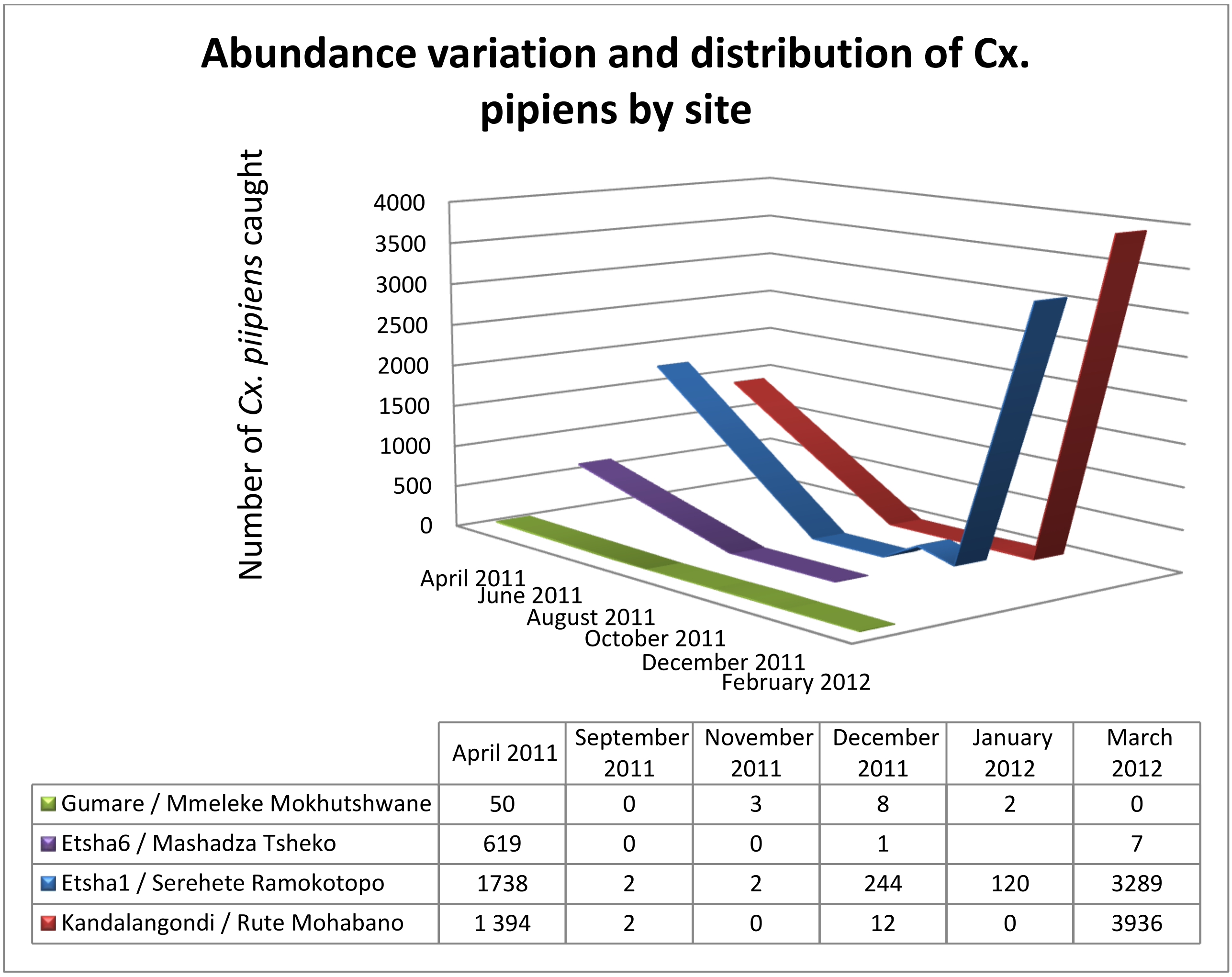


Figure 9 Key parameters contributing to aggregated outputs' variance under the *scenario 1*.

The understanding of environmental conditions that led to an increase in mosquito population is essential in the prevention of possible disease outbreaks and maximization of control efficiencies (Loncaric & Hackenberger 2013). Indeed, weather conditions are expected to affect the dynamics and intensity of the mosquito-borne disease outbreaks. In our case, the increased abundance of *Cx pipiens* suggested by the model in December is consistent with the higher seroprevalences of RVF observed in human blood samples collected in December 1984 two months after the beginning of rain, as suggested by Tessier *et al.* (1987).

Over a long time scale, the characterization of the environmental influence on population dynamics can be extremely relevant in the context of climate change. In one hand, some researchers believe that the effect of temperature on insects probably largely overwhelms the effects of other environmental factors (Bale *et al.* 2002). It has been estimated that with a 2°C temperature increase insects might experience one to five additional life cycles per season (Yamamura & Kiritani 1998). In addition, our model has highlighted the important influence of water availability in our study area. The three climatic factors identified are relevant to predict vector population increase, which can be the first step to establish maps of risk of emergence of mosquito-borne diseases such as RVF. Climate change forecasts predict an increase in the frequency of extreme weather events, such as tropical cyclones, floods, droughts and hurricanes. These changes may destabilise and weaken the ecosystem and modify the equilibrium. In parallel, tiny tectonic movements may cause subtle changes in elevation which result in significant changes in the distribution of flows across the Delta (Mendelson *et al.* 2010) and consequently in the distribution of breeding sites. Agreeing to previous studies which evidence that extreme weather events might create the necessary conditions for RVF to expand its geographical range northwards and cross the Mediterranean and Arabian seas, with an unexpected impact on the animal and human health of newly affected countries (Martin *et al.* 2008; Tourre *et al.* 2009; Tabachnick 2010; Konrad & Miller 2012), our model could eventually help to predict the expansion of vector populations on the basis of climatic forecasts.

Moreover, the identification of key parameters driving the mosquito population dynamics has allowed to affine our functions and to reach the actual model, and should be a valuable tool to discuss possible *scenario* of RVF control strategies. Indeed, these parameters represent potential control points in the biological system when they can be managed in the field. Acting on these parameters should be an efficient way to control mosquito population dynamics. Our results shown that, in our study area, mosquito's control strategies should be centre on the adult stage rather than on the aquatic stages.



	April 2011	September 2011	November 2011	December 2011	January 2012	March 2012
🟩 Gumare / Mmeleke Mokhutshwane	50	0	3	8	2	0
🟪 Etsha6 / Mashadza Tsheko	619	0	0	1		7
🟦 Etsha1 / Serehete Ramokotopo	1738	2	2	244	120	3289
🟥 Kandalangondi / Rute Mohabano	1 394	2	0	12	0	3936

Figure 10 Trapping of *Culex pipiens* over time by site.

RECOMMENDATIONS AND PERSPECTIVES

To improve the significance of our study, we should:

- Complete the sampling *i)* by catching different mosquito life stages (adult/eggs/larvae/pupae), in order to evaluate the response of the model for the entire cycle, and *ii)* by catching during several years or at least each month during one complete year, in order to check if the model is still predictive under condition of inter-annual variability (Is the abundance variation estimated quantitative or qualitative?). Set up a meteorological station on the study area to evaluate the relevance of our climatic data at local level.
- Implement experimental studies to assess the ecology and behaviour of *Cx. pipiens* and its competence to maintain RVFV.
- Undertake complementary studies on mosquito and virus populations genetic in different areas exposed to different water influence regimes (e.g. Chobe District), in order to understand the hydrological impact on the routes of biological dispersal which could furnish information about previous outbreaks and processes acting during the inter-epidemic period.
- Another perspective of the use of our model concerns the assimilation of the predicted abundance of host-seeking mosquitoes into a mechanistic risk transmission model adapted from (Guis *et al.* 2012). Such an approach could provide maps of the entomological risk, taking into account the seasonal variations of host and vector distributions, and allows establishing assumptions about the effect of the environmental factors on the RVF transmission.

To summarize, outbreak prediction, control and increased knowledge on RVFV epidemiology requires additional field data, continued development, and refinement of modeling techniques for exploring plausible disease transmission and emergence mechanisms and the potential impact of intervention strategies.

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Modélisation de l'impact des facteurs environnementaux et météorologiques sur la dynamique des populations de moustiques vecteurs de la fièvre de la Vallée du Rift au nord du Botswana.

Résumé :
Suite à une étude épidémiologique mettant en évidence la circulation du virus de la fièvre de la Vallée du Rift dans la région du Delta de l’Okavango au Botswana, l’identification des facteurs impliqués dans la dynamique des populations des vecteurs de cette maladie s'avère indispensable. La compréhension des facteurs impliqués dans le déclenchement d’une épidémie restent à ce jour mal connus et une forte augmentation de la quantité de moustiques vecteurs reste l’hypothèse la plus probable. L'objectif principal de cette étude est donc d’adapter un modèle de dynamique des populations de moustiques à cette région, dans le but de *i)* déterminer l’influence relative de la température, de la pluviométrie et de la proportion de surfaces inondées sur les variations d’abondance des vecteurs et *ii)* de tester la généricité de ce modèle. Les résultats de captures mensuelles de moustiques effectuées sur quatre sites à la frontière nord-ouest du Delta entre 2011 et 2012 ont été analysés. Quatre *scenarii* impliquant différentes associations de facteurs ont été testés et analysés. Nos principaux résultats indiquent (1) la prépondérance de l’espèce *Culex pipiens* et la très faible présence d’*Aedes spp.* sur l’ensemble des sites, (2) une variabilité spatiale forte dans les captures, (3) une influence significative et équivalente de la pluie et des inondations, (4) une certaine généricité du modèle. Les conséquences de ces résultats sur la dynamique de la fièvre de la Vallée du Rift ont été discutées. Cette analyse s'inscrit dans une étude des modalités d’émergence de la fièvre de la Vallée du Rift dans la région de du Delta de l’Okavango analysant la réponse des populations de vecteurs aux variations environnementales. Il ressort de cette étude la nécessité compléter les connaissances biologiques et les échantillonnages des vecteurs, ainsi que la pertinence de ce type d’outils pour décrire et prévoir l’évolution des populations et ainsi mettre en place des stratégies de surveillance et de contrôle des maladies vectorielles.

Mots clés : dynamique de population, modèle basé sur le climat, écologie des vecteurs, fièvre de la Vallée du Rift, *Culex pipiens.*

Modeling the impact of meteorological and environmental factors on the population dynamics of the vectors of Rift Valley fever in Northern Botswana.

Abstract :
Following an epidemiological study highlighting the Rift Valley fever virus (RVFV) circulation in the region of the Okavango Delta in Botswana, the identification of the factors involved in the population dynamics of vectors of this disease proves to be essential. Knowledge on the epidemiological patterns leading to the emergence of RVFV outbreaks is still limited and a significant increase in the mosquito abundance remains the most likely hypothesis. The main objective of this study is to adapt a mechanist model of population dynamics for mosquitoes from this area, in order to *i)* determine the relative influence of temperature, rainfall and flooding on the vectors abundance and *ii)* to test the genericity of this model. The results of monthly mosquito catches conducted in four sites at the northwest border of the Delta between 2011 and 2012 were analysed. Four *scenarii* involving different combinations of environmental factors were assessed. Our main results indicate (1) the overabundance of the *Culex pipiens* and the very low occurrence of *Aedes spp.* in all sites, (2) a strong spatial variability between the catching sites, (3) a significant and equivalent influence of rainfall and flooding, (4) the genericity of the model in different environments. The implications of these results on the dynamics of fever Rift Valley were discussed. This analysis is part of a study about the conditions leading to the Rift Valley fever emergence by analysing the response of vector populations to environmental change. The study highlights the importance to continue biological and field studies concerning vector dynamics and the relevance of this type of tool to describe and monitor the vector population evolution and develop surveillance and control strategies for vector-borne diseases.

Keywords: Population dynamics, climate driven model, vector ecology, Rift Valley fever, *Culex pipiens*