Master Thesis

Feasibility of cowpea pest *Maruca vitrata* classical biological control in the context of climate change-induced increasing temperatures

submitted by

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Affidavit

I hereby declare that I have authored this master thesis independently, and that I have not used any assistance other than that which is permitted. The work contained herein is my own except where explicitly stated otherwise. All ideas taken in wording or in basic content from unpublished sources or from published literature are duly identified and cited, and the precise references included.

I further declare that this master thesis has not been submitted, in whole or in part, in the same or a similar form, to any other educational institution as part of the requirements for an academic degree.

I hereby confirm that I am familiar with the standards of Scientific Integrity and with the guidelines of Good Scientific Practice, and that this work fully complies with these standards and guidelines.

Vienna, August 21, 2022 Vladimir MISIN *(manu propria)*

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Abstract

The legume pod borer *Maruca vitrata* is devastating the staple food crop cowpea (*Vigna unguiculata*) in West Africa, costing 3 billion USD per year, where control largely relies on the application of chemical insecticides. Classical biological control is researched as a feasible way to address this issue. *Therophilus javanus* and *Apanteles taragamae* are parasitoids from Asia introduced to West Africa to mitigate impact of *M. vitrata*. To study their effect on *M. vitrata* in relation to future warmer temperature, a tritrophic model is conceptualized and implemented using Universal Simulator software with the average daily temperature as the model driver. Three different parasitoid immigration rate scenarios are considered within temperature data for 2020 – 2050, where either of the parasitoids immigrates alone or both together. The effect of the introduced parasitoids varies depending on the parasitoid immigration rate and year, reducing *M. vitrata* young larvae population per m^2 by 20 – 99%. In all three experimental immigration rate scenarios throughout the years 2020 – 2050, *T. javanus* has the strongest effect reducing young larvae produced per m^2 by 40 – 99%. Increasing parasitoid immigration rate increases the reduction effect, while increasing temperature until 2050 does not negatively influence the effect of the parasitoids. On the contrary, the effect markedly increases in the year 2030, when the temperature is above the upper thermal development threshold of *M. vitrata* young larvae. Simulation experiments show that *T. javanus* is more effective in reducing *M. vitrata* population than *A. taragamae* and that it will be such at least until 2050 with the potential for each of the parasitoids being more effective in face of increasing temperatures. Studies related to thermal requirements of the parasitoids and studies to identify and quantify the effect of rainfall on immigration rates of *M. vitrata* are needed to build a more inclusive model.

Kurzfassung

Der Hülsenfruchtschotenbohrer *Maruca vitrata* schädigt die Augenbohne (*Vigna unguiculata*), ein Grundnahrungsmittel in Westafrika, und verursacht dort jährliche Kosten in Höhe von 3 Milliarden US-Dollar. Die Bekämpfung des Schädlings beruht in Westafrika noch weitgehend auf dem Einsatz chemischer Insektizide. Klassische biologische Kontrolle wird als eine mögliche Option angesehen. *Therophilus javanus* und *Apanteles taragamae* sind Parasitoide aus Asien, welche nach Westafrika eingeführt wurden, um den Schädling *M. vitrata* zu bekämpfen. Um deren potentielle Wirkung auf *M. vitrata* im Kontext künftiger Temperaturen zu untersuchen, wird ein tritrophes Modell konzipiert und anhand der Universal Simulator Software umgesetzt, mit der durchschnittlichen Tagestemperatur als Modelltreiber. Drei verschiedene Einwanderungsraten-Szenarien der Parasitoide werden für Temperaturdaten von 2020-2050 betrachtet, bei denen die Parasitoide jeweils einzeln und gemeinsam einwandern. Innerhalb der drei Einwanderungsraten-Szenarien der Parasitoide über die Jahre 2020 – 2050, hat *T. javanus* die größte Wirkung mit einer Reduktion der jungen Larvenpopulation um 40 – 99% pro m^2. Eine Zunahme der Parasitoid-Einwanderungsrate erhöht den Reduktionseffekt, während zunehmende Temperaturen bis 2050 die Wirkung der Parasitoide nicht negativ beeinflussen. Im Gegenteil, die Wirkung nimmt im Jahr 2030 deutlich zu, wenn die Temperatur die obere thermische Entwicklungsschwelle von jungen *M. vitrata* Larven übersteigt. Die Simulationsexperimente zeigen auf, dass *T. javanus* bei der Reduktion der *M. vitrata* Population wirksamer sein könnte als *A. taragamae* und das bis mindestens 2050. Um das Modell zu verbessern, sind weitere Untersuchungen zur thermischen Reaktion der Parasitoide und zur Identifizierung und Quantifizierung der Auswirkungen von Niederschlag auf die Einwanderungsraten von *M. vitrata* erforderlich.

1. Introduction

Health of cultivated cowpea *Vigna unguiculata* Walp in African context is researched for more than half a century, but the biotic constraints, such as insects and diseases manage to suppress potential cowpea yield by 70-90% (Ehlers & Hall, 1997; Tamò et al., 2019). An estimated annual 3 billion USD worth of economic loss throughout West Africa is caused just by one insect pest *Maruca vitrata* – a pest of major economic importance (Ba et al., 2019; Souna, Bokonon-Ganta, Ravallec, Volkoff, & Tamò, 2018).

In Africa cowpea is grown commercially with an annual production of 6.97 million metric tons, which accounts for 94% of global production. In Africa, the semi-arid Sahelian zone is a substantial production area encompassing northern and central Senegal and southern Mauritania, central Sudan, central Mali, northern Burkina Faso, central Chad, southern Niger (second biggest producer in 2018 with 2.38 million metric tons) and northern Nigeria (biggest producer of cowpea in 2018 with 2.6 million metric tons) (FAO, 2020). Cultivation of cowpea in these countries is critical, because the majority of the population consists of rural, resource-poor households that are engaged in cowpea production for sustenance (AFD, 2019; FAO, 2015). (Dabiré et al., 2012; Gómez, 2004). At the same time, management of *M. vitrata* still relies largely on the application of chemical insecticides with all their unintended side effects (Agyekum, Donovan, & Lupi, 2016; Tamò et al., 2019). Reliance on synthetic insecticides as the only pest control measure undermines sustainable alternatives, poses health risks and environmental hazards (Agyekum et al., 2016; Tamò et al., 2019).

Classical biological control of *M. vitrata* is a feasible alternative with a lot of research behind it (Tamò et al., 2019). In short, classical biological control is the use of a population of one organism to reduce the population of another organism. It implies that the pest is invasive and that the natural enemy has to be collected from the area of the origin of the pest (van Lenteren, Bolckmans, Köhl, Ravensberg, & Urbaneja, 2018). After the natural enemy is released by professionals no further intervention is needed, because it is expected to spread by itself. However, it is an approach highly susceptible to climate change-induced disturbances (Crowder & Harwood, 2014). Temperature is identified as the dominant abiotic factor directly affecting development, survival, dispersal and abundance of herbivorous insects (Bale et al., 2002). Consequently, rising temperatures can result in a disruption of current rhythms in an agro-ecosystem, potentially making a natural enemy of a pest appear too early or too late to achieve a desired impact (Bale et al., 2002; Both, van Asch, Bijlsma, van den Burg, & Visser, 2009; Harrington & Woiwod, 1999; Welch & Harwood, 2014).

Recently three exotic parasitoid species have been introduced to West Africa, namely *Apanteles taragamae, Therophilus javanus* and *Phanerotoma syleptae*. While there is controversy related to *A. taragamae* establishment, the latter two show initial success in reducing *M.vitrata* populations (B. Pittendrigh, 2013; Tamò et al., 2019). In the context of rising temperatures exploring effect of parasitoids in terms of population dynamics can be a useful tool in evaluating the short and long-term feasibility of *M. vitrata* classical biological control projects (Welch & Harwood, 2014).

2. Aim and objectives

Overall aim of the study is to examine the tritrophic population dynamics within the cowpea agro-ecosystem. More specifically, the effect that the introduced exotic parasitoids *T. javanus* and *A. taragamae* have on *M. vitrata* population density per m^2 in the northern part of West Africa. The objectives are:

- To describe the cowpea agro-ecosystem and identify key components
- To conceptualize the model
- To implement the model
- To evaluate the model
- To apply the model in a simulation experiment

3. Materials and methods

3.1. System analysis

The strategy is comprised of an initial systematic literature search on “Scopus” (Table 1), reading the literature, following up on relevant in text references and organizing literature in “Citavi” referencing software.

Table 1 Initial key words and their combinations used for literature search in “Scopus” with the number of results yielded.

Entry	Search terms	Publication year	Results
1	TITLE-ABS-KEY ("cowpea production" AND "africa")	All	63
2	TITLE-ABS-KEY ("cowpea cultivation" AND "west africa")	All	5

Table 1 continued

Entry	Search terms	Publication year	Results
3	TITLE-ABS-KEY ("cowpea" AND "west africa")	All	316
4	TITLE-ABS-KEY ("maruca vitrata" AND cowpea)	All	102
5	TITLE-ABS-KEY ("biological control" AND "maruca vitrata")	All	32
6	TITLE-ABS-KEY ("biological control" AND "pod borer")	All	58
7	TITLE-ABS-KEY ("biological control" AND "pod borer" AND "cowpea")	All	17
8	TITLE (“maruca vitrata”)	All	156
9	TITLE-ABS-KEY ("therophilus javanus")	All	4
10	TITLE-ABS-KEY ("phanerotoma syleptae")	All	2
11	TITLE-ABS-KEY ("apanteles taragamae")	All	23

3.2. Model conceptualization

Conceptualization of the model is done in a general style of showing system components and their relationships through a diagram, where various boxes and arrows are used to provide a visual representation of a system (Jackson, Trebitz, & Cottingham, 2000). The components and their relationships to be included in the model conceptualization are chosen based on the findings of the earlier system analysis. In the conceptual model diagram, the boxes represent the population density (also called ‘state variables’) of each of the phenological stages, while the arrows represent the movement of these populations (also called ‘flow’) and ecological interactions such as competition, parazitation and herbivory (Jackson et al., 2000).

3.3. Model implementation

The model is implemented in terms of its conceptualization and according to the traditional Waterfall approach. It is a linear approach, where the completion of one stage is needed to continue to the next (Insight, 2016). It provides a logical structure for the implementation process to progress steadily in accordance to the requirements established at the beginning (Hughey, 2009). The actual transformation of the model concept into a code happens in a text editor out of building blocks called boxes. When building a model in a text editor, a user defined language called a “box script” is used. It follows a few rules and allows to declare which boxes the model consists of, how the boxes are organized and how they interact. In a text editor it is possible to connect the boxes thanks to the inflow and outflow ports of each box. The boxes themselves are written in C++. The model is run with the help of Universal Simulator software. It is an open source software used for ecological modelling. Universal Simulator runs the models, however to see the model output an R software is needed. By default Universal Simulator comes with an already built in number of boxes written in C++, ready to be used as boxes in a text editor to build a model. Additional boxes can be written in C++ and added to the existing library (Holst, 2018).

3.4. Model evaluation

Model behavior is first evaluated in terms of development rate dependence on temperature (thermal time). It is tested by simulating *M. vitrata* population without any trophic interactions in two different geographic areas, which respectively have daily temperatures falling inside or outside of thermal developmental threshold range of *M. vitrata*. Consequently, the daily average temperature is looked at against the daily day-degrees. Also, the interaction between the daily day-degrees and the temporal development of density per m^2 is looked at to help visualize the impact on the duration of a single phenological stage. Additional simulation shows an example, when temperatures exceed *M. vitrata* thermal developmental threshold and *M. vitrata* is coupled to a resource, again looking at daily average temperature, corresponding daily day-degrees and the impact on temporal development of density per m^2 of a single phenological stage of *M. vitrata*.

Trophic interactions are tested in terms of the effect of experimental model parameters on response model parameters, where in each simulation one of the experimental model parameters is fixed. In the case, where parasitoids compete the experimental model parameters vary with each simulation.

In order to validate the model in terms of temporal *M. vitrata* population density development per m^2 a series of considerations are taken into account: location, planting date, planting density per m^2, flowers per plant, daily *M. vitrata* immigration rate per m^2, peak flower infestation density m^2 and *M. vitrata* consumption demand. If values needed to run the simulation are not reported, they are estimated based on scientific literature or tuned. When the values for the simulation are estimated both the reported and simulated temporal density developments are compared.

3.5. Simulation experiment

The experiment is set up to simulate three distinct scenarios, where the first two respectively represent the immigration of only *T. javanus* or *A. taragamae*, and a third scenario where parasitoids immigrate together. Simulations take into account geographic location (i.e. temperature data), cowpea variety, cowpea planting date, cowpea planting density per m^2, amount of flowers per m^2, immigration rate of *M. vitrata* adult females per m^2, demand of flowers per larvae, immigration rate of parasitoid adult females per m^2 and parasitoid demand (Table 2). In scenarios with only one parasitoid, the immigration rate of each of the parasitoids is set to be at 10%, 20% and 50% of the *M. vitrata* immigration rate. In a scenario, where parasitoids immigrate together their immigration rates are split equally still adding up to the 10%, 20% and 50% of the immigration rate of *M. vitrata*. The latter scenario accounts for competition between the parasitoids with their immigration rates being the same and chances of finding the prey split equally at 50% each. The experiment is based on temperature from 2019 (NCEI, 2022) and future temperatures 2020 – 2500 provided by the Copernicus Climate Change Service, where 2019 temperature data acts as a historical event compared to predictions (C3S, 2022; Pachauri & Mayer, 2015). Future temperatures are estimated by NorESM1-M (NCC, Norway) model according to RCP 4.5 trajectories (greenhouse gas concentration prediction, based on an intermediate intervention by mitigation policies resulting in a likely temperature increase of 1.5 °C in 2081 – 2100 relative to the 1850 -1900) in Sokoto, Nigeria (C3S, 2022; Pachauri & Mayer, 2015).

Table 2 Parameters used in the simulation experiment, parameter values and parameter value origins.

Model parameters	Value	Parameter status*
Location temperature data*	Sokoto, Nigeria	Known
Cowpea variety	Early maturing, non-photo sensitive	Known
Planting date	1st of August	Known
Planting density plants m^{-2}	13	Known
Flowers $plant^{-1}$	40	Estimated
Immigrating *M. vitrata* adults m^{-2} day^{-1}	1.3	Control
Immigrating parasitoid adults m^{-2} day^{-1}	% of *M. vitrata* immigration	Experimental
Life cycle flower demand of *M. vitrata* larva	3 flowers $larva^{-1}$	Estimated
Life cycle *M. vitrata* larva demand of parasitoids.	1 larva egg^{-1}	Known
Chances of finding prey between the parasitoids	50% each	Experimental

* Known – parameter values are either precise data (as in temperature data and parasitoid to host demand) or recommended values found in scientific literature (as in recommended planting density and planting date); Estimated – parameter values are chosen based on values found on the topic in the scientific literature; Experimental – parameter values chosen to investigate their effect on studied parameters; Control – parameter value is chosen to represent heavy infestation by the pest to act as a control scenario to study the effect of pest control by the parasitoids.

4. Results

4.1. System analysis

4.1.1. Cowpea *Vigna unguiculata*

Cultivated cowpea is an annual herbaceous legume belonging to the family Fabaceae. There exist five cultivars of cowpea, differentiated mainly by pod, seed and ovule characteristics (Pasquet, 2000). *Unguiculata* comprises the largest cultivar group (Xu et al., 2010). It is usually considered to be drought resistant, which is crucial to Sahel and Sudan regions, where drought often occurs (Dancette & Hall, 1979). Cultivating this crop in Sahelian environment with only 181 mm of rainfall and high evaporative demand can yield as much as 1000 kg of dry grain (Ehlers & Hall, 1997).

In Africa cowpea can be cultivated up to 1800 altitude, but is mainly cultivated at low elevations in hot equatorial and subtropical areas with the majority of production and production area located in sub-Saharan Africa (Ehlers & Hall, 1997). West Sudanian Savana region countries like Nigeria and central Burkina Faso are the biggest and the third biggest producers of cowpea in 2018 respectively with 2.6 million metric tons and 0.6 million metric tons. The Semi-arid Sahelian zone is also a substantial production area with southern Niger being the second biggest producer in 2018 with 2.38 million metric tons (FAO, 2020).

Cowpea can be grown using irrigation water, residual moisture along river or lake flood plains, however predominantly it is a rainfed crop. The latter is a major influence in determining the cropping cycle i.e. the timing of sowing and maturity must correspond with rainfall (Dancette & Hall, 1979). However, there is substantial variation in rainfall, onset and duration of the rainy season across West Africa (A. Y. Kamara, Omoigui, Kamai, Ewansiha, & Ajeigbe, 2018). Hence, breeders in West Africa have developed a range of cultivars, focusing on characteristics that play a key role in growth and development of cowpea (Table 3) (A. Y. Kamara et al., 2018; OECD, 2016).

Table 3 Classification of cowpea based on key characteristics related to growth and development. Source: Ehlers and Hall (1996).

Trait	Response		
Response to photoperiodism	Day – neutral (insensitive. flowering is not influenced by photoperiod, but by temperature)	Quantitative short day (photoperiod longer than a critical value delays, but does not prevent flowering)	Obligate short day (flowering occurs only in short days)
Juvenility period (time for floral bud appearance under short days)	Short	Intermediate	Long
Heat induced floral bud suppression	No suppression	Partial suppression	Complete suppression
Pod setting ability under hot long days		Low	High

The possibility to control the period of growth of cowpea in different climatic conditions and in varying onset of the rainy season comes from selecting the cultivar based on differing degrees of photosensitivity or differences in juvenility (Table 4). Cultivars with different time to juvenility and photoperiodism response give a degree of control to the farmer regardless of the planting date in terms of crop reaching the maturity at the end of a rainy season or ensuring that the critical growth stages, such as flowering are coinciding with the availability of sufficient water (Steele & Mehra, 1980).

Table 4 Different types of cowpea cultivars in terms of key characteristics. Source: B. Singh, Chambliss, & Sharma (1997).

Juvenility in days	Response to photoperiodism	Type and purpose
Extra-early 60-70 days	Non-photosensitive	Grain type for use as a sole crop or intercrop and short rainy seasons
Medium 75-90 days	Non-photosensitive	Grain type for use as a sole crop and intercrop
Late 85-120 days	Non-photosensitive	Grain and leaf type (dual purpose) for use as a sole crop and intercrop
Early 70-80 days	Photosensitive	Grain type for intercropping
Medium 75-90	Photosensitive	Grain and fodder type (dual purpose) for intercropping
Late 85-120	Photosensitive	Fodder type for intercropping

In the drier Sahelian zones cowpea cultivars are adapted to a short growing season in accordance to a short rainy season (Table 5). Usual cultivars include erect day-neutral cultivars with a short maturation period, which need 60 days to mature, prostrate day-neutral with a slightly longer maturation period of 70 days, and a dual-purpose, prostrate, short-day cultivars for hay and grain, which need 90 days to mature. (Ehlers & Hall, 1996). Early maturing cultivars can escape the end-of-season drought that often occurs in semi-arid zones such as the Sahel (Ehlers & Hall, 1997). What is more, short time from planting to harvest is especially important for the Sahel region in terms of providing early food supplies (Ehlers & Hall, 1996). Additionally, day-neutral/photo insensitive varieties display a stable growing period, because flowering is not influenced by photoperiod, but by temperature, which is relatively constant in tropical zones (**Table 6**) (Anthony E. Hall, 2004; OECD, 2016).

Table 5 Example of different planting dates depending on the beginning of the rainy season in accordance to the types of cowpea in dry savanna regions of West Africa. Source: Dugje et al. (2009).

Rainy season	Cowpea cultivars	Planting date
May – October	Erect early and extra early maturing	August, week 2
	Semi erect intermediate maturing	August, week 1
	Prostrate late maturing	August, week 2
June – October	Erect early and extra early maturing	August, week 3
	Semi erect intermediate maturing	August, week 1
	Prostrate late maturing	August, week 3
June/July – October	Erect early and extra early maturing	End of July
	Semi erect intermediate maturing	End of July
	Prostrate late maturing	August, week 1

Table 6 Thermal thresholds (T_0-lower, T_{opt} optimal and T_{max} upper) and thermal time of developmental processes and events in cowpea cultivars of Nigeria. Source: Craufurd, Summerfield, Ellis, & Roberts (1997).

Process/event	Thermal thresholds in °C			Thermal time in day-degrees d°C
	T_0	T_{opt}	T_{max}	
Seed germination	8-11	35	43	35
Seedling emergence	11	-	-	43
Leaf appearance	7-10, 16	≥ 28	-	30-60
First visible bud	8-10	27-29	-	350-580
First open flower	8-10	27-29	36	550-830
First ripe pod	8	≥ 28	-	940-1130

The medium maturing varieties that develop in 75-90 days perform well both in the semi-arid and the sub-humid zones. They can be used if a full-season cowpea variety is required to fit the prevalent cropping system, soil type, and rainfall pattern. These varieties combine multiple disease and insect resistance (B. Singh et al., 1997). In the wetter Sahelian and Sudanian zones to the south the short-day cultivars are adopted (OECD, 2016). Planting is recommended to occur between mid-July to mid-August, because planting early in the rainy season (June or early July) will delay flowering and promote excessive vegetation leading to low yield (A. Y. Kamara et al., 2010). Further south in the wetter sub-humid Sudan and humid Guinea zones medium and late maturing varieties should be planted from mid-August to early September to avoid higher incidence of diseases and produce significantly higher yield in comparison to cowpea planted in June and July (A. Y. Kamara et al., 2018).

In terms of reproductive efficiency there is a significant difference between the cultivars for total number of flowers produced, flower retention, pod drop and yield. The average of total flowers produced per single plant ranges from 28 to 50 with percent flower retention ranging from 35% to 52% and pod drop ranging from 22% to 40% (Ogunbodede, 1990). The reproductive capacity depends on the capacity to produce flower buds, develop them into flowers, the ability to retain formed flowers until they form fruits that produce mature seeds. 70% to 80% flowers buds are shed before anthesis of the flower, resulting in 6 – 16% mature fruits out of the initial flower buds (Ojehomon, 1968). Major reason for dropping flowers and pods is damage caused by pests (S. R. Singh, 1977).

4.1.2. Legume pod borer *Maruca vitrata*

M. vitrata is a moth belonging to Lepidoptera order and Crambidae family. The life cycle consists of egg, larva, pupa and adult stages (Figure 1). Depending on temperature and food quality the durations of each stage can differ (Ba et al., 2019). On cowpea the duration of the whole life cycle is 13 – 27 days (Table 7).

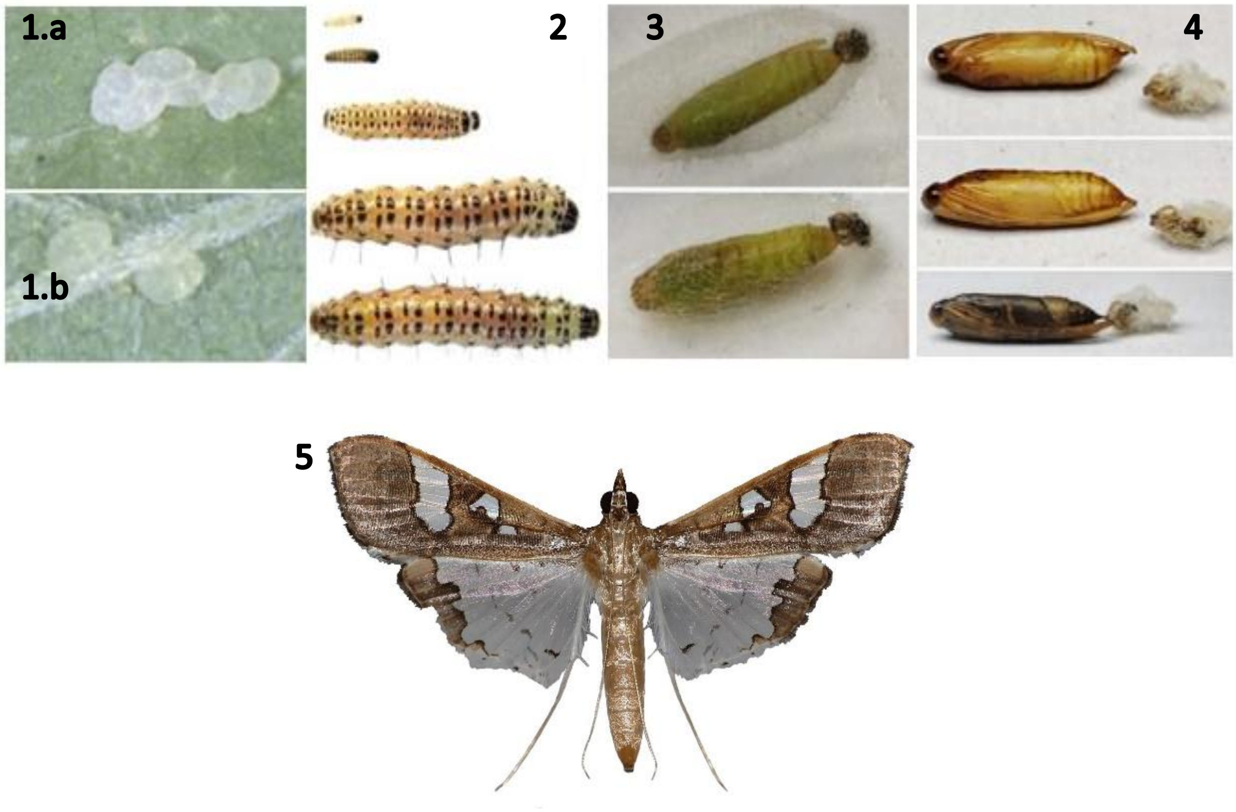

Figure 1 Maruca vitrata life cycle. 1.a and 1.b – single eggs deposited in batches on the lower surface of the leaf (Sharma, Saxena, & Bhagwat, 1999); 2 – all larval instar stages from 1st to 5th instar (Dannon, 2011) ; 3 – pre-pupal stage and 4 – late pupal stages and pupa (Pal, 2020); 5 – adult *Maruca vitrata* moth (Dupont, 2017).

In terms of temperature the developmental period of eggs, larvae and pupae gets shorter as temperature increases from 14.4 °C to 29.3 °C, but starts to get longer at 31.9 °C, and at 34.3 °C it is the same as at 19.5 °C and 24.3 °C. Temperatures below 10.5 °C and above 34.3 °C are sub-optimal for egg development. Pupal period for males is significantly longer than for females between 14.4 – 29.3 °C (Adati, Nakamura, Tamó, & Kawazu, 2004). The optimum curve of intrinsic rate of increase is at temperatures 26 – 30 °C (Dannon, Tamò, van Huis, & Dicke, 2010).

Table 7 Development time of *Maruca vitrata* in days on a cowpea plant.

Egg	Larva	Pre-pupa	Pupa	Total	Reference
-	7 – 12	-	6 – 10	13 – 25*	(Atachi & Ahounou, 1995)
-	9 – 11	2	6 – 7	19 – 22*	(Akinfenwa, 1975)
2 – 3	8 – 13	1 – 2	6 – 7	17 – 25	(Taylor, 1967)
3	8-14	1	5 – 14	25 – 27	(Okeyo-Owour & Ochieng, 1981)
3.1	13.9	1.8	6.9	25.7	(Ramasubramanian & Babu, 1988, 1989)
2.5	9.7	2.1	8	22.3	(Naveen, Naik, Manjunatha, Shivanna, & Sridhar, 2009)

-: indicates that data is not determined
*: does not include time needed for egg hatching

Development times are also reported on a temperature dependant scale expressed in day-degrees (Table 8). A total lifetime duration of 366.3 degree-days and overall lower development threshold of 10.5 °C is derived from a temperature range of 20-30 °C. (Dannon et al., 2010). In a temperature range of 14.4 – 29.3 °C the duration for eggs is 51.1 d°C above lower temperature threshold of 10.5 °C, duration of larvae is 234.7 d°C above lower temperature threshold of 10 °C and for pupae it is 116.5 d°C above lower temperature threshold of 10.9 °C. Pupal period for males is significantly longer than for females between 14.4 – 29.3 °C, where female pupa development lasts 110 d°C, while male pupa development lasts 122.7 d°C (Adati et al., 2004).

Table 8 Temperature dependent development times in day-degrees together with corresponding lower temperature thresholds for development (T_o) calculated from linear regression in a temperature range of 14.4-29.3 °C. Source: Adati et al., (2004).

Stage	Regression equation	Day-degrees d°C	T_o °C
Egg	$y = 0.0247x - 0.260$	51.1	10.5
1st larva instar	$y = 0.0255x - 0.293$	50.8	11.5
2nd larva instar	$y = 0.0338x - 0.351$	40	10.4
3rd larva instar	$y = 0.0337x - 0.351$	40.1	10.4
4th larva instar	$y = 0.0229x - 0.183$	51.8	8
5th larva instar	$y = 0.0156x - 0.152$	73.6	9.7
Pre-pupa	$y = 0.0486x - 0.372$	28.2	7.7
Cumulative (larvae+pre-pupa)	$y = 0.0045x - 0.044$	234.7	10
Pupa	$y = 0.0095x - 0.104$	116.5	10.9
Pupa female	$y = 0.0101x - 0.114$	110.0	11.2
Pupa male	$y = 0.0089x - 0.0.96$	122.7	10.7

M. vitrata presents itself as a serious pest in the tropics and sub-tropics distributed across Asia, Africa, Australia and the Americas (Figure 2) (Sharma et al., 1999).

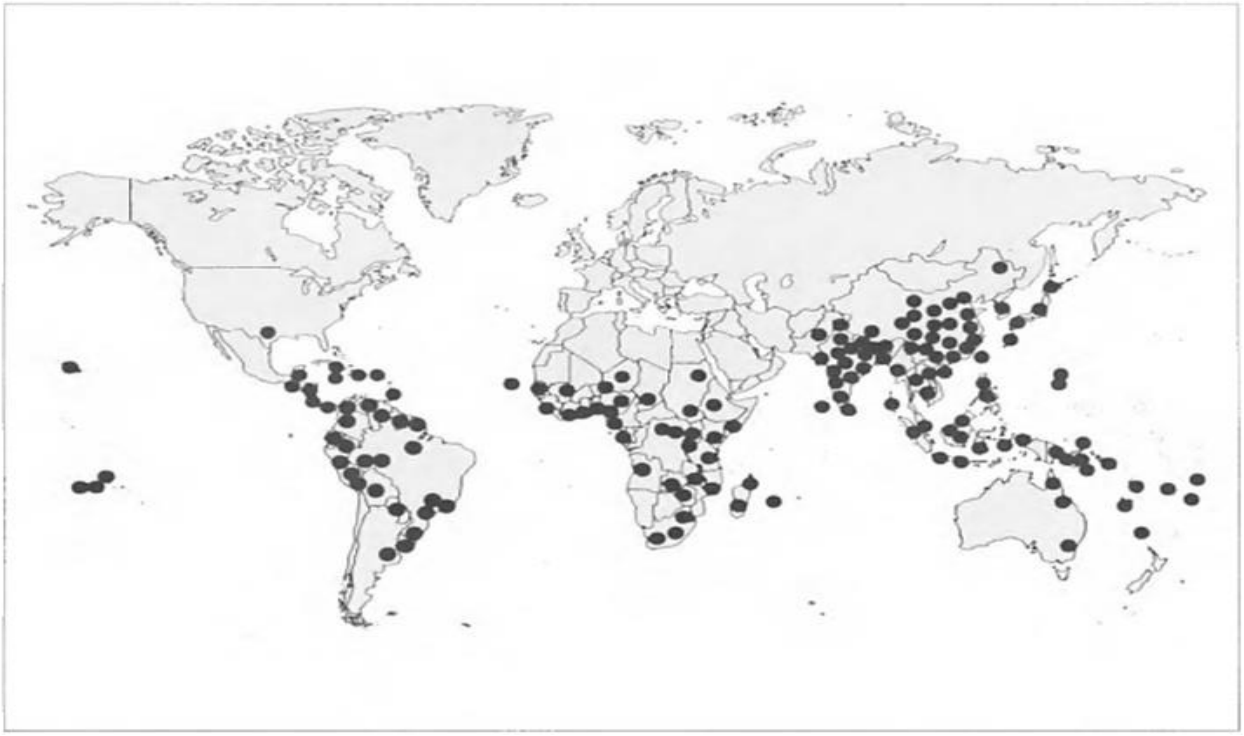

Figure 2 Geographical distribution of the legume pod borer *Maruca vitrata*. Source: International Institute of Entomology (1996)

M. vitrata does not undergo diapause in Africa (Adati, Tamò, Koji, & Downham, 2012; Arodokoun, Tamò, Cloutier, & Adeoti, 2003; Okeyo-Owour & Ochieng, 1981; Taylor, 1967) and the population is always maintained on a range of alternative wild and cultivated hosts (Table 9) (Arodokoun et al., 2003; Tamò et al., 2002).

Table 9 Family Fabaceae wild host plants of *M. vitrata* in Africa. Sources: Benin – Arodokoun et al., (2003) and Tamò et al., (2002), Burkina Faso – Traore et al. (2014) , Niger and Nigeria – Margam et al., (2010).

Benin	Burkina Faso	Niger[1] and Nigeria[2]
Afromosia laxiflora (Benth) Harms	*Crotalaria ochroleuca* G. Don	*Afrormosia laxiflora*[2]
Andira inernis (Wright) D.C.	*Daniella oliveri* (Rolfe.) Hutch. & *Dalziel*	*Crotalaria senegalensis* [2]
Carnavalia ensiformis (L.) D.C.	*Mucuna poggei* Taub.	*Tephrosia uniflora*[1]
Carnavalia virosa (Roxb.)	*Rhynchosia hirta* (Andrews) Meikle and Verdc.	*Tephrosia bracteolata*[1]
Centrosema pubescens	*Rhynchosia pycnostachya* (DC) Meikle	*Sesbania sesban*[1, 2]
Dolichos africanus	*Sesbania pachycarpa* DC.	*Sesbania pachycarpa*[1].
Esclerotona dolabriformis (coll.)	*Tephrosia bracteolata* (Guill. & Perr.)	
Lonchocarpus sericeus (Poir) H.B.K	*Tephrosia candida* (Roxb.) DC.	

Table 9 continued

Benin	Burkina Faso	Niger[1] and Nigeria[2]
Lonchocarpus cyanescens (Schum & Thonn)	*Tephrosia nana* Schweinf	
Milletia thonningii	*Vigna gracilis* (Guill. & Perr.) Hook.f.	
Pacchyrrhizus angulatus (Rich.)	*Vigna nigritia* Hook.f.	
Pterocarpus erinaceus (Poir)		
Pterocarpus santalinoïdes (l'Her. ex D.C.)		
Psophocarpus palustris (Deso.)		
Pueraria phaseoloides		
Sesbania pachycarpa DC.		
Tephrosia humilis (Guill. & Perr.)		
Tephrosia platycarpa Guill. & Perr.		
Tephrosia candida		
Vigna racemosa (G.Don) Hutch. & *Dalziel*		
Xerroderri sulthmanii (Taub.) Mend & Sous.		

Alternative hosts plants belong to the Fabaceae family and are important to the population dynamics of *M. vitrata*, because the insect feeds and reproduces on them when migrating from the coast to the dry savannas of West Africa (Bottenberg et al., 1997). Studies suggest that cowpea infestations in northern regions are the result of pest's windborne immigration from permanent populations in the southern regions at the onset of the rainy season (Figure 3) (Adati et al., 2012; Ba et al., 2009; Margam et al., 2010; Tamò et al., 2002).

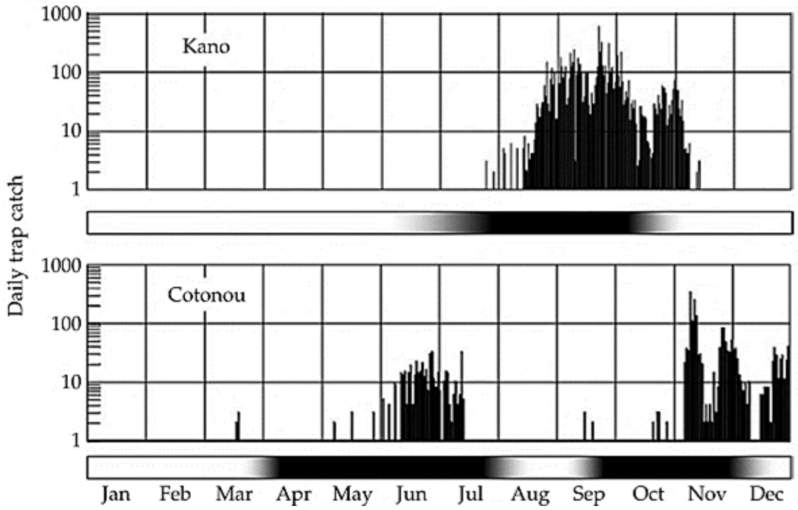

Figure 3 Daily light-trap catches of *Maruca vitrata* at Kano, Nigeria in northern West Africa and Cotonou, Benin in the southern West Africa in 2002. Kato is located in the Sahelian ecological zone, while Cotonou is in the Sudanian. Dark zones in the horizontal bars under the horizontal axis indicate rainy seasons. Source: Adati et al. (2007).

Throughout the year higher numbers of *M. vitrata* population are found in the southern regions of cowpea producing areas as compared to the northern regions *viz.* Sudanian zone with a relatively high rainfall in the south and the drier Sahelian zone further to the north (Figure 4) (Adati et al., 2012; Ba et al., 2009). As the pest population migrates it finds favorable conditions on different host plants and increases in size in each new generation, eventually reaching main cowpea production areas in the northern areas (Tamo, Bottenberg, Arodokoun, & Adeoti, 1997). In the lower latitudes of West Africa *M. vitrata* thrives on alternative host plants without any reliance on cowpea e.g. during the main dry season in southern and central Benin, *Pterocarpus santalinoides* tree provides a favorable habitat, while during the short dry season, when previous cowpea is harvested in early August and second cropping starts in mid-September, several *Tephrosia* and *Sesbania* species are available (Tamò et al., 2002). On the other hand, in Nigeria and Niger a relatively small number of alternative host plants is available, thus it is difficult for *M. vitrata* to survive in the off season, after cowpea is harvested (Jackai, Ochieng, & Raulston, 1990; Margam et al., 2010).

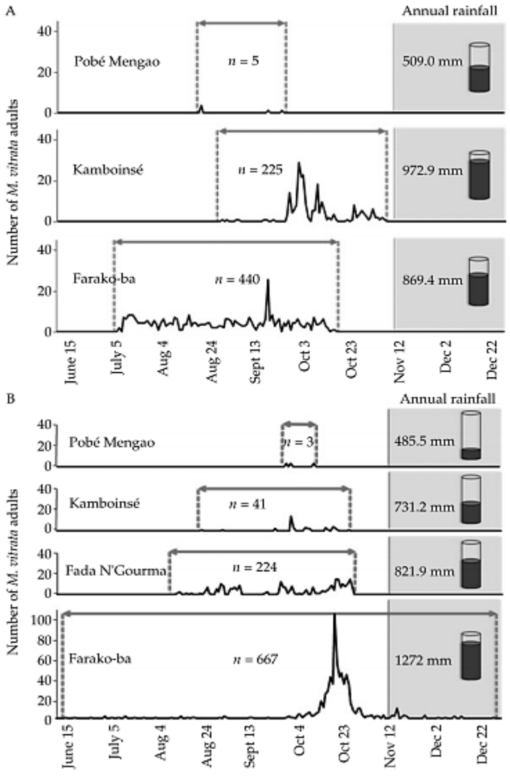

Figure 4 Adult *Maruca vitrata* catches in light traps in 2005 from June 15 until December 22 in various locations in Burkina Faso: A (Farako-ba, Kamboinsé and Pobé Mengao) and in 2006 from June 15 to December 22 in four four locations B (Farako-ba, Fada N'Gourma, Kamboinsé and Pobé Mengao). n indicates the total number of adults caught during the year, while total annual rainfall is indicated on the right specific to each location. Source: Ba et al. (2009).

Initial infestation starts with adults invading cultivated fields from alternative hosts. Adults are inactive during the day, when they rest on lower leaves of host plants (Lu, Qiao, Wang, Wang, & Lei, 2007). Females deposit eggs on leaves, vegetative buds and flowers with highest preference for lower surfaces of the leaves (Figure 1) (Okeyo-Owour & Ochieng, 1981). There is a pre-oviposition period of 3 – 4 days with peak oviposition occurring 6 – 8 days after mating (Ke. L. D., Fang, & Li, 1985; Tumuhaise, 2015). When it comes to choosing an oviposition site in the presence of conspecific larvae, adult *M. vitrata* females are shown to prefer to lay eggs on non-infested flowers as opposed to infested flowers (Osei-Owusu et al., 2020).

Eggs are laid singly or in batches and hatch within 2 – 3 days. Depending on the environment one female can lay up to 600 eggs (Table 10). Humidity is shown to be a main factor in reproduction of *M. vitrata* (Appert & Deuse, 1982; Busoli, Lara, & Silveira, 1981; Ochieng, Okeyo-Owuor, & Dabrowski, 1981; Okeyo-Owuor & Ochieng, 1981).

Table 10 Lifetime fecundity per *Maruca vitrata* female and egg survival in laboratory conditions.

Eggs	Survival	Rearing medium	Temperature	Relative humidity	Reference
140	ns	Semi-synthetic	20-30 C°	Ns	(Dannon et al., 2010)
ns	93.1%	Semi-synthetic	14.4-31.9 °C	Ns	(Adati et al., 2004)
97.6	39.9%	Cowpea flowers	ns	Ns	(Sharma et al., 1999)
568.6	57.1%	48 h soaked sprouting grains of 3 cowpea cv.	25.5 °C	81.5%	(Wetro et al., 2014)
137-275	ns	Flowers of various cultivars	22 °C	57%	(Oigiangbe, Jackai, Ewete, & Lajide, 2000)
362.7	ns	Artificial diet	22 °C	57%	(Oigiangbe et al., 2000)
126.8	95.45%	Cowpea flowers	ns	Ns	(Naveen, Naik, Manjunatha, Shivana, & Sridhar, 2009)
617	81.8%	Various cowpea floral parts	25-32 °C	60-80%	(Traore, Dabire-Binso, Ba, Sanon, & Pittendrigh, 2013)

ns – not specified by the author

The larval stage consists of five instars, which is completed within 8 – 14 days (Adati et al., 2004; Okeyo-Owour & Ochieng, 1981; Ramasubramanian & Babu, 1989; S. R. Singh & Allen, 1980; S. R. Singh & Jackai, 1985). Larvae emerge early in the evening and are mainly nocturnal found together within individual flowers in their first instar stage, but later disperse and move individually from one flower to another capable of consuming from 4 to 6 flowers before larval development is complete and being able to develop all the way to adulthood on any single component of the cowpea flower (Gblagada, 1982; Traore et al., 2013; Usua & Singh, 1979).

Damage to the flower can lead to a loss of an entire potential pod (Atachi & Gnanvossou, 1989; Sharma, 1998; Taylor, 1967). On the other hand, it is known that older larvae instars can feed and pupate in pods (Okeyo-Owour & Ochieng, 1981). After the initial phase of young larvae appearance on floral parts there is a period of “harmonization”, where different larval stages are distributed almost homogenously across flower parts and pods (Atachi & Gnanvossou, 1989). The first three instars are less mobile (Jackai & Daoust, 1986). First two instars are usually found on flowers, while fourth and fifth are found on the pods (Figure 5) (Liao & Lin, 2000; Okeyo-Owuor, Agwaro, & Simbi, 1983; Okeyo-Owuor & Ochieng, 1981). First instar larvae can sometimes also be found in young pods (Traore et al., 2013). Larvae of *M. vitrata* are responsible for the substantial damage done to plants by feeding inside flowers, flower buds and pods, thus reducing potential for flowering and fruit setting (Sharma et al., 1999). Even 1 larva per flower is enough to cause significant yield losses (Atachi & Ahohuendo, 1989). A population of 12 – 15 larvae per plant can cause a 100% yield loss, despite plant looking healthy in growth (Taylor, 1967).

Figure 5 Larvae of *Maruca vitrata* feeding on a 1 – flower and 2 – a pod. Source: Tumuhaise (2015).

There is a high degree of variation in levels of infestation depending on cowpea cultivar, date of planting and whether pest management is in place or not, however *M. vitrata* is consistently present in higher numbers in more humid zones (Ba et al., 2009; Baoua et al., 2011). Some peak density infestation values found in literature are presented in Table 11.

Table 11 Location and the prevalent rainfall pattern, cultivation season, cowpea cultivar and the maximum *M. vitrata* larvae infestation.

Location and rainfall pattern	Season	Peak larvae infestation	Cowpea cultivar and its traits	Reference
Glazoue, Central Benin; bimodal	April – July	3.5 plant^{-1}	Wankoun semi-erect 65-70 day cycle	(Joelle et al., 2020)
Djakotomey, Southern Benin; bimodal	April – July	5 plant^{-1}	Sakaouga semi-erect 65-70 day cycle	(Joelle et al., 2020)
Agonkamey, Southern Benin; bimodal	April – July Sept. – Nov.	0.6 inflorescence^{-1} 0.3 inflorescence^{-1}	Kpodjiguégué duration to harvest 70 days	(Arodokoun et al., 2003)
Southern Benin; bimodal	June – Sept.	0.34 flower^{-1} 0.18 pod^{-1}	IT84D449	(Sokame et al., 2015)
Farako-ba, South-western Burkina Faso; unimodal	June – Oct.	13.5 flower^{-20}* 11.7 flower^{-20}* 16.3 flower^{-20}* 9.2 flower^{-20}*	KVx 404-8-1 (60 days) early maturing KVx 61-1 (70 days) early maturing KVx 396-4-5-2D (70 days) early maturing Moussa local (85 days) late maturing	(Traore et al., 2014)
Farako-ba, South-western; Burkina Faso; unimodal	Aug – Oct.	3.9 plant^{-1} 4 plant^{-1} 2.2 plant^{-1}	KVx 404-8-1 (60 days) early maturing KVx 61-1 (70 days) medium maturing Moussa local (85 days) late maturing	(Baoua et al., 2011)
Samaru, Northern Nigeria		25.17 flower^{-20}* 13.89 pod^{-1*}	IAR-48/SAMPEA 7 Photo insensitive early maturing	(Muhammad, Malgwi, & Adamu, 2017)
Kano, Northern Nigeria; unimodal	June – Oct.	0.13-0.92 flower^{-1}	A range from a variety of cultivars planted across a range of dates	(Asante, Tamó, & Jackai, 2001)
Kano, Northern Nigeria; unimodal	July – Nov.	3.2 flower^{-1}**	IT86D-715 (extra-early maturity) Dan Ila (local cultivar, spreading type)	(Bottenberg et al., 1997)
	Residual	0.12 flower^{-1}	Unspecified	
	Irrigated	1.2 flower^{-1}	TVx 3236	
Maradi, Niger; unimodal	July – Sept.	0.9* plant^{-1} 0.6* plant^{-1} 0.04* plant^{-1}	IT 97k-499-38 (60 days) early maturing TN-256-87 (90 days) medium maturing Dan-Dame (100 days) late maturing	(Baoua et al., 2011)

*average of 2 consecutive seasons.
**average across varieties given in the table.

The prepupal stage takes 1 – 2 days and the pupal stage lasts 5 – 27 days (Table 7). Adult emergence from pupa throughout the day with peak emergence at night (C. C. Huang & Peng, 2001; Lu et al., 2007). Mating takes place between fourth and twelfth hour of darkness when temperature is 20 – 25 ℃ and relative humidity is greater than 80% (Hassan, 2007; Jackai et al., 1990). Females usually mate once (IITA, 1981), while males may mate multiple times (Jackai et al., 1990). Mating activity is highest 3 – 5 days after females emerge from pupation (Jackai et al., 1990; Lu et al., 2007).

Sex ratio varies, but is shown to be close to 1:1 in laboratory conditions (Table 12) (Ba et al., 2019; Dannon et al., 2010; Lu et al., 2007). On the other hand, light trap catches suggest that in nature it might be different, where it is season and location related. For example in northern Nigeria and northern Benin the ratio is 1:1 except the months of August – October, where females constitute a majority of the population (Adati et al., 2012). In southwestern Burkina Faso females are also reported to constitute the majority of the population in the same months of late August – mid October with an average of 66% (Traore et al., 2014). However, throughout the months of June – December in southern, central and northern parts of Burkina Faso almost 70% of *M. vitrata* adults caught in light traps are male (Ba et al., 2009). In the south of Benin the population is male dominated from July to August and female dominated in November – January (Adati et al., 2012). In laboratory conditions no correlation between sex ratio and temperature is found (Dannon et al., 2010).

Table 12 Percent female progeny of *Maruca vitrata* in laboratory conditions and percent females caught in light traps studies.

% females	Setting	Rearing medium	Temperature	Relative humidity	Reference
47	Lab	Cowpea flowers and pods	29 ℃	75-80%	(Lu et al., 2007)
38	Lab	48 h soaked sprouting grains of 3 cowpea cultivars	25.5 °C	81.5%	(Wetro et al., 2014)
47	Lab	Semi-synthetic	20-30 C°	ns	(Dannon et al., 2010)
30	Light traps	-	Across Burkina Faso		(Ba et al., 2009)
63	Light traps	-	South Western Burkina Faso		(Traore et al., 2014)

- not specified by the author

Depending on temperature and food quality adults lifespan can differ, however females generally live longer (Ba et al., 2019). In laboratory conditions it is shown that females live longer when reared on cowpea flowers, while males outlive females when reared on a semi-synthetic diet (Table 13). There is also an observed negative correlation between temperatures in a range of 20 – 30 °C and adult longevity, when reared on a semi-synthetic diet (Dannon et al., 2010).

Table 13 *Maruca vitrata* adult longevity in days in laboratory conditions.

Male	Female	Rearing medium	Temperature	Relative humidity	Reference
10.82	12.41	Cowpea flowers	ns	Ns	(Naveen, Naik, Manjunatha, Shivana, & Sridhar, 2009)
13.7	17.06	Cowpea flowers	25–32 °C	60–80%	(Traore et al., 2013)
12.68	11.8	Semi-synthetic	20-30 C°	Ns	(Dannon et al., 2010)

ns – not specified by the author

Mortality rates vary (Table 14). Field mortality rates from egg to adulthood are reported to be high reaching 98.2 – 99.4%, where development from egg to 3rd instar is the most susceptible. (Okeyo-Owour, Agwaro, & Simbi, 1983). Parasitoids and pathogens contribute 41% and 36% to the total generation mortality, while predation accounts to about 60%. When *M. vitrata* is reared on a semi-synthetic diet the average larvae (including pre-pupae) survival is 62.8% and survival of pupae is 83.9% between 14.4 – 31.9 °C (Adati et al., 2004). Between 20 – 30 °C the survival decreases as temperature increases with an average survival rate of larvae and pupae of 74% (Dannon et al., 2010). The percentage adult emergence is in a range of 45 – 67%, when reared on various cultivated cowpea flowers (Oigiangbe et al., 2000), while it is 94.2% on average, when reared on various parts of cowpea flower (Traore et al., 2013).

Table 14 Mortality of various stages of *Maruca vitrata* in laboratory conditions.

Stage	Survival	Rearing medium	Temperature	Relative humidity	Reference
Egg-adult	45-67%	Flowers of various cultivars	22 °C	57%	(Oigiangbe et al., 2000)
Egg-adult	92.2%	Artificial diet	22 °C	57%	Ibid
Egg	93.1%	Semi-synthetic	14.4-31.9 °C	ns	(Adati et al., 2004)
Larvae	81.7%	48 h soaked sprouting grains of 3 cowpea cultivars	25.5 °C	81.5%	(Wetro et al., 2014)
Larvae	81.5%	Artificial diet	25 °C	ns	(Dannon, Tamò, Agboton, van Huis, & Dicke, 2012)
Larvae	90.5%	Artificial diet	29 °C	ns	Ibid
Larvae	74%	Cowpea flowers	25 °C	ns	Ibid
Larvae	84.5%	Cowpea flowers	29 °C	ns	Ibid
Larvae and pre-pupae	62.8%	Semi-synthetic	14.4-31.9 °C	ns	(Adati et al., 2004)
Larvae and pupae	74%	Semi-synthetic	20-30 C°	ns	(Dannon et al., 2010)
Pupae	94.2%	Various cowpea floral parts	25-32 °C	60-80%	(Traore et al., 2014)
Pupae	83.9%	Semi-synthetic	14.4-31.9 °C	ns	(Adati et al., 2004)
Adult	46.08%	48 h soaked sprouting grains of 3 cowpea cultivars	25.5 °C	81.5%	(Wetro et al., 2014)

ns – not specified by the author

4.1.3. *Apanteles taragamae*

In Taiwan a green manure crop *Sesbania cannabina* is infested with *M. vitrata.* This leguminous species presents a good opportunity to study natural enemies of the pest, because chemical pesticides are rarely applied to it. Results show that a predominant portion of natural enemies consist of parasitoids, where a wasp *Apanteles taragamae* alone accounts for 92.2%. Previously, this parasitoid is not generally associated with *M. vitrata*, nor does it attack *M. vitrata* on any *Vigna* species in Taiwan (C. C. Huang, Peng, & Talekar, 2003). The parasitoid also occurs in India where it attacks some pests of economic importance e.g. a pest of coconut *Opisina arenosella* and a pest of various species of gourds *Diaphania indica* (Ghosh & Abdurahiman, 1988; Peter & David, 1990). However, the parasitoid shows a strictly specialist behavior in presence of six other lepidopteran species related to the cowpea agro-ecosystem in West Africa (Dannon, Tamò, van Huis, & Dicke, 2012).

Small scale field trials of *A. taragamae* inoculative releases between February and June 2007 in Nigeria, Ghana and Benin result in unsuccessful parasitoid recovery attempts lasting until mid-2008 (Tamò et al., 2012). On the other hand *Sesbania cannabina* plots artificially infested with *M. vitrata* and planted at 5 and 25 meters from the release point of *A. taragamae* were all infested with the parasitoid (B. R. Pittendrigh, 2011). Short range dispersal studies show that *A. taragamae* dispersal from the release site is subject to prevailing wind direction. Even though results show effective targeting of *M. vitrata* and good field dispersal, the low recovery rates point to poor ecological adaptation, more specifically to major wild host plants of *M. vitrata* such as *Lonchocarpus* spp., *Pterocarpus santalinoides,* and *Milletthia thonningii* (Ba et al., 2019; Tamò et al., 2019). There is however and indirect evidence of *A. taragamae* presence in the environment. The *Mavi*MNPV virus is found close to the parasitoid release sites, even though it is not known to naturally infect *M. vitrata* there. This discovery leads to testing *A. taragamae* in its ability to transmit the virus, which turns out to be true (Tamò et al., 2012). What is more, two years after the last *A. taragamae* inoculation the parasitoid is retrieved from *M. vitrata* feeding on *L. sericeus* tree flowers (B. Pittendrigh, 2013).

The parasitoid successfully parasitizes 1, 2 and 3 day old (first and early second instar) larvae of *M. vitrata* with an observable host density-dependence. There is no significant impact of host age at the time of parazitation on subsequent development time of the parasitoid (Table 15). However, 1 day old larvae are parasitized 50% less compared to 2 and 3 day old larvae with only males emerging from the 1 day old larvae (Dannon et al., 2010). When parasitizing a 2 day old *M. vitrata* larvae fed *V. unguiculata* flowers, it takes 5.4 days to complete egg to cocoon development and 5.3 days to complete cocoon to adult development with a longevity of 4.7 days and 4.3 days for combined male and female and just female adults respectively at 29 °C (Dannon, Tamò, Agboton, et al., 2012). When parasitizing 1, 2 and 3 day old *M. vitrata* larvae fed artificial diet in laboratory conditions at 25 °C, it takes on average 8 days to complete egg to cocoon and 5 days to complete cocoon to adult with a longevity of 12.3 days and 9.9 days for combined male and female and just female adults respectively. When looking at *A. taragamae* development time averaged across 5 temperatures in a 2 day old parasitized *M. vitrata* larvae fed artificial diet it takes the parasitoid on average 8 days to complete egg to cocoon development and 5.9 days to complete cocoon to adult development with a longevity of 11.1 days and 11 days for combined male and female and just female adults respectively (Dannon et al., 2010).

Table 15 Development times of *Apanteles taragamae* stages from egg to cocoon and from cocoon to adult together with adult longevity in laboratory conditions.

Stage	Temperature and duration in days	Conditions	Reference
Egg – cocoon	At 25 °C: ud At 29 °C: 5.4	From 2 day old parasitized *M. vitrata* larva fed *V. unguiculata*	(Dannon, Tamò, Agboton, et al., 2012)
	At 25 °C: 8	Average from 1, 2 and 3 day old parasitized *M.vitrata* larvae fed artificial diet	(Dannon et al., 2010)
	At 20 °C: 13.7 At 24 °C: 7.9 At 26 °C: 6.9 At 28 °C: 5.7 At 30 °C: 5.7 Average: 8	Average across 5 temperatures from a 2 day old parasitized *M. vitrata* larvae fed artificial diet	
	26 °C: 7.97	From a 2 day old *M. vitrata* larvae fed germinated cowpea grains.	(Wetro et al., 2014)

Table 15 continued

Cocoon – adult	At 25 °C: ud At 29 °C: 5.3	From 2 day old parasitized *M. vitrata* larva fed *V. unguiculata*	(Dannon, Tamò, Agboton, et al., 2012)
	At 25 °C: 5	Average from 1, 2 and 3 day old parasitized *M.vitrata* larvae fed artificial diet	(Dannon et al., 2010)
	At 20 °C: 11.3 At 24 °C: 4.8 At 26 °C: 5.2 At 28 °C: 4.4 At 30 °C: 3.9 Average: 5.9	Average across 5 temperatures from a 2 day old parasitized *M. vitrata* larvae fed artificial diet	
	26 °C: 5.81	From a 2 day old *M. vitrata* larvae fed germinated cowpea grains.	(Wetro et al., 2014)
Adult	At 25 °C: no development At 29 °C: 4.7; F 4.3	Average (male + female) and just females from 2 day old parasitized *M. vitrata* larva fed *V. unguiculata*	
	At 25 °C: 12.3; F 9.9	Average (male + female) and just female from 2 and 3 day old parasitized *M.vitrata* larvae fed artificial diet. No females emerge from 1 day old parasitized larvae	(Dannon et al., 2010)
	At 20 °C: 20.1; F 21.9 At 24 °C: 13.8; F 12 At 26 °C: 11.5; F 9.2 At 28 °C: 6.5: F 7.7 At 30 °C: 3.6: F 4.1 Average: 11.1; F 11	Average (male + female) and just female across 5 temperatures from a 2 day old parasitized *M. vitrata* larvae fed artificial diet	
	26 °C: 16.03; F 19.03	From a 2 day old *M. vitrata* larvae fed germinated cowpea grains.	(Wetro et al., 2014)

ud – unsuccessful development

A. taragamae is pro-ovigenic and emerges with all of the eggs already mature. Lifetime fecundity of *A .taragamae* female in laboratory conditions varies (Table 16). Lifetime fecundity of females resulting from parasitizing a 2 day old *M. vitrata* larva fed *V. unguiculata* is 7 eggs at 29 °C (Dannon, Tamò, Agboton, et al., 2012). Fecundity of females resulting from parasitizing 1, 2 and 3 day old *M.vitrata* larvae fed artificial diet is on average 48.9 eggs at 25 °C, without significant impact of host age at the time of parazitation, except for only male appearing from 1 day old parasitized larvae (Dannon et al., 2010). Across 5 temperatures lifetime female fecundity is 62.8 eggs on average, when looking at females formed from a 2 day old parasitized *M. vitrata* larvae fed artificial diet (Dannon et al., 2010).

Table 16 Lifetime fecundity of adult *Apanteles taragamae* female in laboratory conditions.

Parameter	Temperature and eggs	Conditions	Reference
Fecundity (cocoons per female)	At 25 °C: unsuccessful development At 29 °C: 7	From 2 day old parasitized *M. vitrata* larva fed *V. unguiculata*	(Dannon, Tamò, Agboton, et al., 2012)
	At 25 °C: 48.9	Average from 2 and 3 day old parasitized *M. vitrata* larvae fed artificial diet. No females emerge from 1 day old parasitized larvae	(Dannon et al., 2010)
	At 20 °C: 123.3 At 24 °C: 73.2 At 26 °C: 64.7 At 28 °C: 46.7 At 30 °C: 5.9 Average: 62.8	Average from 2 and 3 day old parasitized *M.vitrata* larvae fed artificial diet. No females emerge from 1 day old parasitized larvae	
	26 °C: 57.43	From a 2 day old *M. vitrata* larvae fed germinated cowpea grains cv. Tawa	(Wetro et al., 2014)

A.taragamae progeny sex ratio in laboratory conditions is relatively stable (Table 17). The percentage of female progeny resulting from parasitizing a 2 day old *M. vitrata* larva fed *V. unguiculata* is 16.9% at 29 °C (Dannon, Tamò, Agboton, et al., 2012). Percentage of female progeny of resulting from parasitizing 1, 2 and 3 day old *M.vitrata* larvae fed artificial diet is on average 33.9% at 25 °C (Dannon et al., 2010). Female progeny constitutes on average 33.9% across 5 temperatures, when looking at population formed in a 2 day old parasitized *M. vitrata* larvae fed artificial diet (Dannon et al., 2010).

Table 17 *Apanteles taragamae* progeny sex ratio in laboratory conditions.

Parameter	Temperature and eggs	Conditions	Reference
Sex ratio (% females progeny)	At 25 °C: ud At 29 °C: 16.9	From 2 day old parasitized *M. vitrata* larva fed *V. unguiculata*	(Dannon, Tamò, Agboton, et al., 2012)
	At 25 °C: 33.9	Average from 2 and 3 day old parasitized *M. vitrata* larvae fed artificial diet. No females emerge from 1 day old parasitized larvae	(Dannon et al., 2010)
	At 20 °C: 34.7 At 24 °C: 33.3 At 26 °C: 34.3 At 28 °C: 34 At 30 °C: 33.3 Average: 33.9	Average from 2 and 3 day old parasitized *M.vitrata* larvae fed artificial diet. No females emerge from 1 day old parasitized larvae	
	At 26 °C Average: 35	Average from 1,2 and 3 day old *M. vitrata* larvae fed 3 different germinated grains of cowpea	(Wetro et al., 2014)

ud – unsuccessful development

Survival rates of *A. taragamae* might vary (Table 18). The survival rate of parasitized larvae resulting from parasitizing a 2 day old *M. vitrata* larva fed *V. unguiculata* flowers is 53.5% at 29 °C. A large percentage of larvae parasitized by *A. taragamae* is killed by *Mavi*MNPV (Dannon, Tamò, Agboton, et al., 2012). In laboratory conditions the rate of cocoons resulting from parasitized larvae at 25 °C is on average 53.7%, when parasitizing 1, 2 and 3 day old *M.vitrata* larvae fed artificial diet (Dannon et al., 2010). In laboratory conditions adult emergence rate from cocoon, which formed from parasitizing a 2 day old *M. vitrata* larva fed *V. unguiculata* flowers is 83.3 % at 29 °C (Dannon, Tamò, Agboton, et al., 2012). However, emergence rate is on average 32% at 25 °C, when looking at the cocoons formed from 1, 2 and 3 day old parasitized *M.vitrata* larvae fed artificial diet. The survival rate of *A. taragamae* larvae on a 1 day old larvae is only 7% (Dannon et al., 2010). Emergence rate is on average 73% across 5 temperatures, when looking at the adult emergence rate from cocoons formed in a 2 day old parasitized *M. vitrata* larvae fed artificial diet (Dannon et al., 2010).

Table 18 Survival of *Apanteles taragamae* egg, larvae and cocoon developmental stages as well as adult emergence from cocoon in laboratory conditions.

Stage	Temperature and % survival	Conditions	Reference
Egg	At 25 °C : ud 1 day old: 35% 2 day old: 67% 3 day old: 56% Average: 53.7%	Average from 1, 2 and 3 day old parasitized *M.vitrata* larvae fed artificial diet.	(Dannon et al., 2010)
Larvae	At 25 °C: ud At 29 °C: 52.5%	From 2 day old parasitized *M. vitrata* larva fed *V. unguiculata* flowers	(Dannon, Tamò, Agboton, et al., 2012)
Percentage of *M. vitrata* killed by *Mavi*MNPV – major mortality contributor	At 25 °C: 75% At 29 °C: 37%		
Larvae and cocoon (until adult emergence)	At 25 °C: 32%	Average from 1, 2 and 3 days old parasitized *M.vitrata* larvae fed artificial diet. Survival rate on a 1 day old larvae is only 7%	(Dannon et al., 2010)
	At 20 °C: 71% At 24 °C: 81.7% At 26 °C: 76% At 28 °C: 69.3% At 30 °C: 67.3% Average: 73%	Average across 5 temperatures from a 2 day old parasitized *M. vitrata* larvae fed artificial diet	
Cocoon (until adult emergence)	At 25 °C: ud At 29 °C: 83.3%	From 2 day old parasitized *M. vitrata* larva fed *V. unguiculata*	(Dannon, Tamò, Agboton, et al., 2012)

ud – unsuccessful development

4.1.4. *Therophilus javanus*

T. javanus is a larval parasitoid wasp found in Malaysia and Vietnam, whose host continues to feed and grow after the parazitation. Olfactory studies of *T. javanus* show that its parasitism competence is influenced by different host plant species of *M. vitrata* in West Africa (Souna et al., 2019). Infested cowpea pods and flowers are preferred over non-infested parts, while infested pods are preferred over infested flowers. What is more, non-infested pods are preferred over infested flowers. In terms of 3 alternative host plants of *M. vitrata viz. L. sericeus*, *S. rostrata* and *T. platycarpa* only the *T. platycarpa* significantly attracts *T. javanus*, where infested flowers are preferred over the non-infested flowers.

In laboratory *T. javanus* successfully parasitizes first and second larvae instars 80% of the time (Souna et al., 2021). The full life cycle of *T. javanus* takes 15.35 – 16.73 days depending on the age of the host at the time of parazitation, where development is faster on a 2 and 3 day old *M. vitrata* larvae compared to 4 day old larvae (Table 19). Egg development takes 1.94 days. There are three larval stages (Figure 6), which last 3.04, 2.04 and 1.84 days respectively. Approximately 8 days after parasitism the third instar larva egresses from the host and keeps feeding on the host by sucking contents through the egression hole. When the host contents are empty the third instar larva spins a cocoon and enters a prepupal stage. Duration of prepupal and pupal stages is 1.1 and 5.65 days respectively (Souna et al., 2018).

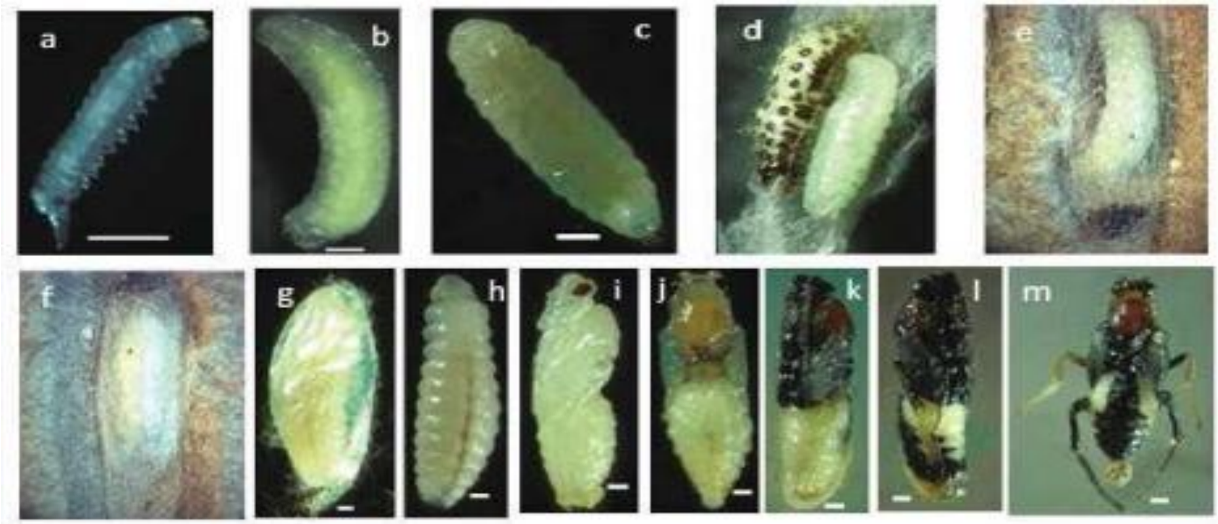

Figure 6 Development of immature stages of *Therophilus javanus*. a-first larval instar, b-second larval instar, c-third larval instar, d-third larval instar egressed from *Maruca vitrata* caterpillar, e-third larval instar inside the silken cocoon of *M. vitrata*, f-aspect of silken cocoon of *M. vitrata* after formation of *T. javanus* cocoon, g-cocoon of *T. javanus*, h-pre-pupa, i-hyaline pupa, j-m-progressive body pigmentation during pupation.

The longevity of adult females is not significantly dependent on the age of the host at parazitation (Table 19). When larvae of *M. vitrata* are 2, 3 and 4 days old the longevity of *T. javanus* females is 5.46, 5.63 and 4.53 days respectively. The total development time from egg to adult is shorter when parasitizing younger instar larvae of *M. vitrata* with durations of 15.35, 15.43 and 16.73 days respectively when parasitizing 2, 3 and 4 day old larvae (Souna et al., 2018).

The age of host at parazitation impacts both the daily and the total amount of host parasitized, where parazitation is lowest on 4 day old *M. vitrata* larvae with the mean daily 10.67 and total 35.93 host parasitized. In comparison daily parazitation is 16.66 and 18.68 hosts with total parazitation of 66.63 and 92.03 hosts respectively, when parazitation occurs on 2 and 3 day old *M. vitrata* larvae. Mean number of cocoons formed (parazitation success) and adult emergence are also affected by host age at parazitation with the highest number observed when a 2 day old larvae is parasitized with values of 32% and 25% respectively. When a 3 day old larva is parasitized the values are 22% and 16% respectively. (Souna et al., 2018). Survival rate of the host is not affected by the age of the host at parazitation. Overall, the mortality of parasitized *M. vitrata* is higher than successful *T. javanus* cocoon formation and adult emergence with 30% and 20% of the parasitized host forming a complete pupa ,when parasitized at 2 days and 3 days old respectively (Souna et al., 2018). *T. javanus* is a synovigenic and emerges with only part of all of its eggs already mature, while continuing to mature the rest throughout the life. There is a high degree of variation in the number of ovarioles, with the most ovarioles being present in females that emerge from second instar of *M. vitrata* (Souna et al., 2017). There is also a tendency for more eggs being carried by older females, hence the highest number of mature eggs is reported in 5 day old *T. javanus* females that emerged from second instar of *M. vitrata*. The number of adult offspring produced per female is 66.63, 92.03 and 35.93 respectively when parasitizing 2, 3 and 4 day old *M. vitrata* (Souna et al., 2018; Souna et al., 2021).In terms of sex ratio of the parasitoid's progeny there is a tendency for a higher male proportion 55-60% regardless of the host's age at the moment of parazitation (Souna et al., 2018).

Table 19 Life history parameters of *Therophilus javanus*. Source: Souna et al., (2018).

Parameter	Value	Conditions
Egg-cocoon development time in days	At 26 °C: E 1.94 L1 3.04 L2 2.04 L3 1.84 Average: 8.86	Average of egg and first three instar larvae from 3 day old parasitized *M. vitrata* larvae fed sprouting cowpea grains
Cocoon formation success rate %	At 26 °C: 2 day old: 0.32 3 day old: 0.22 Average: 5.2	From 2 and 3 days old parasitized *M. vitrata* larvae fed sprouting cowpea grains
Cocoon – adult development time in days	At 26 °C: PP 1.1 P 5.65 Average: 6.75	Average of pre-pupae and pupae inside the cocoon from 3 day old parasitized *M. vitrata* larvae fed sprouting cowpea grains
Adult emergence %	At 26 °C: 2 day old: 25% 3 day old: 16% Average: 20%	From 2 and 3 days old parasitized *M. vitrata* larvae fed sprouting cowpea grains
Female longevity in days	At 26 °C: 2 day old: 5.46 3 day old: 5.63 4 day old: 4.53 Average: 5.2	Average of female longevity from 2, 3 and 4 days old parasitized *M. vitrata* larvae
Sex ratio (% females progeny)	At 26 °C: 2 day old: 39 3 day old: 42 Average: 40.5	Average from 2 and 3 days old parasitized *M. vitrata* larvae fed sprouting cowpea grains
Fecundity	At 26 °C: 2 day old: 66.63 3 day old: 92.03 4 day old: 35.93 Average: 64.9	Average fecundity from 2, 3 and 4 days old parasitized *M. vitrata* larvae fed sprouting cowpea from a 5 day year old *T. javanus*
Parazitation daily and total	At 26 °C: 2 day old: 16.66 and 66.63 3 day old: 18.68 and 92.03 4 day old: 10.67 and 35.93 Average: 15.43 and 64.86	Average of 2 and 3 days old parasitized *M. vitrata* fed sprouting cowpea grains
Survival rate of parasitized *M. vitrata* %	At 26 °C: 2 day old: 30% 3 day old: 20% Average: 25%	Average from 2 and 3 days old parasitized *M. vitrata* larvae fed sprouting cowpea grains that successfully completed pupa development

4.2. Model conceptualization

System analysis suggests a number of important system components some of which are used in conceptualizing the model (Table 20). The exotic parasitoid *P. syleptae* is omitted, because there is a lack of published scientific literature in terms of life table parameters.

Table 20 System components and their inclusion/exclusion in the model conceptualization.

Components	Inclusion	Conceptualization
Cowpea		
Response to photoperiodism	Not included	Non-photosensitive variety – flowering is not influenced by photoperiod, but by temperature
Time to maturity	Included	Early maturing variety – 60 days to maturity
Variety of geographical locations	Not included	Only Sahel region is represented in terms of prevalent variety and sowing dates
Rainfall pattern	Included	Beginning of cowpea development date is in accordance to the prevailing onset of rainfall in the region
Flowering capacity	Included	Amount of flowers per plant in accordance to the variety
Life cycle	Included	Development stages include pre-vegetative (seed germination), seedling emergence, vegetative (leaf appearance), flowering and maturity stages
Maruca vitrata		
Migration pattern based on alternative host plants, winds or rainfall	Not included	Influence of availability of alternative host plants, prevalent wind directions or rainfall on migration of *M. vitrata* is not taken into account
Immigration into cowpea fields	Included	Immigration begins if cowpea flowers are present in the field. Immigration rate depends on maximum infestation value
Feeding behavior	Included	Larvae consume flowers based on their reported capacity to consume flowers through life
Infestation levels	Included	Infestation levels vary year to year and region to region. However the maximum infestation value reported in the Sahel region determines the immigration rate of *M. vitrata*
Life cycle	Included	Development stages include egg, larvae, pupa and adult stages
Life table parameters	Included	Only the duration of each of the development stages, the oviposition capacity of adult females and the sex ratio of the progeny are considered.
Humidity effect on oviposition capacity	Not included	The oviposition capacity of *M. vitrata* is shown to be affected by humidity levels, however oviposition is fixed in the model.
Exotic parasitoids		
Host search on different alternative host plants	Not included	The efficacy of the exotic parasitoids might vary depending on what *M. vitrata* host plant it has to prey on, however these attributes are not considered.
Competition	Included	Competition between *A. taragamae* and *T. javanus* in terms of allocating available prey to them e.g. 50/50.

Table 21 continued

Components	Inclusion	Conceptualization
Exotic parasitoids		
Immigration into cowpea fields	Included	Immigration begins if *M. vitrata* larvae are present
Feeding behavior	Included	When preying on *M. vitrata* larvae every parazitation/attack is considered successful
Life cycle	Included	Development stages include egg, cocoon and adult stages
Life table parameters	Included	Only the duration of each of the development stages, the oviposition capacity of adult females and the sex ratio of the progeny are considered. Duration in days. However, *A. taragamae* sex ratio depends on age of *M. vitrata* at parazitation, which is not included in the model.
Reproductive biology	Not included	The egg load of *T. javanus* is influenced by both the age of *M. vitrata* larva at parazitation and the age of *T. javanus* female, however oviposition per female is fixed in the model
Virus vectoring	Not included	*A. taragamae* has the capacity to transmit *M. vitrata* specific nucelopolyhedrosis virus (*Mavi*MNPV), however the impact of this virus on the population dynamics is not considered

Out of 21 components 7 are not included in the model conceptualization. Firstly, the variety of geographical locations across West Africa is not considered due to a substantial variation in rainfall, onset and duration of the rainy seasons with consequent variation of cowpea cultivars tailored to the prevalent conditions in terms of purpose, response to photoperiodism and time to juvenility. However, it is still crucial to think about West African landscape in terms of annual precipitation, because it helps to correlate a cultivar with a geographical location and to determine the planting dates in accordance to the prevalent rainfall pattern (Figure 7).

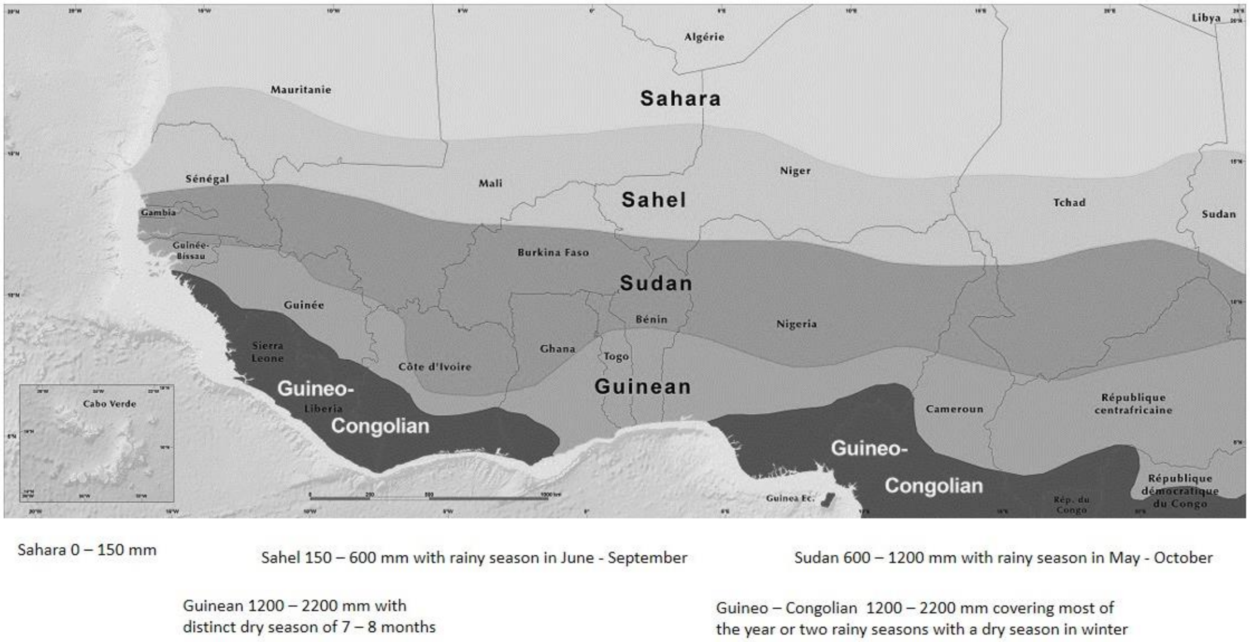

Figure 7 Climate zones, rainfall and period of rainfall in West Africa. Source: USGS (2019). Rainy season occurrence rainfall and the duration of rainy season gradually increase from Sahara to Guineo-Congolian zone. In the latter there is a possibility for two cropping seasons, because of two distinct rainy seasons throughout the year (C. S. Kamara & Godfrey-Sam-Aggrey, 1979).

Second and third components not to be included have to do with alternative host plants of *M. vitrata* and respectively the impact the alternative host plants have on both the migration patterns of *M. vitrata* and the parasitizing capacity of exotic parasitoids. The fourth omitted component has to do with humidity effect on oviposition capacity of *M. vitrata. A. taragamae*’s ability to transmit a pathogenic virus to *M. vitrata* and hence the consequences on the population dynamics it has are not included either. The last component not to be included is the reproductive biology of *T. javanus*, where it emerges with a certain amount of mature eggs and keeps maturing new eggs throughout its lifetime with a dependency of the egg load on the age of the host at parazitation as well as the age of *T. javanus* female.

Even though life table parameters are included they only cover duration of various development stages, the fecundity of adult females and the sex ratio of the offspring, while mortality rates of various development stages or successful pupa/cocoon formation or adult emergence are omitted. Life table parameters are used together with life cycles and temperature data to conceptualize the model in a stage structured approach (Figure 8) i.e. all phenological stages are conceptualized as separate populations, which are connected to each other and through which the initial population moves as it ages. The duration of developmental stages is temperature dependent and lasts in degree-days wherever possible, otherwise the duration is in days. When population moves from the *‘Oviposition’* stage it is multiplied by the average female lifetime fecundity adjusted for the sex ratio.

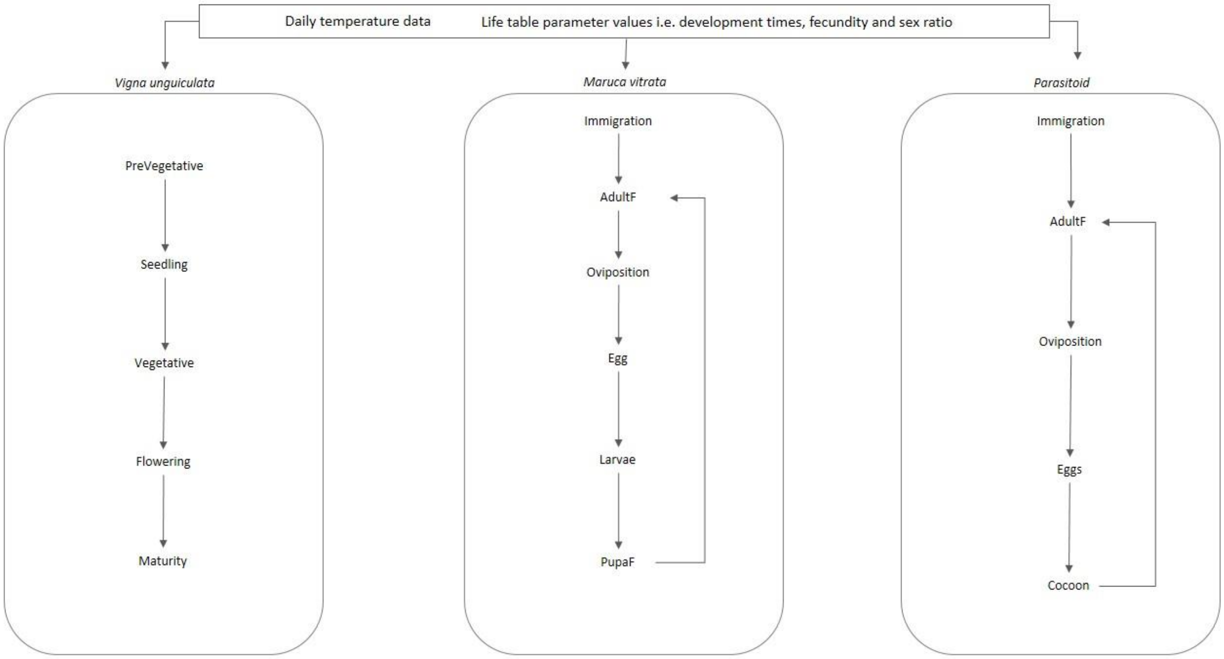

Figure 8 Stage structured approach to modelling cowpea, *M. vitrata* and parasitoids. Respective population goes through a series of phenological stages connected via inflow and outflow of each stage.

While life table parameters and life cycles are crucial for the stage structured conceptualization, the flowering capacity of cowpea, immigration levels, infestation levels and feeding behaviors of *M. vitrata* and of the exotic parasitoids are crucial for conceptualizing the trophic interactions. Initial population of either *M. vitrata* or the exotic parasitoids depends on their immigration when their respective prey is present (Figure 9) i.e. *M. vitrata* is immigrating if cowpea flowers are present, while exotic parasitoids immigrate if *M. vitrata* larvae are present. The rate of immigration of *M. vitrata* depends on its reported maximum infestation density level, while the rate at which the exotic parasitoids immigrate is to be investigated.

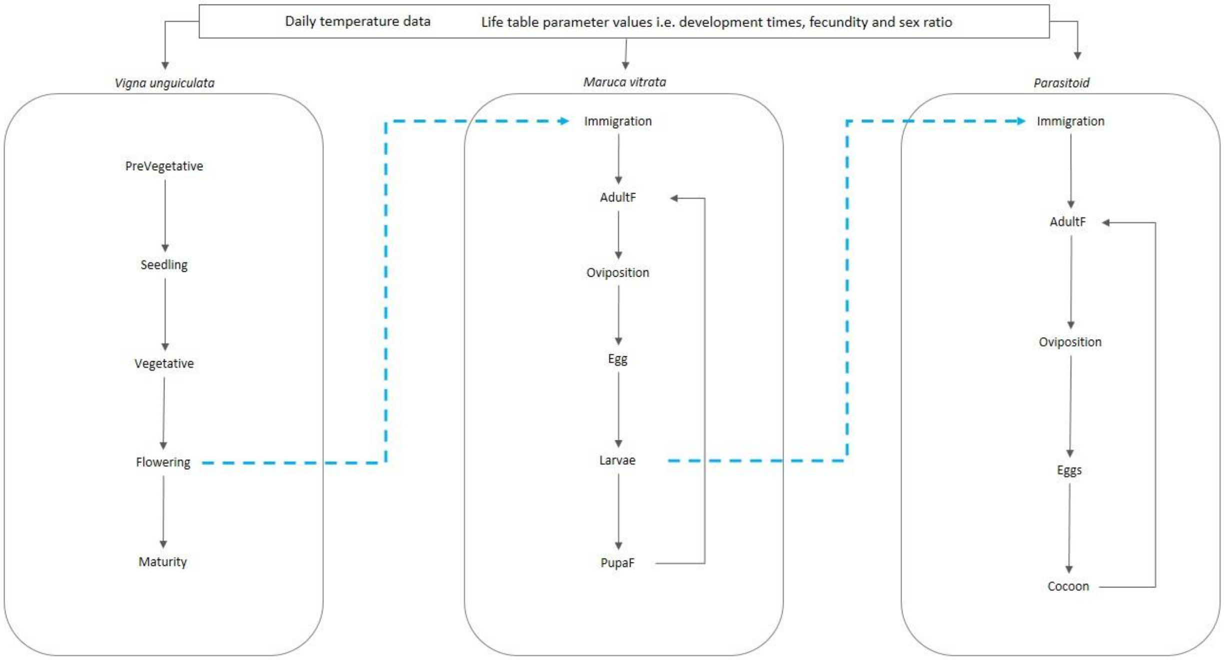

Figure 9 Initial populations of the pest moth *Maruca vitrata* and the exotic parasitoids *Apanteles taragamae* and *Therophilus javanus* are initiated by immigration of adult females to the cowpea field at a fixed rate and begins respectively, when *Vigna unguiculata* flower population and *M. vitrata* larvae population values are higher than 1 and stops, when the values are lower than 1

In terms of feeding behavior the distinction between the larvae of *M. vitrata* is made, where 1st and 2nd larvae are grouped to represent young larvae, while 3rd, 4th and 5th represent old larvae. Only the young larvae prey on cowpea flowers. The dependence of *M. vitrata* larvae population on the availability of cowpea flowers is conceptualized in terms of outflowing egg population representing a demand for potential *M. vitrata* larvae i.e. egg can turn to larvae, if there is enough flowers for the larvae to finish their development. Such relationship reduces cowpea flowers, based on the amount of eggs to be hatched, making *M. vitrata* larvae population limited by the availability of cowpea flowers i.e. if larvae demand is 3 flowers and there are 150 eggs of *M. vitrata*, but only 30 flowers of cowpea, then only 10 larvae of *M. vitrata* will come about, while cowpea will lose all 30 flowers. The resulting young larvae of *M. vitrata* become a resource for the exotic parasitoids, where the same principle applies i.e. outflowing parasitoid eggs represent a demand for *M. vitrata* larvae. The only difference is that *M. vitrata* needs 3 flowers of cowpea to come about, while either of the parasitoids needs 1 larva of *M. vitrata* to come about (Figure 10).

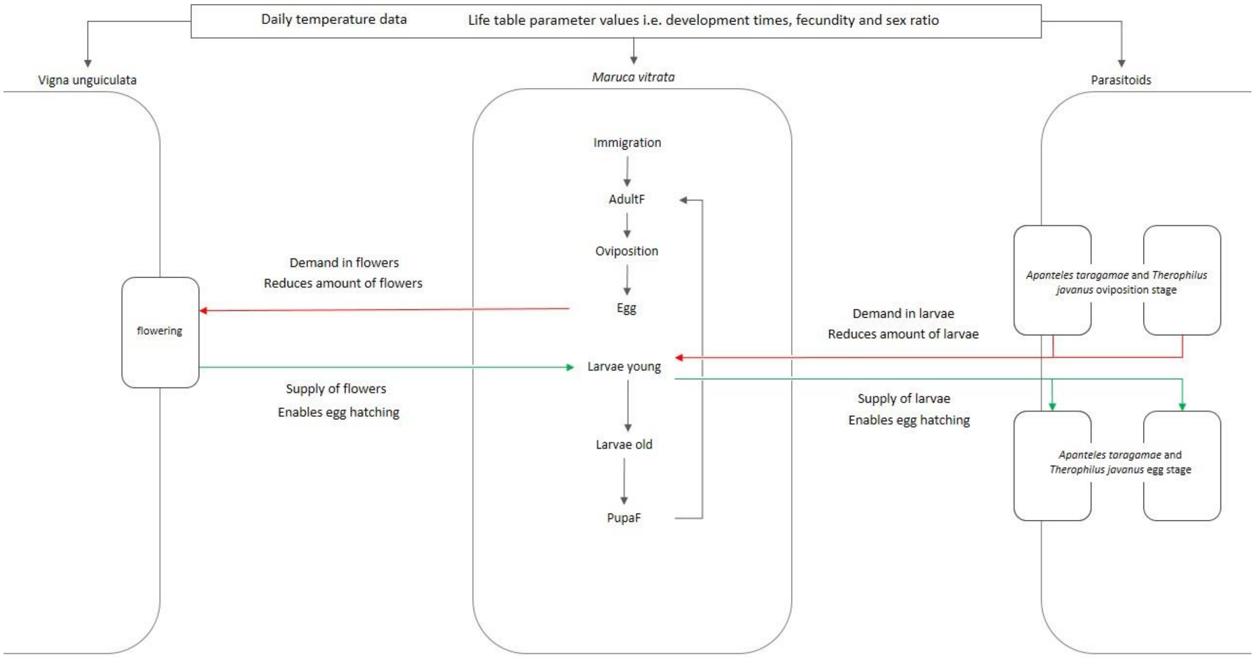

Figure 10 Conceptualized trophic interactions between cowpea, *Maruca vitrata* and either of the exotic parasitoids *Apanteles taragamae* or *Therophilus javanus*. The acquired resources turn into consumers' population growth.

Lastly, the model can be conceptualized with either of the parasitoids immigrating alone or together. The latter represents competition between the *A. taragamae* and *T. javanus* in terms of allocating available prey to them e.g. 50/50 (Figure 11).

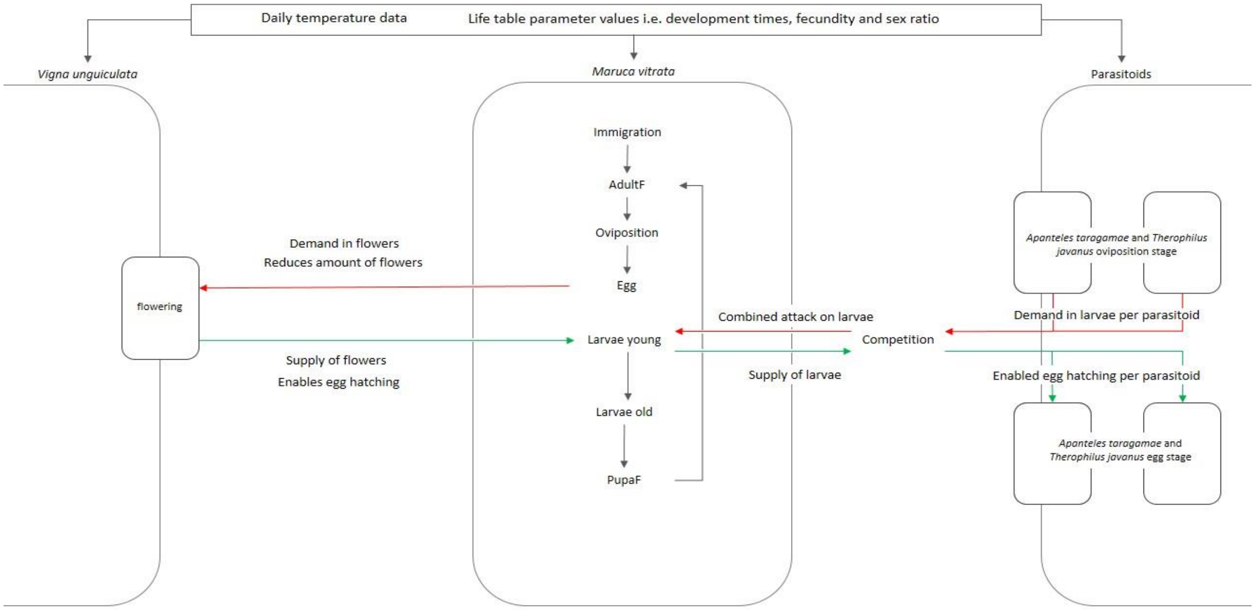

Figure 11 Conceptualized trophic interactions between cowpea, *Maruca vitrata* and both of the exotic parasitoids *Apanteles taragamae* and *Therophilus javanus*. The acquired resources turn into consumers' population growth.

4.3. Model evaluation

4.3.1. Temperature dependent development – thermal time scale

Simulation of *M. vitrata* population with unlimited resources starts on July 1st of 2009 in Maradi, Nigeria and July 1st of 2017 in Save, Benin with respective location temperature data. The average daily temperature falls within *M. vitrata's* developmental lower and upper thermal thresholds in Save, while in Maradi it sometimes falls above the upper thermal threshold. Consequently, the daily day degrees are being accumulated continuously in Save and interruptedly in Maradi (Figure 12). The closer the daily average temperature is to the optimal development temperature, the more day degrees per day are accumulated and the shorter the development period. When the average daily temperature is above the upper thermal threshold or below the lower thermal threshold the temporal development stops, because daily day degrees are not being accumulated in this period and the population cannot outflow into the next stage. Larvae population hangs until the temperature is within the thermal thresholds again resulting in a longer larvae development time in Maradi.

Additionally, one simulation is run in Maradi 2009 on July 16th with 0.1 *M. vitrata* adult females immigrating per m^2, where *M. vitrata* depends on cowpea flowers. In this scenario *M. vitrata* population can be increasing even if the daily temperature is outside the thermal thresholds, because new larvae are hatching from eggs (Figure 13).

The model behaves accordingly to the prevalent temperature, where development rate increases above the lower threshold for development (T0) until it reaches the optimal development threshold (Topt), where it starts to decrease until the upper development threshold (Tmax), where development ceases. Additionally, if the daily average temperature is outside lower or upper thermal thresholds, development ceases until average daily temperature falls within the thermal thresholds again, hence increasing duration of development and affecting the population density. However, when trophic interactions are involved the population in question can keep increasing instead of stagnating, because the inflow into the population depends on the availability of resources and thermal thresholds of the previous phenological stage.

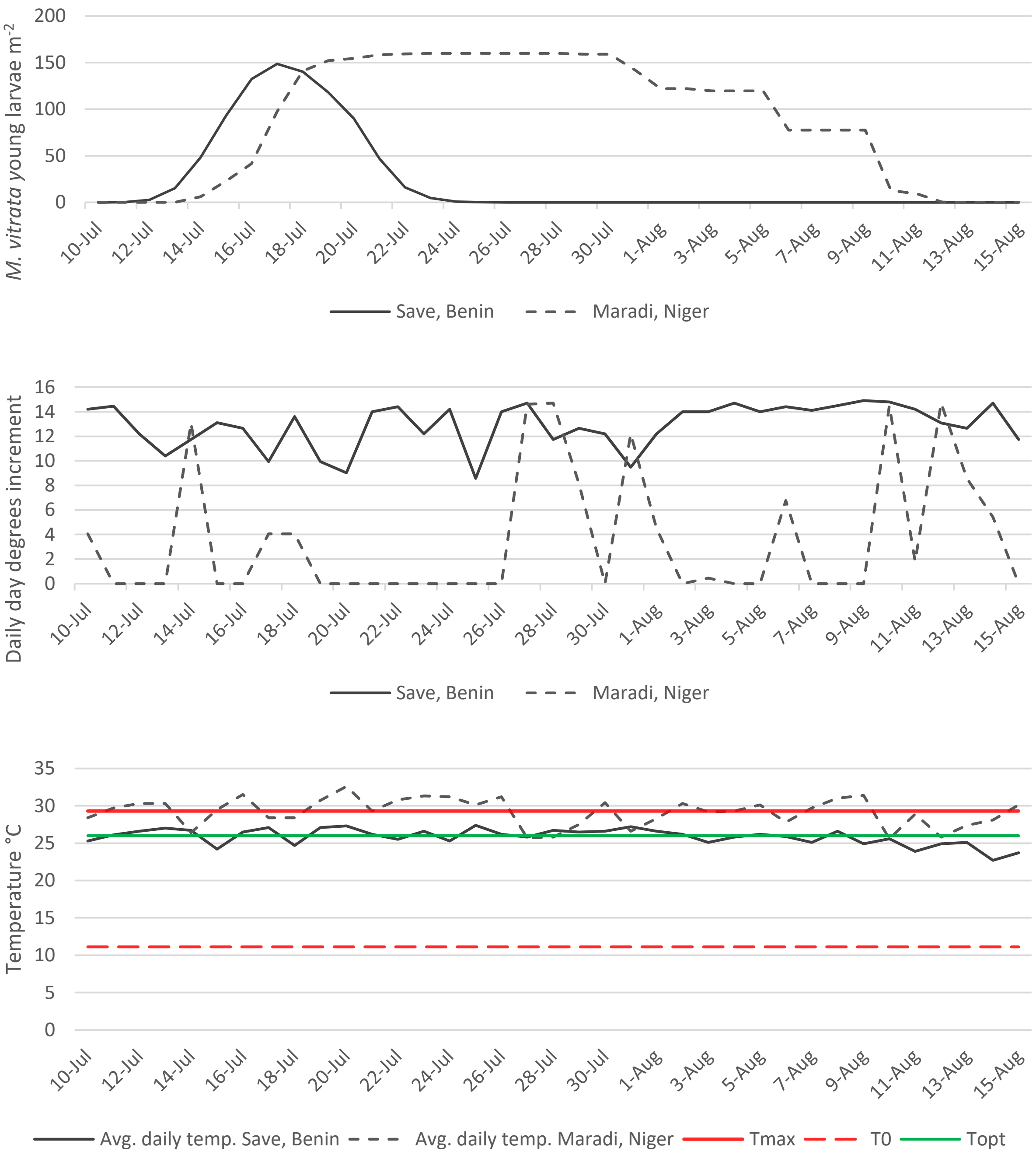

Figure 12 Temporal development of young *M. vitrata* larvae (1st and 2nd larvae instars) population density m^{-2}. Daily average temperature is close to the optimal development temperature (Topt) in Save, Benin 2017 and above the Topt and sometimes above the upper thermal threshold (Tmax) of in Maradi, Niger 2009. The further the daily average temperature is from the T_{opt} the less day degrees are accrued on a given day. When daily average temperature is above the Tmax, then the daily day degrees increment is equal to 0 (red boxes). As a result in Save, Benin temporal development of *M vitrata* population density m^{-2} is shorter compared to Maradi, Niger.

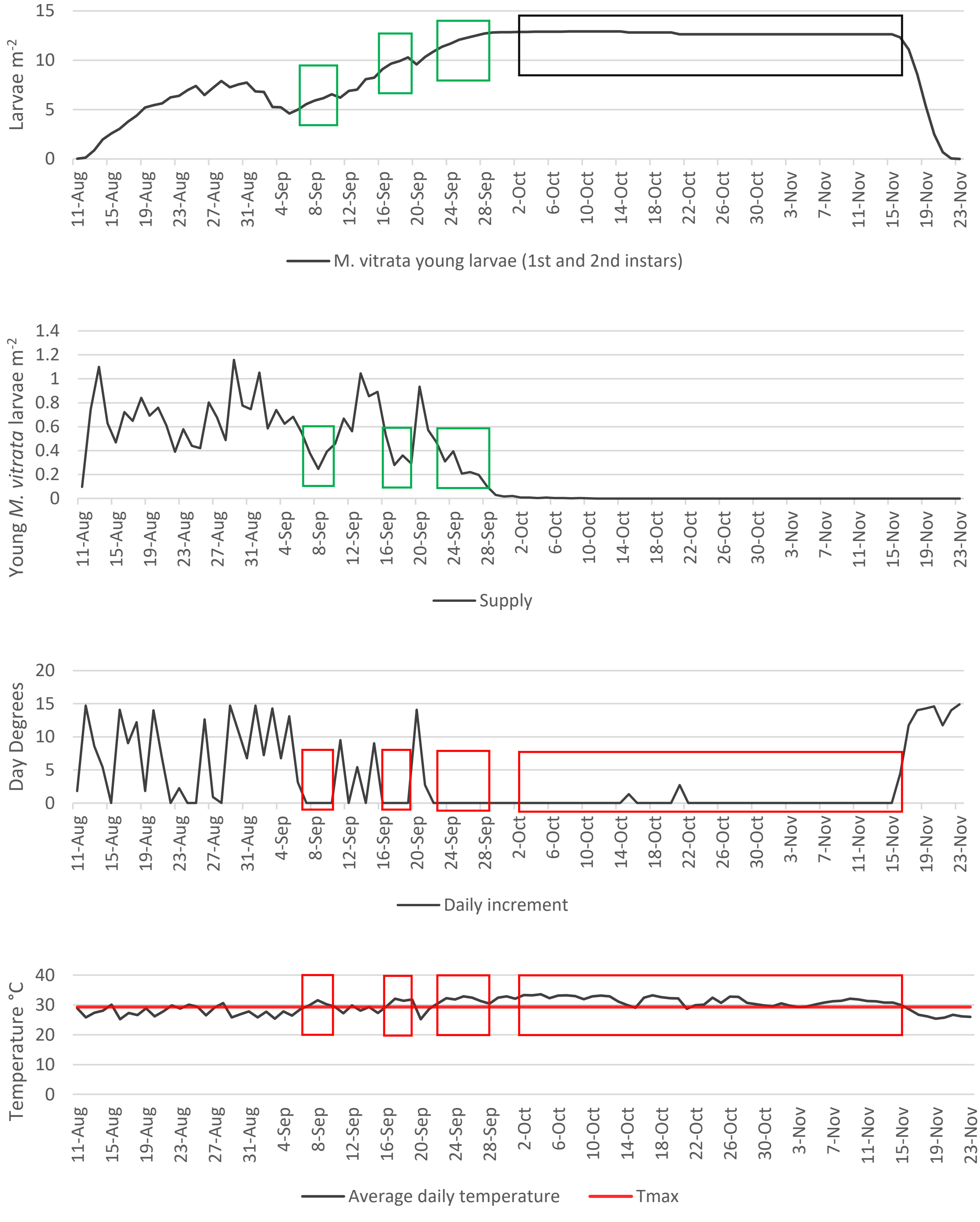

Figure 13 Temporal development of young *M. vitrata* larvae (combined 1st and 2nd) population density m^{-2}. When daily average temperature is above the upper thermal threshold Tmax, then the daily day degrees increment in this period is equal to 0 (red boxes). As a result, larvae population density both stagnates (black box), because there is no new larvae hatching and keeps increasing (green boxes), because there are available resources in terms of cowpea flowers for new larvae to be supplied. Location and temperature data: Maradi, Niger 2009.

4.3.2. Trophic interactions

4.3.2.1. *M. vitrata* and cowpea

First trophic interaction to be tested is between cowpea and *M. vitrata*. A series of simulations are run, where the number of cowpea flowers produced per m^2 and the number of young *M. vitrata* larvae produced per m^2 are the response parameters, while the number of immigrating adult *M. vitrata* females per m^2 per day and *M. vitrata*'*s* demand in cowpea flowers per young larva are the experimental model parameters. The relationship between cowpea and *M. vitrata* is tested when simulation runs with one of the experimental model parameters fixed and the other varied, consequently looking at the output values of response variables (Table 21).

When consumption demand of *M. vitrata* decreases, more *M. vitrata* larvae can appear. However, because larvae consume less overall, more total cowpea flowers are present. Respectively, as immigration rate of *M. vitrata* increases, the total larvae infestation increases and the total amount of cowpea flowers decreases (Figure 14).

Table 21 Effect of experimental model parameters (a) adult *M. vitrata* females immigrating m^{-2} per day and (b) *M. vitrata* young larvae demand on response variables (c) cowpea flowers produced per m^2 and (d) young *M. vitrata* larvae produced per m^2. Cowpea is simulated as being planted on 1st of August 2019 in Sokoto, Nigeria at a density of 13 plants per m^2 and 40 flowers per plant resulting in 520 flowers produced m^{-2} without immigrating pest *M. vitrata* (first line in the table). Consequent immigration of *M. vitrata* begins when cowpea begins to flower and the simulation experiment is carried out with one of the experimental model parameters being fixed, while the other varies (varying experimental model parameters are shaded in grey). Development of both cowpea and *M. vitrata* is simulated based on temperature data of 2019 in Sokoto, Nigeria.

Experimental model parameters		Response parameters	
(a) *M. vitrata* adult females immigrating m^{-2} per day	(b) *M. vitrata* demand in flowers $larva^{-1}$	(c) *V. unguiculata* cowpea flowers produced m^{-2}	(d) *M. vitrata* young larvae produced m^{-2}
0	0	520	0
0.02	3	495.712	8.09611
0.05	3	462.721	19.0929
0.1	3	411.298	36.2341
0.4	3	167.605	117.465
0.05	1	498.904	21.0956
0.05	3	462.721	19.0929
0.05	10	350.201	16.9799
0.05	20	218.389	15.0805

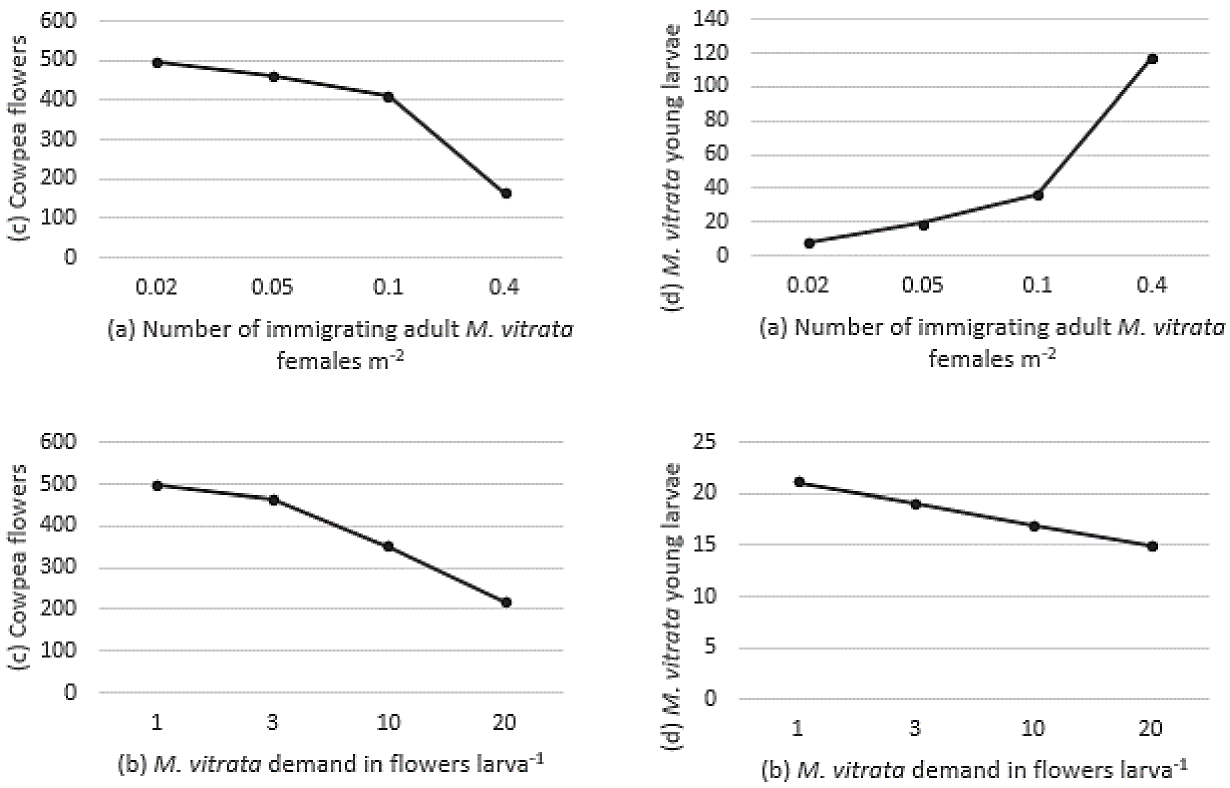

Figure 14 Effect of experimental model parameters (a) adult *M. vitrata* females immigrating m^{-2} and (b) *M. vitrata* young larvae demand on response variables (c) cowpea flowers produced per m^2 and (d) young *M. vitrata* larvae produced per m^2.

4.3.2.2. *M. vitrata* and *T. javanus*

Next trophic interaction is tested between *M. vitrata* and its parasitoids. A series of simulations are run, where the number of young *M. vitrata* larvae produced per m^2 per day and the number of *T. javanus* cocoons produced per m^2 are the response parameters, while the number of immigrating adult *T. javanus* females per m^2 per day and the attack rate (number of attacks per number of hosts per day, where 1 attack equals 1 kill) of *T. javanus* are the experimental model parameters. Similarly to the previous experiment the relationship between *M. vitrata* and *T. javanus* is tested when simulation runs with one of the experimental model parameters fixed and the other varied, consequently looking at the output values of response variables (Table 22).

With an increasing attack rate of *T. javanus*, the population of young *M. vitrata* larvae decreases, while more parasitoid cocoons are produced. Respectively, when the immigration rate of *T. javanus* increases, the parasitoid cocoon population increases, while *M. vitrata* young larvae population decreases (Figure 15).

Table 22 Effect of experimental model parameters (a) adult *T. javanus* females immigrating m^{-2} and (b) *T. javanus* attack rate (number of attacks per number of hosts per day) on response variables (c) young *M. vitrata* larvae produced per m^{2} and (d) *T. javanus* cocoon produced per m^{2}. Cowpea is simulated as being planted on 1st of August 2019 in Sokoto, Nigeria at a density of 13 plants per m^{2} and 40 flowers per plant with *M. vitrata* immigrating at a rate of 1 adult female m^{-2} per day with a lifetime demand of 3 flowers per larva, resulting in 172.6 young larvae of *M. vitrata* produced per m^{-2} (first line in the table). Consequent immigration of *T. javanus* begins when *M. vitrata* young larvae are available and the simulation experiment is carried out with one of the experimental model parameters being fixed, while the other varies (varying experimental model parameters are shaded in grey). Development of both *M. vitrata* and *T. javanus* is simulated based on temperature data of 2019 in Sokoto, Nigeria.

Experimental model parameters		Response parameters	
(a) *T. javanus* adult females immigrating m^{-2} per day	(b) *T. javanus* attack rate	(c) *M. vitrata* young larvae produced m^{-2}	(d) *T. javanus* cocoon produced m^{-2}
0	0	172.6	0
0.01	0.95	148.549	24.0235
0.2	0.95	53.0825	119.49
0.5	0.95	7.90825	164.664
0.9	0.95	5.7637	166.809
2	0.95	4.30808	168.264
0.5	0.1	35.7616	136.811
0.5	0.2	17.7843	154.788
0.5	0.5	9.00201	163.57
0.5	0.75	8.12082	164.452
	0.95	7.90825	164.664

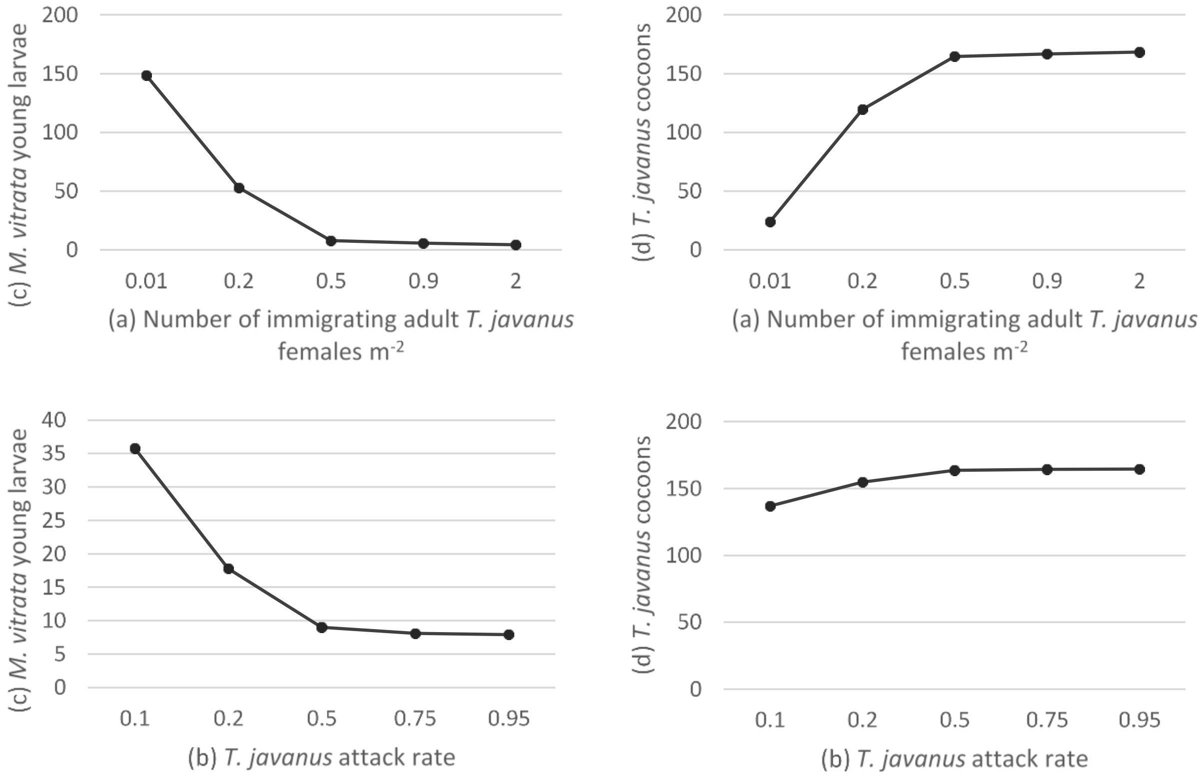

Figure 15 Effect of experimental model parameters (a) adult *T. javanus* females immigrating m^{-2} and (b) *T. javanus* attack rate (number of attacks per number of hosts per day) on response variables (c) cowpea flowers produced per m^{2} and (d) young *M. vitrata* larvae produced per m^{2}.

4.3.2.3. *T. javanus* and *A. taragamae* competition

Last trophic interaction is tested between the parasitoids *A. taragamae* and *T. javanus*. It is a competition simulation based on parasitoids' chances of finding the prey and the affect it has on their respective population size. A series of simulations are run, where *T. javanus* cocoons produced per m^2 and *A. taragamae* cocoons produced per m^2 are the response parameters, while *T. javanus* chances of finding prey and *A. taragamae* chances of finding prey are the experimental model parameters. The relationship between the parasitoids is tested when simulation runs with parasitoids having different chances of finding the available prey (i.e. if *T. javanus* chances of finding the prey are 40% then only 40% of the total available prey is available to the *T. javanus*, while the rest 60% is available to *A. taragamae*). Consequently, the effect on the output values of response variables is looked at (Table 23).

With increasing or decreasing chances of finding the prey the population of the parasitoid increases or decreases respectively (Figure 16).

Table 23 Effect of experimental model parameters (a) *T. javanus* chances of finding prey and (b) *A. taragamae* chances of finding prey on response variables (c) *T. javanus* cocoons produced per m^2 and (d) *A. taragamae* cocoons produced per m^2. Cowpea is simulated as being planted on 1st of August 2019 in Sokoto, Nigeria at a density of 13 plants per m^2 and 40 flowers per plant with *M. vitrata* immigrating at a rate of 1 adult female m^{-2} per day with a lifetime demand of 3 flowers per larva. Consequent immigration of *T. javanus* and *A. taragamae* of 0.5 adult females m^{-2} per day begins when *M. vitrata* young larvae are available, with both parasitoids' attack rate (number of attacks per number of hosts per day with 1 attack resulting in 1 kill) of 0.95, resulting in 112.926 and 52.0193 cocoons respectively (first line in the table). The simulation experiment is carried out with both of the experimental model parameters being varied. Development of cowpea, *M. vitrata*, *T. javanus* and *A. taragamae* is simulated based on temperature data of 2019 in Sokoto, Nigeria.

Experimental model parameters		Response parameters	
(a) *T. javanus* chances of finding the prey	(b) *A. taragamae* chances of finding the prey	(c) *T. javanus* cocoons produced m^{-2}	(d) *A. taragamae* cocoons produced m^{-2}
50%	50%	112.926	52.0193
90%	10%	136.942	28.0036
70%	30%	124.937	40.0087
30%	70%	100.911	64.0344
10%	90%	88.8919	76.0193

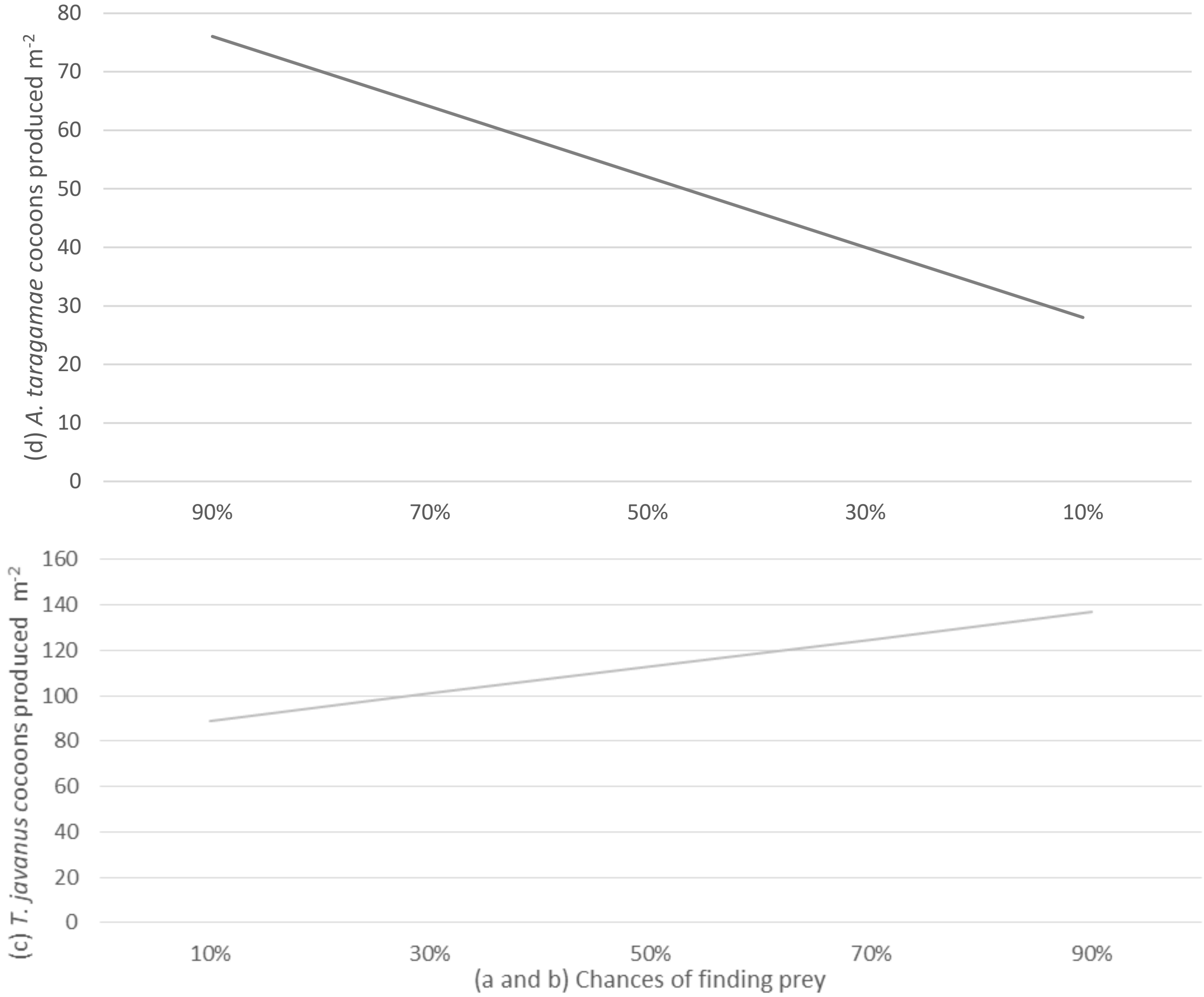

Figure 16 Effect of experimental model parameters (a) *T. javanus* chances of finding prey and (b) *A. taragamae* chances of finding prey on response variables (c) *T. javanus* cocoons produced per m^2 and (d) *A. taragamae* cocoons produced per m^2.

4.3.3. Temporal development

Lastly, the behaviour of the model is tested to simulate the population density of *M. vitrata* young larvae throughout the cowpea growing season. The model simulates Baoua et al. (2011) report about cowpea grown on residual moisture, however only some of the parameter values needed to run the simulation are reported. As a result, the missing values are either worked out by running the model (tuned) or estimated from other scientific literature (estimated) (Table 24). The most important tuning parameter is the immigration rate of adult *M. vitrata* females per m^2 per day, which is tuned to reach the desired peak larval infestation density per m^2 reported by Baoua et al. (2011). What is more, authors do not report the planting date of cowpea, so the date is set to reflect the reported beginning of infestation. Additionally, obtained temperature data for the reported location (Maradi, Nigeria) is sporadic and incomplete, however it is available for the Niamey, which is a city close by on the same latitude (NCEI, 2022).

Table 24 Parameters used in the simulation of Baoua et al. (2011) report about *M. vitrata* population density development, parameter values and parameter value origins.

Model parameters	Value	Parameter status
Location temperature data*	Niamey, Niger*	Known
Planting date	16th of July 2008 17th of July 2009	Tuned
Planting density m^{-2}	7.16	Known
Flowers $plant^{-1}$	40	Estimated
Immigrating *M. vitrata* adults m^{-2} day^{-1}**	0.004 (2008) 0.0835 (2009)	Tuned Tuned
Peak *M. vitrata* flower infestation density m^{-2}***	0.716 m^{-2} (2008) 12.9 m^{-2} (2009)	Known
Life cycle flower demand of *M. vitrata* larva	3 flowers $larva^{-1}$	Estimated

* Model driver. Temperature data for Niamey city located nearby on the same latitude as Maradi is used, because available temperature data for Maradi is not complete (NCEI, 2022).

** Immigration rate m^{-2} day^{-1} is tuned to reflect the peak infestation density of *M. vitrata* m^2.

*** Peak infestation density m^{-2} is the target parameter according to which the immigration rate of *M. vitrata* is being adjusted.

Planted in the middle of July (tuned planting date) at a reported planting density of 7.16 plants per m^2 and immigration rate (tuned) of 0.004 *M. vitrata* adults per m^2 per day for 2008 and 0.0835 adults per m^2 per day for 2009, the model respectively produces the corresponding *M. vitrata* peak larval infestation density of 0.716 larvae per m^2 for 2008 and 12.9 larvae per m^2 for 2009 and density of (Figure 17).

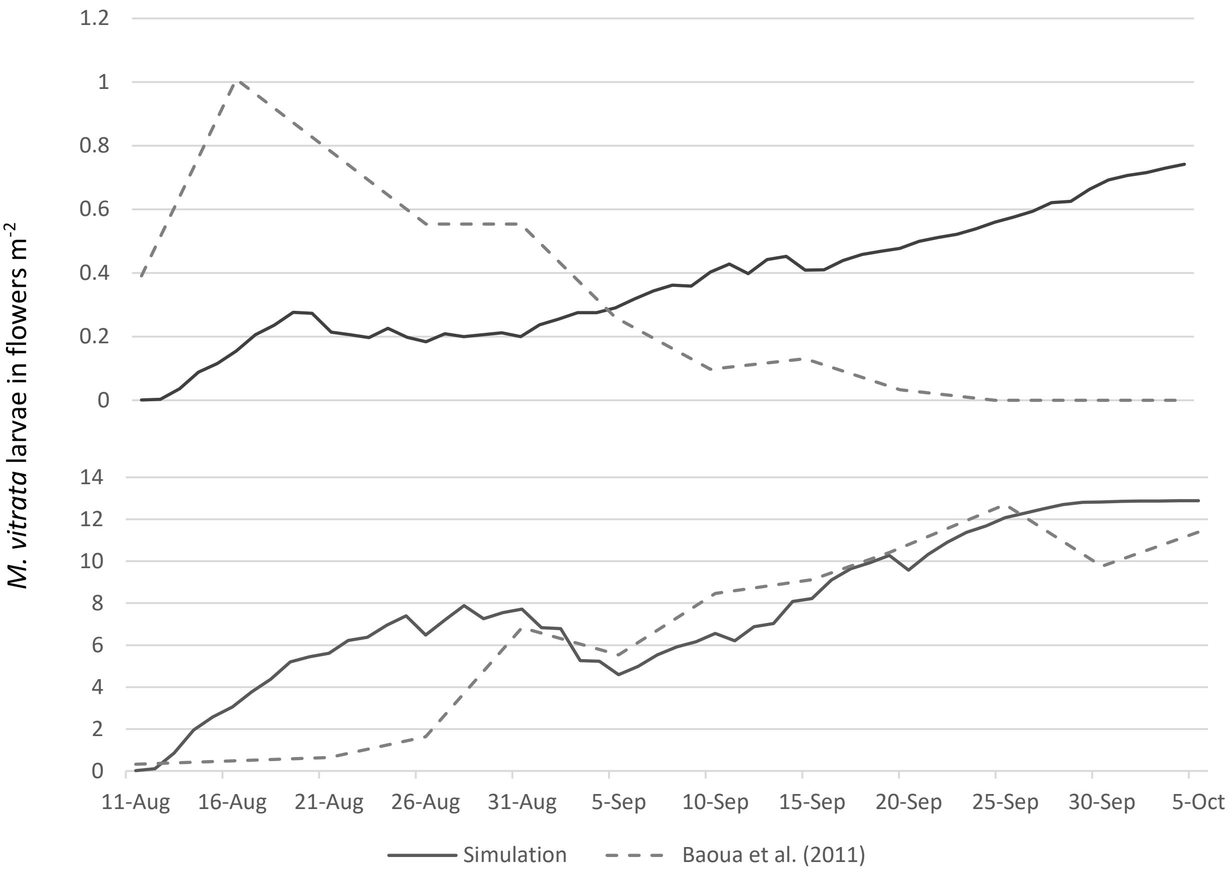

Figure 17 Population of young *M. vitrata* larvae in cowpea flowers in the period of August to October (2008 top chart; 2009 bottom chart) according to the simulation (solid line) and Baoua et al. (2011) (dashed line). Simulation is tuned in accordance to the Baoua et al. (2011) reported peak infestation density values of 0.716 larvae per m^2 for 2008 and 12.9 larvae per m^2 for 2009 in Maradi, Niger, resulting respectively in immigration rate of 0.004 (2008) and 0.0835 (2009) adult *M. vitrata* females per day per m^2. Simulation runs with planting date set to 16th of July for 2008 and 17th of July for 2009 at a planting density of cowpea of 7.16 per m^2 with *M.* vitrata life cycle demand of 3 flowers per larva. Temperature data is used for Niamey, a city located nearby Maradi on the same latitude.

Simulated *M. vitrata* population over the cowpea growing season matches the reported peak infestation densities for both 2008 and 2009 due to tuned immigration rates of *M. vitrata* adult females per m^2 per day. However simulated development of the population density is similar to the field data only for 2009.

4.4. The simulation experiment

4.4.1. Sokoto 2019

In 2019 in Sokoto, Nigeria the effect of the introduced parasitoids on the population of *M. vitrata* varies depending on the parasitoid immigration scenario, reducing young larvae population density per m^2 between 22% – 96.1% (Figure 18). When immigration rates of *T. javanus* are 10%, 20% and 50% of the immigration rate of *M. vitrata*, then the young larvae population per m^2 is respectively reduced by 42.4%, 72.4% and 96.1%, (Table 25). The effect of *A. taragamae* immigration rates equal to 10%, 20% and 50% of the immigration rate of *M. vitrata* reduces total larvae population per m^2 by 22%, 39.6% and 69.5% respectively (Table 26). The effect of combined immigration of *T. javanus* and *A. taragamae* totalling 10%, 20% and 50% of immigration rate of *M. vitrata*, reduces total larvae population per m^2 by 33.2%, 57.7% and 92.3% respectively (Table 27).

Table 25 Effect of three different *Therophilus javanus* immigration rates of adult females per m^2 on *Maruca vitrata* young larvae population, when immigration of *T. javanus* is 10%, 20% or 50% of the 1.3 immigrating adults of *M. vitrata* per m^2.

Therophilus javanus immigration rate	*Maruca vitrata* Young larvae	Effect
0	173.3 m^{-2}	
10% = 0.13 m^{-2}	99.8 m^{-2}	Reduced by 42.4 %
20 %= 0.26 m^{-2}	47.9 m^{-2}	Reduced by 72.4 %
50% = 0.65 m^{-2}	6.7 m^{-2}	Reduced by 96.1 %

Table 26 Effect of three different *Apanteles taragamae* immigration rates of adult females per m^2 on *Maruca vitrata* young larvae population produced per m^2, when immigration of *A. taragamae* is 10%, 20% or 50% of the 1.3 immigrating adults of *M. vitrata* per m^2 daily.

Apanteles taragamae immigration rate	*Maruca vitrata* Young larvae	Effect
0	173.3 m^{-2}	
10% = 0.13 m^{-2}	135.1 m^{-2}	Reduced by 22 %
20% = OR 0.26 m^{-2}	104.7 m^{-2}	Reduced by 39.5 %
50% = 0.65 m^{-2}	52.9 m^{-2}	Reduced by 69.5 %

Table 27 Effect of three different, combined immigration rates of *Therophilus javanus* and *Apanteles taragamae* adult females per ^{m2} on *Maruca vitrata* young larvae population, when combined immigration of the parasitoids is 10%, 20% or 50% of the 1.3 immigrating adults of *M. vitrata* per m^2. Both the immigration rates and chances of finding the prey are split equally.

A. taragamae immigration rates	*T. javanus* Immigration rates	*M. vitrata* Young larvae	Effect
0	0	173.3 m^{-2}	0
5 % = 0.065 m^{-2}	5% = 0.065 m^{-2}	115.7 m^{-2}	Reduced by 33.2 %
10% = 0.13 m^{-2}	10% = 0.13 m^{-2}	73.3 m^{-2}	Reduced by 57.7 %
25% = 0.325 m^{-2}	25% = 0.325 m^{-2}	13.3 m^{-2}	Reduced by 92.3 %

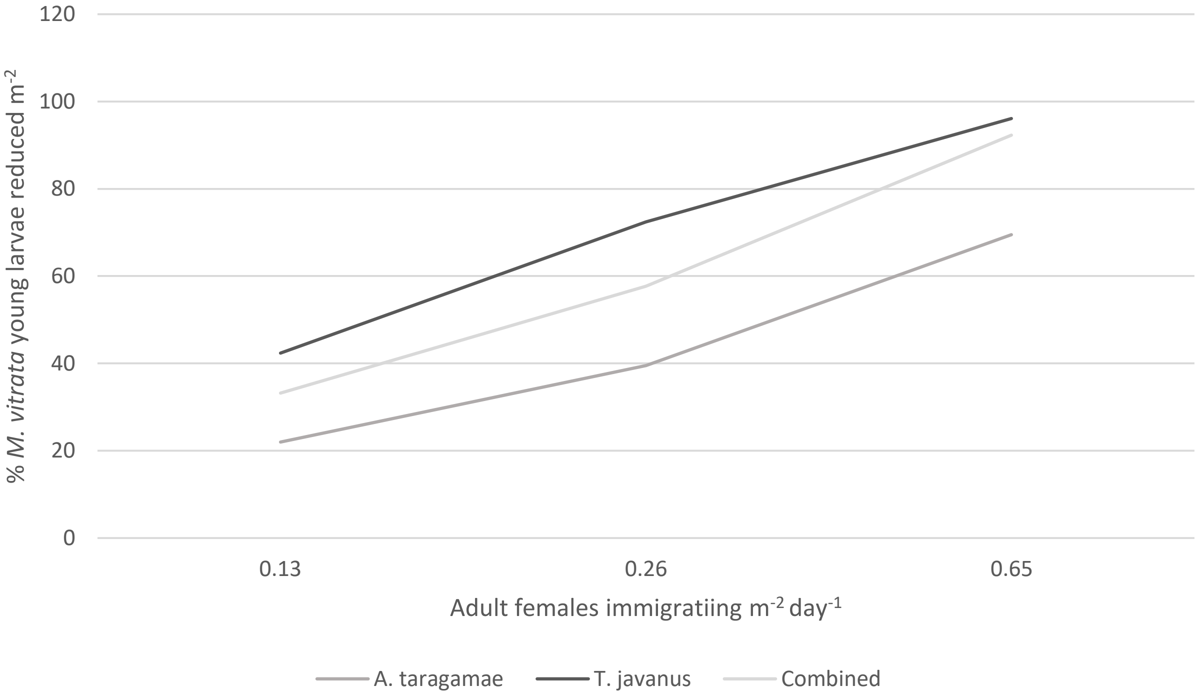

Figure 18 Effect of parasitoids on *M. vitrata* young larvae population in 2019.

4.4.2. Sokoto 2020-2050

In 2020 to 2050 in Sokoto, Nigeria the effect of the introduced parasitoids on the of young *M. vitrata* larvae population per m^2 varies depending on the immigration rate and year, reducing young larvae population per m^2 between 20% - 99%. Increasing immigration rates increase the reduction effect, where immigration at 10% of the *M. vitrata* immigration rate roughly reduces *M. vitrata* per m^2 by 20-40%, at 20%.by 40-70% and at 50% by 50-95%. Future temperature does not change the pattern of how the immigration scenarios affect *M. vitrata* i.e. *T. javanus* shows highest reduction and *A. taragamae* shows the lowest reduction with the combined effect always in between the two (Figure 19).

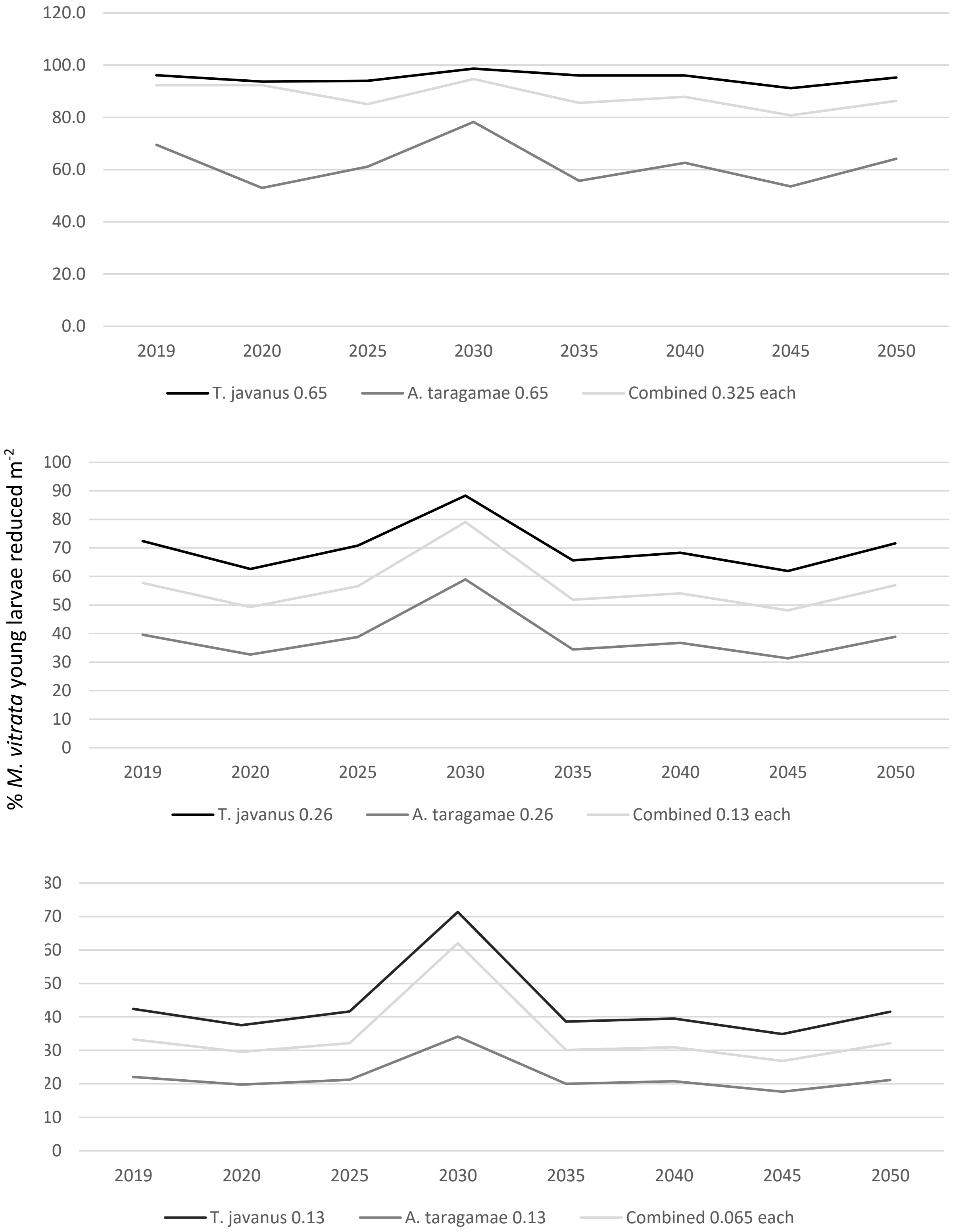

Figure 19 Effect of exotic parasitoids on *M. vitrata* in 2020-2050. Lowest graph shows the effect, when immigration is 0.13, mid graph – 0.26 and upper most – 0.65 adult females per m^2 daily.

5. Discussion

5.1. System analysis and conceptualization

System analysis reveals 21 component out of which 7 are not included into the conceptualization. Some of the excluded components such as cowpea photoperiodism response could be used together with various time to maturity to represent different geographical location with their specific cultivation needs (e.g. a dual purpose, medium maturing, photo-sensitive variety in the south and an early maturing, photoperiod-insensitive variety in the north). Other components such as *M. vitrata* migration pattern based on alternative host plant availability, wind direction and rainfall can enfold the previous two components and result in a model, where *M. vitrata* population dynamics in a cowpea field at a certain location is just a sub-model of the *M. vitrata* population dynamics throughout West Africa on south to north gradient. In such a model *A. taragamae's* virus vectoring ability and parasitoid host searching capacity relative to different alternative host plants can contribute to a more complete set of interactions to better describe effectiveness of exotic parasitoids as classical biological control agents and how they affect *M. vitrata* (Figure 20).

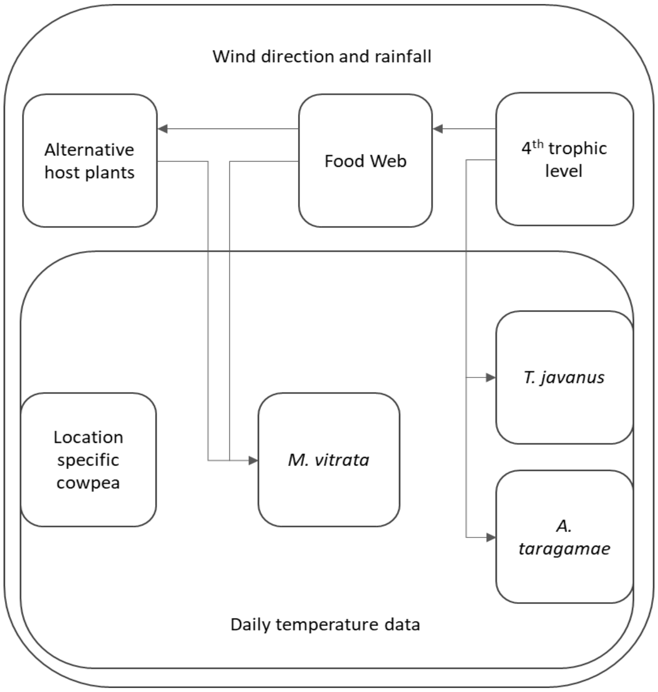

Figure 20 Expanded model of *M. vitrata* population dynamics. The current model is just a part of the bigger model. In addition to temperature data the model is also driven by rainfall and wind direction, which in turn influence the migration rate and time of *M. vitrata*. At the same time *M. vitrata's* food web influences the amount of *M. vitrata* available on the alternative host plants and in cowpea fields, while the 4th trophic level influences both the food web of *M. vitrata and* the parasitoids that act as biological control agents.

So, the current model can theoretically become a sub-model in a more inclusive model, if the above mentioned, excluded system components were to be included. However, in practice there might be a lack of quantified research as is the case with immigration rates of *M. vitrata* in relation to rainfall and humidity effect on oviposition capacity of *M. vitrata*. On the other hand, even when some quantified research is available, as is the case with the reproductive biology of *T. javanus*, the detail is excluded in the current model and oviposition is represented in a fixed estimate, because it presents a technical challenge. The same applies to *A. taragamae* sex ratio, where only males emerge from 1 day old *M. vitrata* larvae. The latter can be remedied with a Food Web approach of the Universal Simulator, where each of the development stages attack specific developmental stages of the host at specific rates and as a result the sex ratio can be more accurate (Holst, 2018). Similarly, the current simulation only focuses on the cowpea flowers and young *M. vitrata* larvae (1st and 2nd larvae instars), whereas it can be extended to include various pod developmental stages and additional *M. vitrata* larvae, which could be useful to estimate grain yield and parasitoids effect in reduction to yield damage (Figure 21).

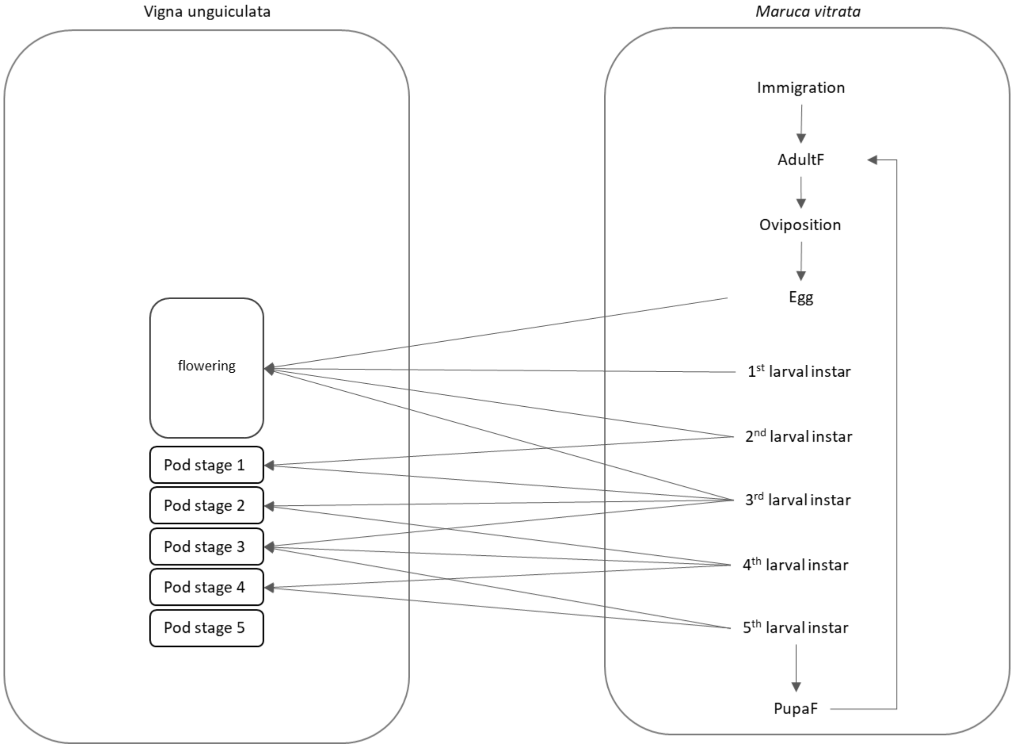

Figure 21 Example of a more detailed feeding behavior of *M. vitrata* on cowpea flowers. Each instar larva attacks a more realistically available development stage of cowpea e.g. 1st larvae instars attacks only the flowers, while the 2nd larvae already has a small chance of attacking the earliest pod, at the same time 3rd larvae instar attacks flowers at a small rate and 1st and 2nd stage pods at a high rate and 3rd stage at a lower rate etc.

What is more, the fixed estimate of *M. vitrata's* feeding behaviour (the amount of flowers per life cycle of *M. vitrata*) can be substituted with cowpea biomass, however this immediately requires extended system analysis and conceptualization of cowpea and *M. vitrata* growth as well as various thresholds e.g. how much biomass consumed results in a "dead" flower or pod.

When it comes to the temperature dependent development the current model has a drawback, because there is no literature on temperature influence on *T. javanus* development. Hence, even though there is research about *A. taragamae* developmental rate across a range of temperatures and hence thermal times can be estimated based on linear regression, neither of the parasitoids in the model depends on temperature in contrast to *M. vitrata* and cowpea.

5.2. Model validation

5.2.1. Temperature dependent development

It is well established that ectothermic species grow and develop in a certain range of temperatures, however it is a question whether species can change their range or whether the range is constrained. In the current model species' thermal range for development is fixed. As temperatures rise, it is expected that the rate of development increases until a certain point, where development stops as enzymes begin to denature. Current model responds to the daily temperatures, lower and upper development thermal thresholds and adjusts the development rate accordingly. When the daily temperature exceeds the upper thermal threshold the development stops. It is achieved by restricting the outflow of the population to the next phenological stage to 0. As a result, the population hangs until the temperature is within the thermal thresholds again to accumulate the needed amount of day degrees to be able to outflow again – to finish the development. This makes the development time longer, but it also can make the duration of the development unrealistic, when temperatures exceed the upper threshold for an extended period of time (Figure 22).

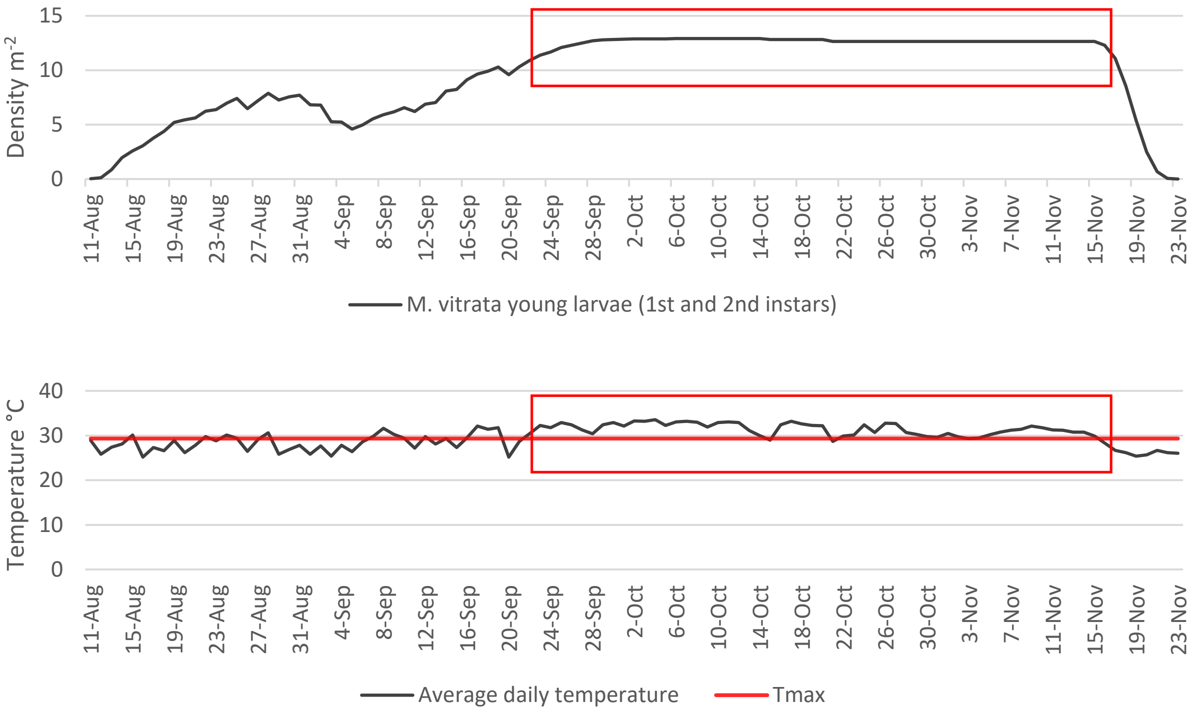

Figure 22 Unrealistic temperature dependent development of young *M. vitrata* larvae instar (combined 1st and 2nd) population density m^{-2}. The daily average temperature is above the upper thermal threshold Tmax of 29.3 °C. The daily day degrees in this period are equal to 0 (red boxes). In this example, when daily average temperature is above Tmax, larvae population density stagnates, because there is no new larvae hatching and no larvae completing their development (red boxes). Location and temperature data: Maradi, Niger 2009.

In the experiment above (Figure 22) this is not of a big concern, because the focus is only on the young *M. vitrata* larvae population density, which are assumed to infest only the flowers of cowpea. As a result, even though the duration of the whole life cycle is unrealistically extended, due to the unrealistic duration of young larvae, the amount of young larvae produced per m^2 is limited by the number of flowers per m^2 and eggs per m^2. Both cowpea flowers and *M. vitrata* eggs have a higher upper thermal threshold than *M. vitrata* young larvae making their development realistic. In case older *M. vitrata* larvae population density is used in the model it has to be looked at only with regards to cowpea flowering period (Figure 23).

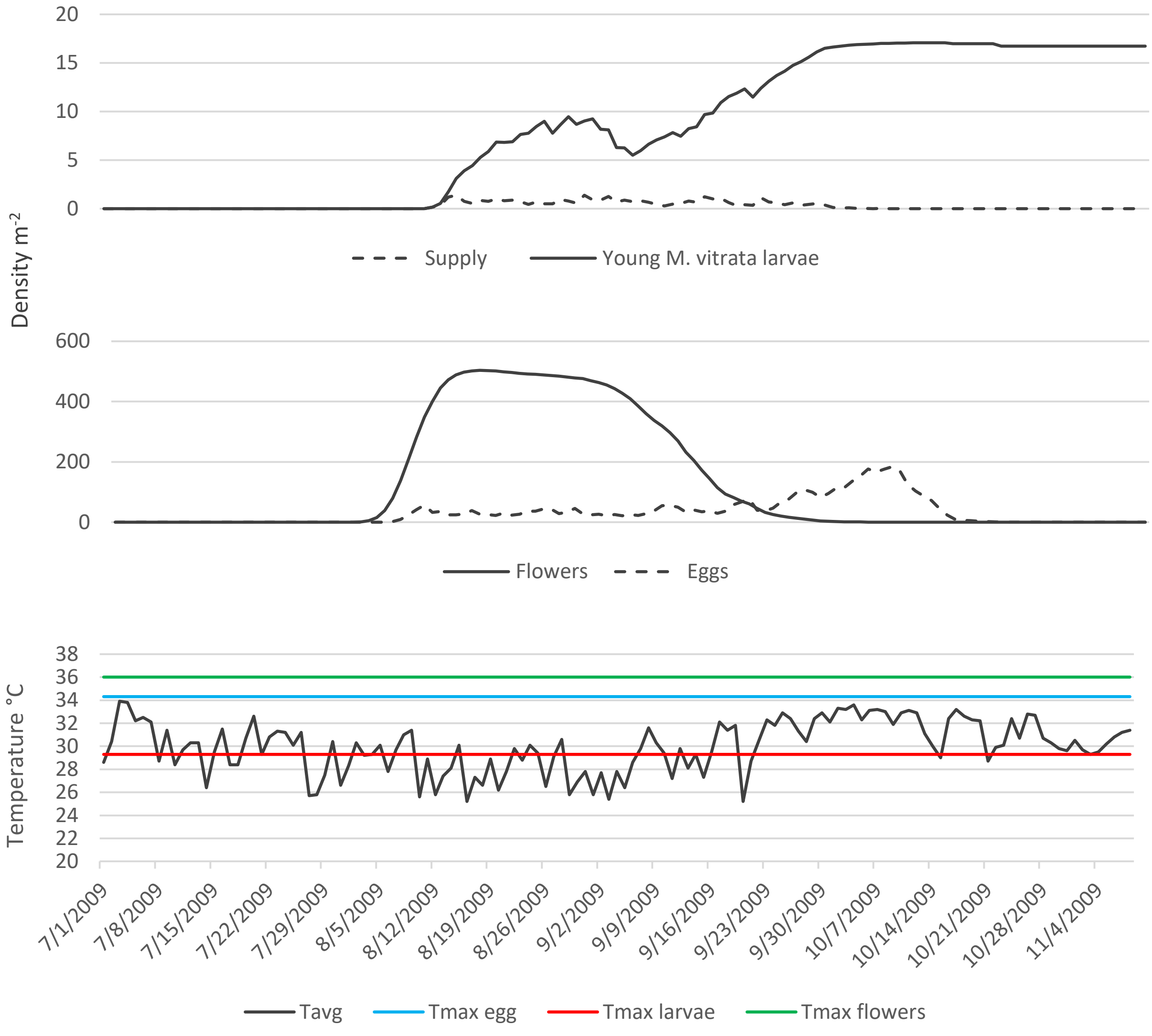

Figure 23 Resource availability and unrealistic temperature dependent. In such a situation the later phenological stages have to be evaluated critically, where the depletion of the resource is an indicator of the end of the current phenological stage i.e. when the resource ends, realistically there should soon not be any individuals left in the population.

5.2.2. Trophic interactions

5.2.2.1. *M. vitrata* and cowpea

Trophic interactions are purely calculative in terms of demand being converted to supply according to the availability of resources. However the relationship is not always straightforward. For example with increasing *M. vitrata* demand per larva the decrease in density is seen in both the cowpea flowers per m^2 and young *M. vitrata* per m^2. It is interesting that larvae population density seems to decrease linearly with the demand per larva increasing from 1 – 20 flowers, while cowpea flower density decreases sharper at higher values (Figure 24).

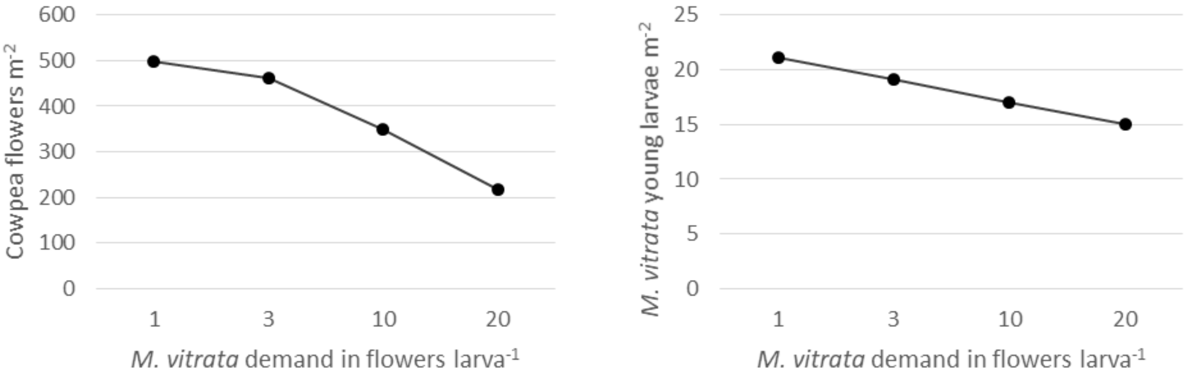

Figure 24 Effect of experimental model parameter *M. vitrata* young larvae demand on response variables cowpea flowers produced per m^2 and young *M. vitrata* larvae produced per m^2 with 0.05 *M. vitrata* adults immigrating daily per m^2. Cowpea is simulated as being planted on 1st of August 2019 in Sokoto, Nigeria at a density of 13 plants per m^2 and 40 flowers per plant resulting in 520 flowers produced m^{-2} without immigrating pest *M. vitrata.* Development of both cowpea and *M. vitrata* is simulated based on temperature data of 2019 in Sokoto, Nigeria.

With an immigration rate of 0.05 adult females per m^2 daily the temporal development of young *M. vitrata* population density is slightly different when demand is 1 – 3 flowers per larva compared to 3 – 20. It differs mainly in the duration of infestation due to a difference in duration of the available resources i.e. the less the demand per larva is, the longer the resources are available, the longer the infestation by young larvae. At the same time reduction of cowpea flowers happens according to the life time demand per larva i.e. higher demand means higher reduction of cowpea flowers. As a result, lower demand results in an additional spike in the population density and a bigger young *M. vitrata* larvae population moving on to the next developmental stage. Such behaviour explains why *M. vitrata* population density decreases as cowpea flower population density decreases (Figure 25).

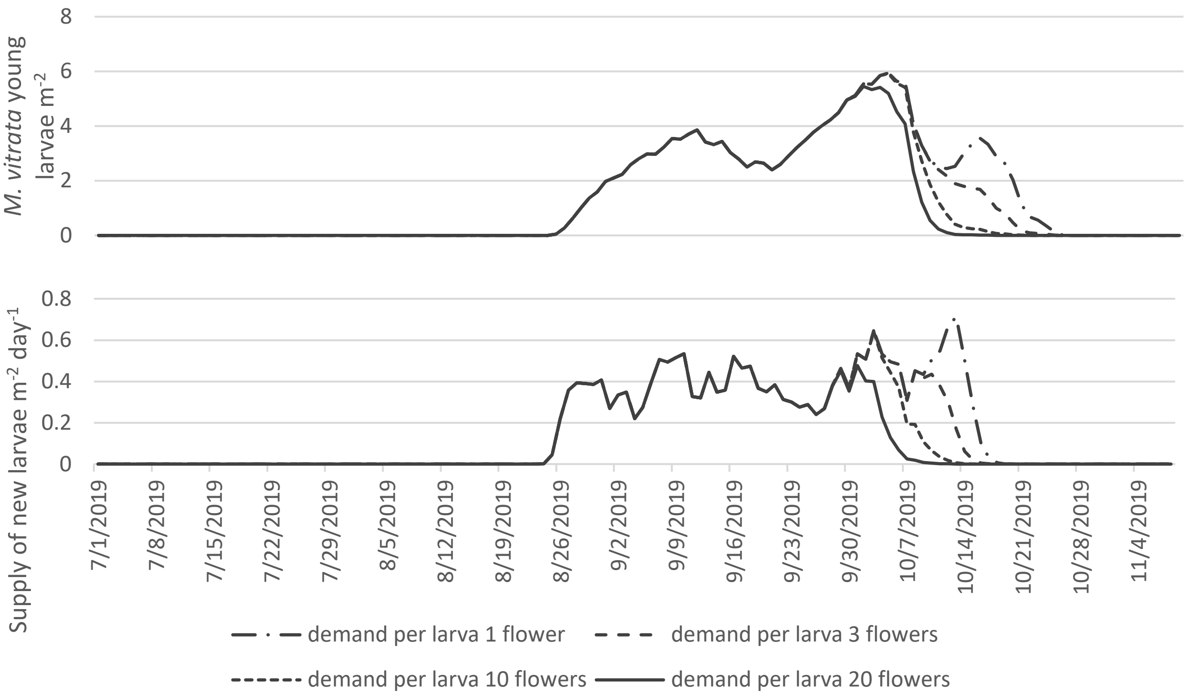

Figure 25 Supply of *M. vitrata* larvae and its effect on *M. vitrata* young larvae population density. Higher demands mean higher cowpea flower reduction, shorter infestation time and a smaller *M. vitrata* young larvae population. Cowpea is simulated as being planted on 1st of August 2019 in Sokoto, Nigeria at a density of 13 plants per m^2 and 40 flowers per plant and an immigration of 0.05 adult *M. vitrata* females per m^2 daily. Development of both cowpea and *M. vitrata* is simulated based on temperature data of 2019 in Sokoto, Nigeria.

Both density of cowpea flowers per m^2 and young *M. vitrata* larvae per m^2 respond almost linearly to the increasing daily immigration rates of *M. vitrata* female adults, however in opposite directions. When daily immigration of adult *M. vitrata* females per m^2 increases, a respective proportional increase in larval density happens. Similarly, cowpea flower density decreases proportionally to the increasing immigration rate (Figure 26).

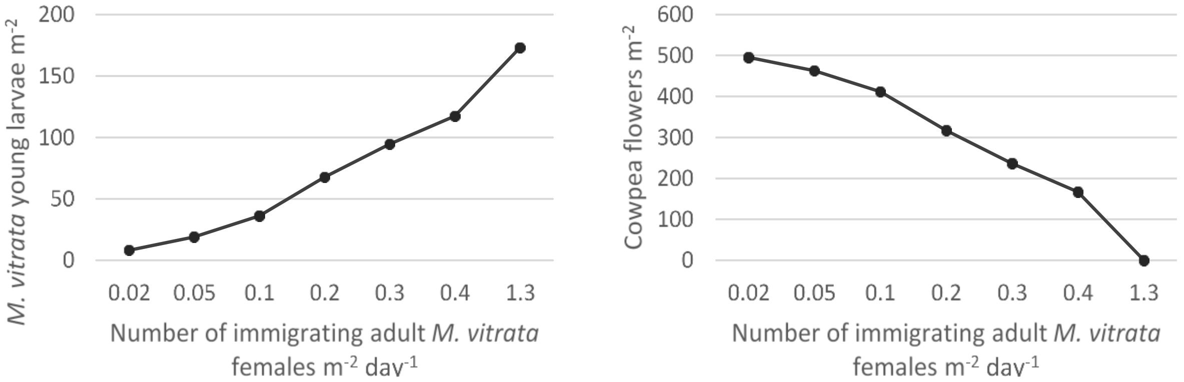

Figure 26 Effect of increasing daily immigrating rates of *M. vitrata* adult females per m^2 with a life cycle demand of 3 flowers per larva. At an immigration rate of 1.3 adult females per m^2 daily all of the cowpea flowers are consumed. Cowpea is simulated as being planted on 1st of August 2019 in Sokoto, Nigeria at a density of 13 plants per m^2 and 40 flowers per plant. Development of both cowpea and *M. vitrata* is simulated based on temperature data of 2019 in Sokoto, Nigeria.

It seems that *M. vitrata* young larvae population density is sensitive to new immigrating female adults in terms of more immigration means bigger population, while the amount the larvae will consume means smaller population. The latter can make realistic sense, because *M. vitrata* avoids laying eggs on already occupied flowers. Cowpea flower density is sensitive to both the demand per larva and *M. vitrata* immigration rate in terms flower density being reduced by both. At the same time, both cowpea flower density and young *M. vitrata* larvae density respond to the immigration rate of *M. vitrata* proportionally, as opposed to the effect of demand per larva, where the effect on flower density varies as demand per larva increases and stays almost the same in young *M. vitrata* larvae population.

5.2.2.2. *M. vitrata* and *T. javanus*

The effect of immigration rates of *T. javanus* in *M. vitrata* and *T. javanus* relationship is similar to what is seen between cowpea and *M. vitrata* relationship with different levels of *M. vitrata* immigration i.e. higher immigration of *T. javanus* means more host consumed and more *T. javanus* cocoons formed. However in contrast to the effect of increasing *M. vitrata* immigration rate, a sharper effect is seen in the lower values of *T. javanus* immigration rates on both the *M. vitrata* larvae population density and *T. javanus* cocoons density, both of which start to flatten as immigration increases above 0.5 *T. javanus* adult female per m^2 daily. In contrast *M. vitrata* has to immigrate at a rate of 1.3 adult females per m^2 daily to deplete the resource completely and reach its maximum production. The same effect is seen with increasing daily immigration of *A. taragamae* female adults, however it starts consuming close to its maximum at an immigration rate above 2 adult females per m^2 daily (Figure 27).

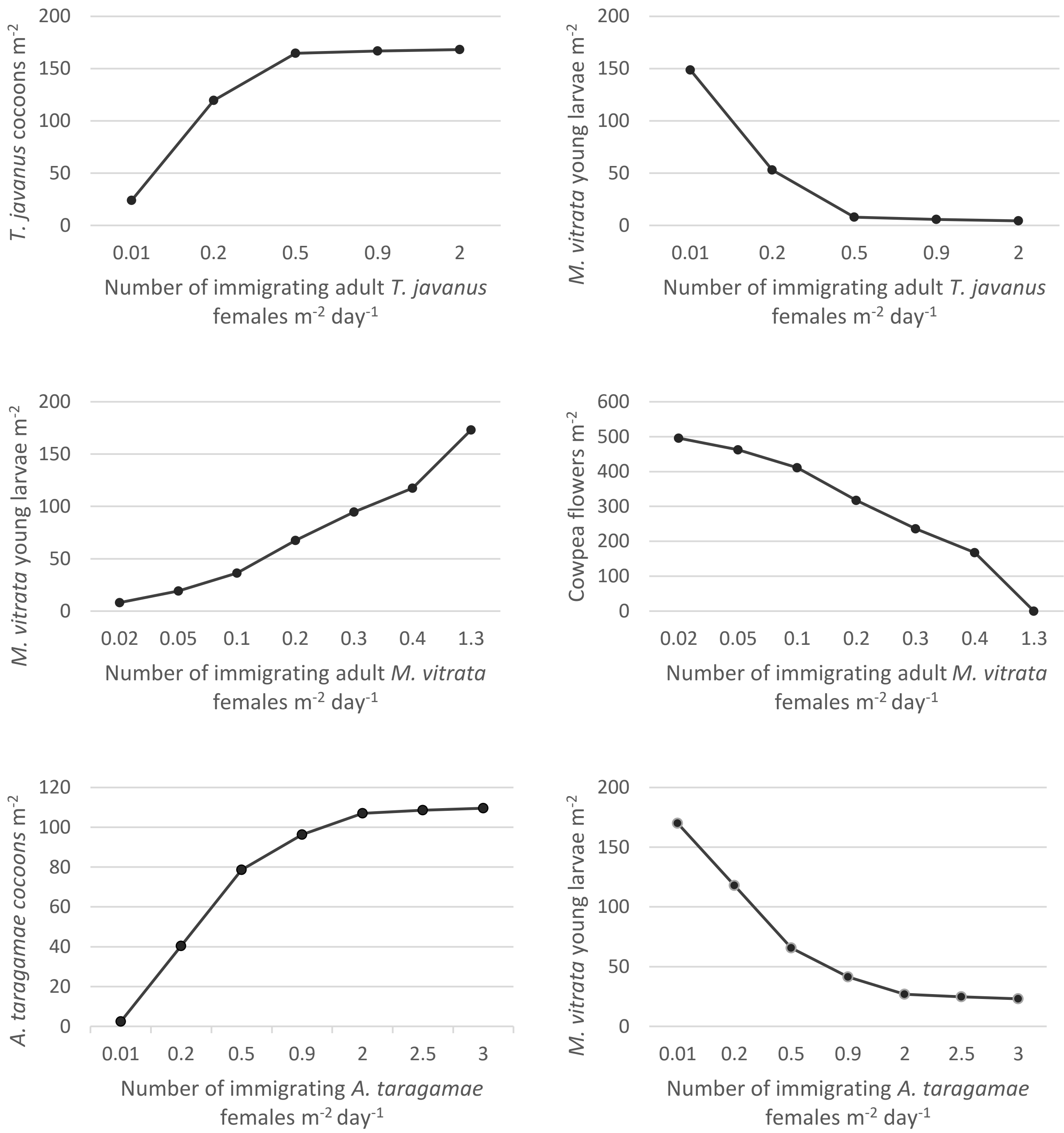

Figure 27 Effect of experimental daily immigration rates per m^2 of adult *M. vitrata, T. javanus* and *A. taragamae* on respective response variables cowpea flowers produced per m^2, young *M. vitrata* larvae produced per m^2 and parasitoid cocoons produced per m^2. Cowpea is simulated as being planted on 1st of August 2019 in Sokoto, Nigeria at a density of 13 plants per m^2 and 40 flowers per plant and *M. vitrata* larval demand of 3 flowers, while parasitoid attack rate is 0.95 (number of attacks per host per attacker per day, where one attack is one kill). Development of both cowpea and *M. vitrata* is simulated based on temperature data of 2019 in Sokoto, Nigeria.

The difference in outcomes between the two parasitoids of the effect of their immigration rates in general depends on the duration of developmental stages and fecundity of the parasitoids. *A. taragamae* has a lower fecundity (24 females for *A. taragamae* and 27.9 females for *T. javanus*) and a longer life cycle duration (25 days for *A. taragamae* and 20.8 days for *T. javanus*). The possible explanation as to why the effect of increasing *T. javanus* immigration rates flattens out earlier than the effect of *A. taragamae* immigration is that *T. javanus* achieves earlier maximum proportion of *M. vitrata* attacked in the growing season due to a shorter life cycle, with a big difference in the initial development, where it takes eggs of *A. taragamae* 8 days to develop in contrast to only 1.95 days to the eggs of *T. javanus*. Longer life cycle also results in longer periods, where the amount of parasitoids exceeds the amount of prey (young *M. vitrata* larvae) present as is the case with *A. taragamae*. As a result, more immigrating adults do not help increase consumption of prey (Figure 28).

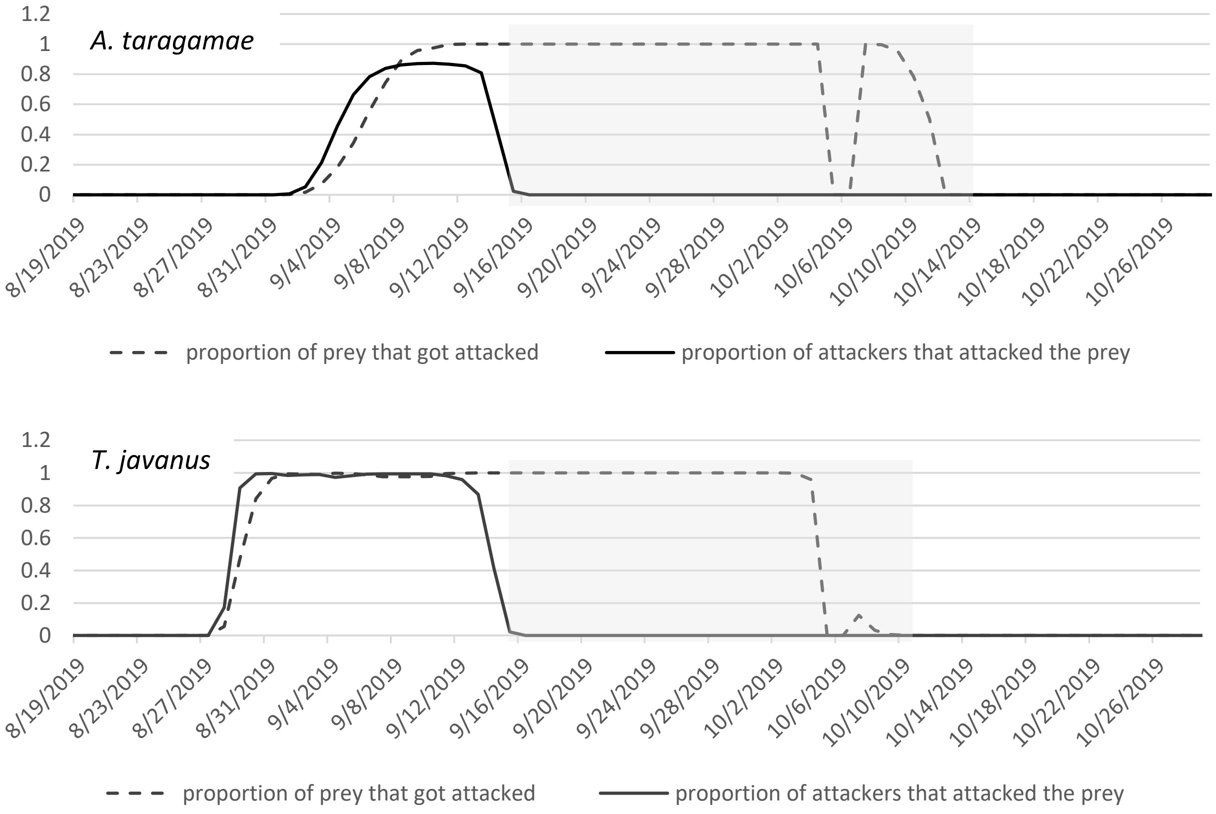

Figure 28 Attacking ratios of *T. javanus* (lower) and *A. taragamae* (upper). Immigration rate is 2 adult females per m^2 daily with an attack rate of 0.95 (number of attacks per host per attacker per day). Shaded areas represent periods with very low proportion of attackers that attack all of the prey (high attacker population, low prey population densities) is a result of an asynchrony in temporal development between prey and attacker.Cowpea is simulated as being planted on 1st of August 2019 in Sokoto, Nigeria at a density of 13 plants per m^2 and 40 flowers per plant and *M. vitrata* larval demand of 3 flowers with an immigration rate of 1 adult female per m^2 daily. Development of both cowpea and *M. vitrata* is simulated based on temperature data of 2019 in Sokoto, Nigeria.

The attack rate (number of attacks per host per attacker per day) of *T. javanus* has a different effect on its own consequent population if compared to the effect of increased demand per *M. vitrata* larva (same difference applies to *A. taragamae*). With an increasing attack rate, the consequent parasitoid population is increasing instead of decreasing, which is the case with increasing demand per *M. vitrata* larva and consequent larva population density (Figure 29).

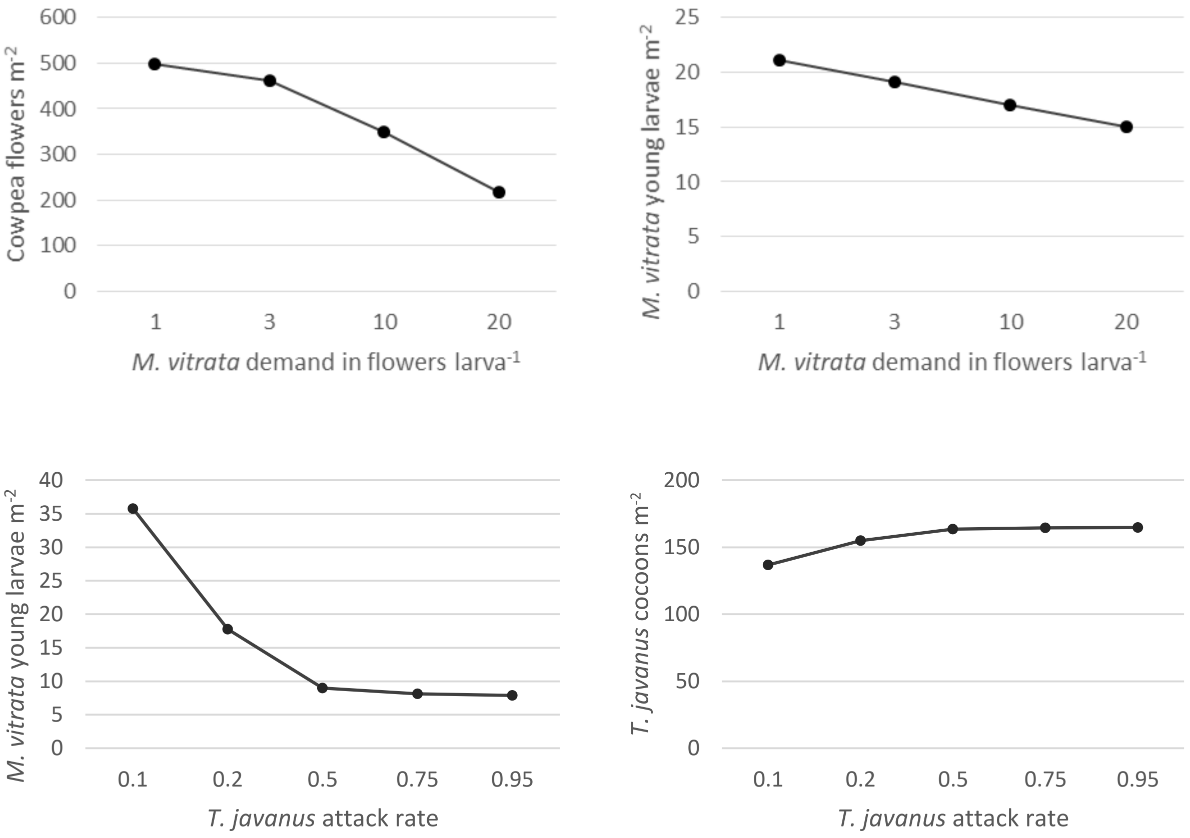

Figure 29 Comparison of the effect of *T. javanus* attack rate and the effect of *M. vitrata* demand per larva on their own and prey populations. Immigration rates are 0.05 adult *M. vitrata* females and 0.5 adult *T. javanus* females daily per m². Cowpea is simulated as being planted on 1st of August 2019 in Sokoto, Nigeria at a density of 13 plants per m² and 40 flowers per plant Developments based on temperature data of 2019 in Sokoto, Nigeria.

It is counter intuitive, because in both cases they consume the resource, which in turn is decreasing. However in the case of cowpea flowers, the increased demand per *M. vitrata* larva results in a faster depletion of cowpea flowers, whereas the duration (availability) of how long the resources that the parasitoid needs is unaffected by the attack rate (Figure 30).

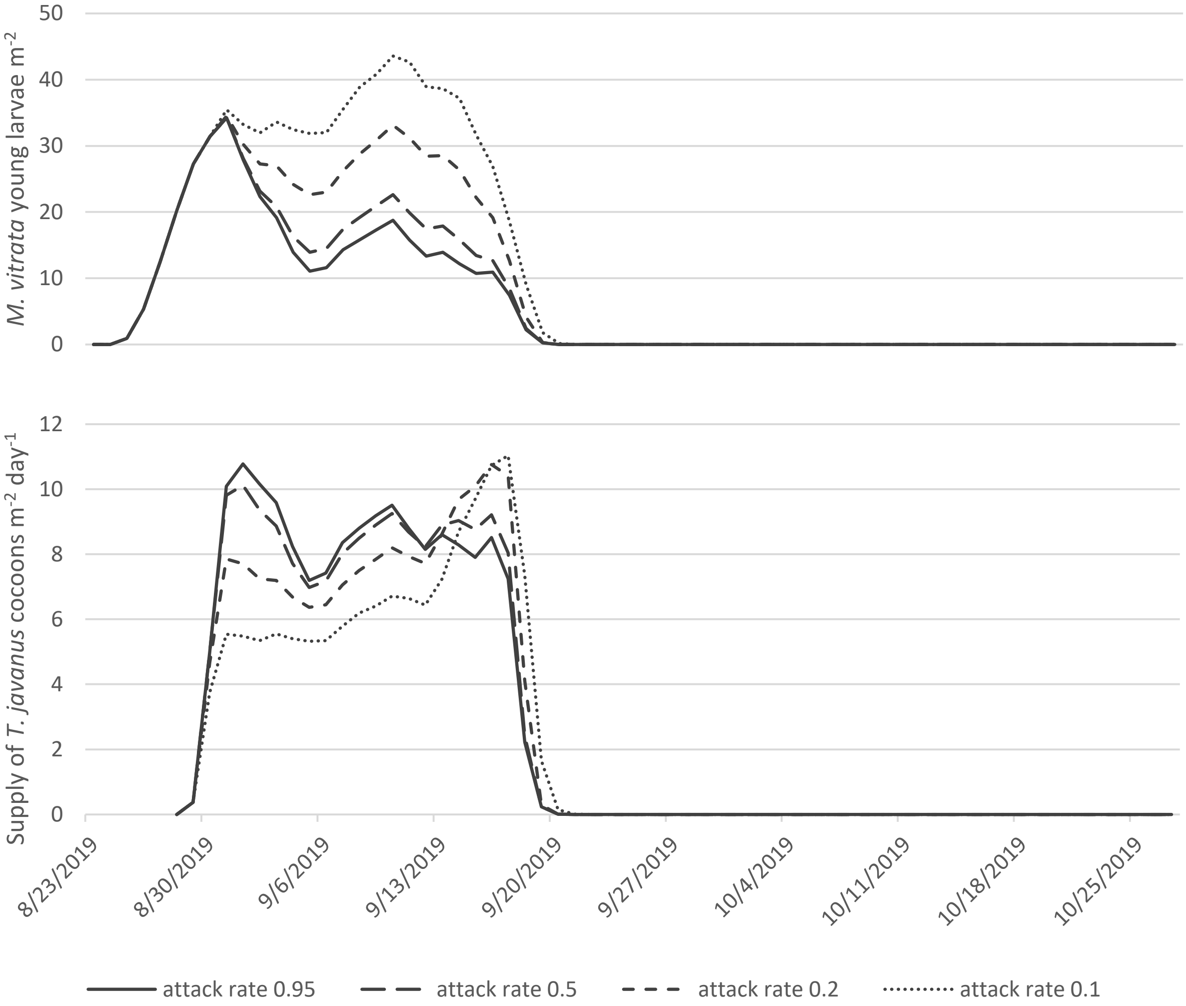

Figure 30 Effect of attack rate on supply of *T. javanus* cocoons. Higher demand means higher cowpea flower reduction, shorter infestation time and smaller *M. vitrata* young larvae population. *T. javanus* immigrates at 0.5 adult female per m^2 daily and *M. vitrata* immigrate at 1 adult female m^{-2} daily with a lifetime demand of 3 flowers per larva. Cowpea is simulated as being planted on 1st of August 2019 in Sokoto, Nigeria at a density of 13 plants per m^2 and 40 flowers per plant. Developments based on temperature data of 2019 in Sokoto, Nigeria.

T. javanus cocoon population seems to be less sensitive to the attack rate than the prey population. At the same time both the consequent parasitoid population and the prey population as sensitive to the immigration rates of the parasitoid.

5.2.2.3. *T. javanus* and *A. taragamae* competition

From interaction between the parasitoids it is clear that the higher the chances to find the prey (i.e. the higher the proportion of prey available to the parasitoid), the higher is the consequent parasitoid population density per m^2. When chances of finding prey between the parasitoids are 50% for each (i.e. half of the available *M. vitrata* young larvae population is available to each of the parasitoids) *T. javanus* cocoon population is 112.9 cocoons, while *A. taragamae* is 52 cocoons per m^2. This is in agreement with previous results, where *T. javanus* is shown to attack *M. vitrata* sooner and has a longer overlap with the prey compared to *A. taragamae* (Figure 28). In terms of proportion of the prey population being attacked, a higher proportion of prey is being attacked earlier compared to when either of the parasitoids attack individually (Figure 31 and Figure 32).

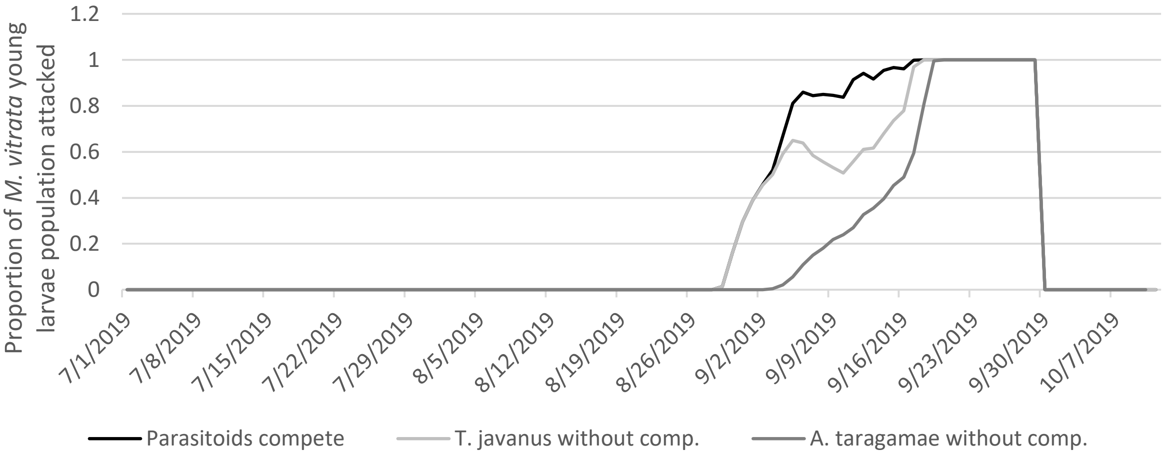

Figure 31 Comparison of the proportion of *M. vitrata* young larvae population attacked, when *T. javanus* and *A. taragamae* attack separately and together. Cowpea is simulated as being planted on 1st of August 2019 in Sokoto, Nigeria at a density of 13 plants per m^2 and 40 flowers per plant with *M. vitrata* immigrating at a rate of 1 adult female m^{-2} daily with a lifetime demand of 3 flowers per larva. Immigration of *T. javanus* and *A. taragamae* of 0.5 adult female m^{-2} per day begins when *M. vitrata* young larvae are available, with both parasitoids' attack rate (number of attacks per number of hosts per day) of 0.95. Development of cowpea and *M. vitrata* is simulated based on temperature data of 2019 in Sokoto, Nigeria, while duration of *T. javanus* and *A. taragamae* is based on duration in days.

At the same time both parasitoids look susceptible to competition in terms of daily amount of hosts parasitized, which decreases with competition (Figure 33). However, total amount of host parasitized is 164.7 for *T. javanus* without competition and 88.9 112.9 and 136.9 respectively, when competing and having 10% 50% and 90% of prey available to it, whereas *A. taragamae* parasitizes 28, 52 and 76.1 respectively with competition and 120.5 without. Thus, it seems that *T. javanus* is more robust in face of competition, where he parasitizes high number of hosts relative to the parazitation without competition, retaining 54%, even when only 10% of prey is available to it, in contrast to *A. taragamae*, which retains 23.2%.

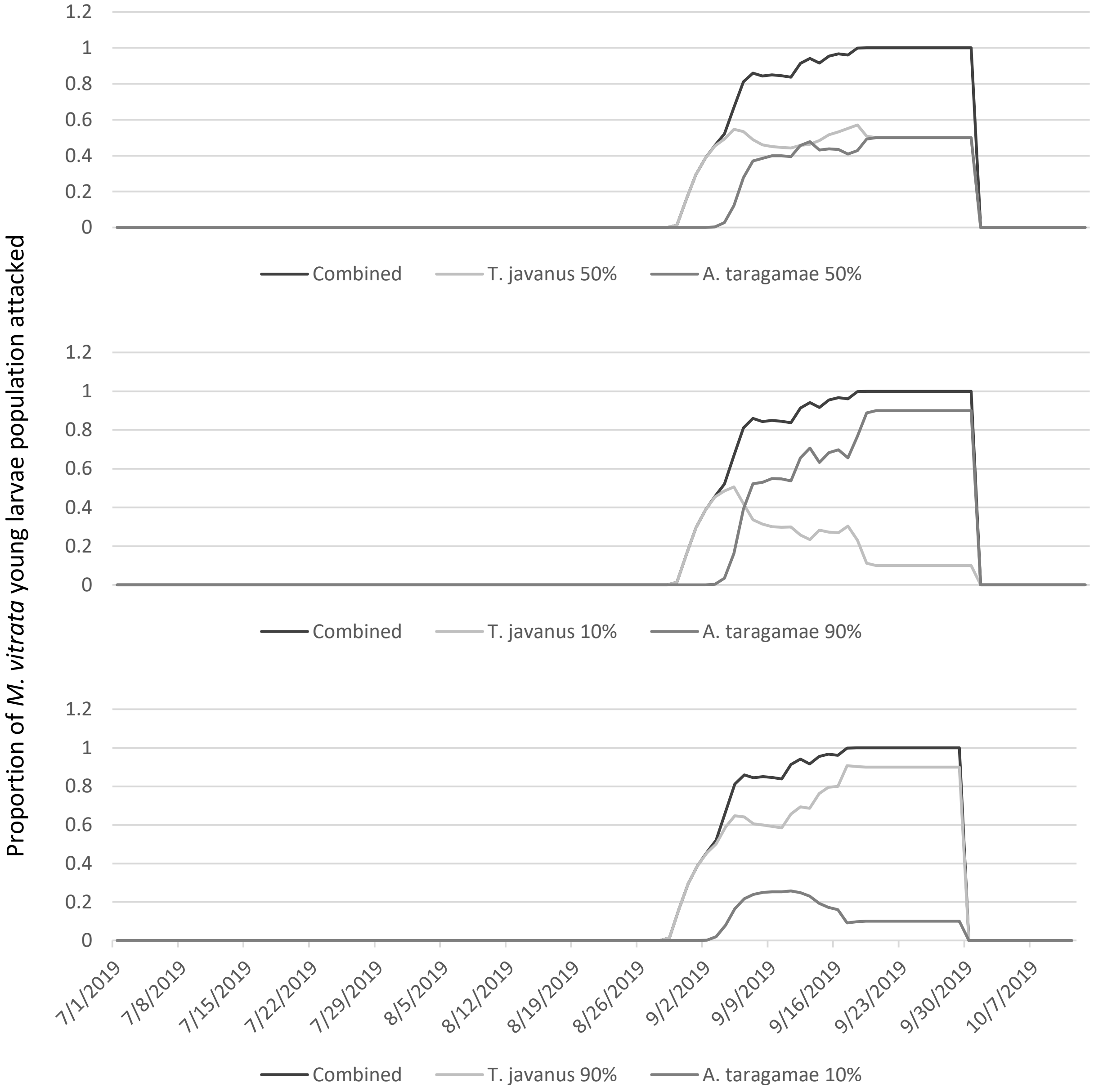

Figure 32 Comparison of the proportion of *M. vitrata* young larvae population attacked, when *T. javanus* and *A. taragamae* compete at different levels. Cowpea is simulated as being planted on 1st of August 2019 in Sokoto, Nigeria at a density of 13 plants per m^2 and 40 flowers per plant with *M. vitrata* immigrating at a rate of 1 adult female m^{-2} daily with a lifetime demand of 3 flowers per larva. Immigration of *T. javanus* and *A. taragamae* of 0.5 adult female m^{-2} per day begins when *M. vitrata* young larvae are available, with both parasitoids' attack rate (number of attacks per number of hosts per day) of 0.95. Development of cowpea and *M. vitrata* is simulated based on temperature data of 2019 in Sokoto, Nigeria, while duration of *T. javanus* and *A. taragamae* is based on duration in days.

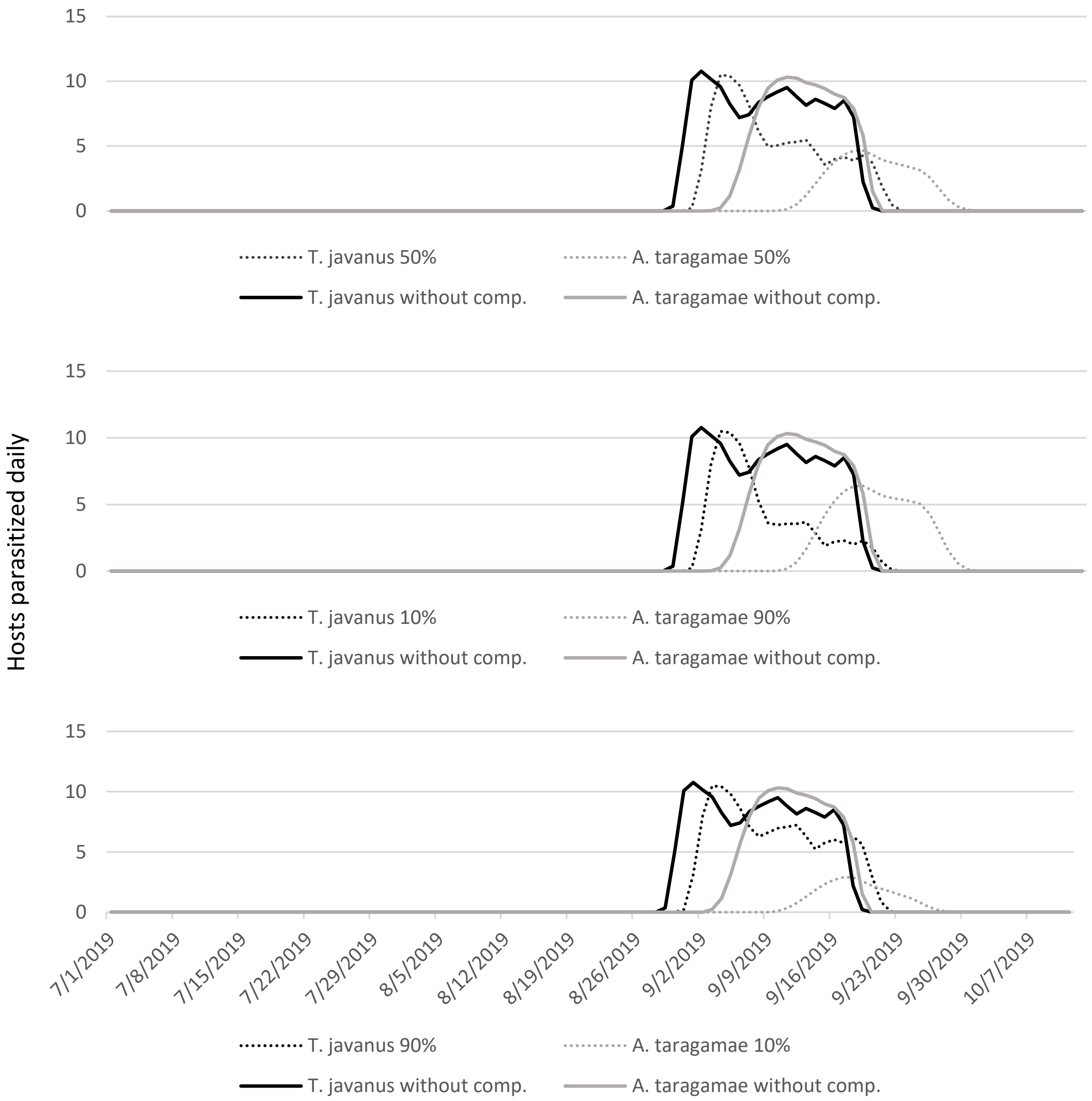

Figure 33 Comparison of the number of hosts parasitized daily, when *T. javanus* and *A. taragamae* compete at different levels and when parasitoids attack without competition. Cowpea is simulated as being planted on 1st of August 2019 in Sokoto, Nigeria at a density of 13 plants per m^2 and 40 flowers per plant with *M. vitrata* immigrating at a rate of 1 adult female m^{-2} daily with a lifetime demand of 3 flowers per larva. Immigration of *T. javanus* and *A. taragamae* of 0.5 adult female m^{-2} per day begins when *M. vitrata* young larvae are available, with both parasitoids' attack rate (number of attacks per number of hosts per day) of 0.95. Development of cowpea and *M. vitrata* is simulated based on temperature data of 2019 in Sokoto, Nigeria, while duration of *T. javanus* and *A. taragamae* is based on duration in days.

5.2.3. Temporal development

Simulated temporal development of *M. vitrata* population young larvae population over the cowpea growing season is highly dependable on the immigration rate value, which is estimated to reach the reported peak larval infestation density of *M. vitrata* reported in the geographical area.

Overall, the immigration rate of adult *M. vitrata* females acts as a sort of an adjustment tap for the whole model. Using this tap a desired peak infestation can be reached easily, however it only represents an immigration scenario, where pest is synchronized with cowpea flowers and pest population doesn't crash before the resource is depleted in contrast to a scenario, where other events influence *M. vitrata* population and result in a relatively low pest population. As already highlighted in the system analysis and model conceptualization discussion, a "complete" model includes additional components such as *M. vitrata* migration pattern based on alternative host plant availability, wind direction and rainfall all of which can influence the migration duration, intensity (amount of females) and geographical distribution. This pest is a short distance flier, and so it moves from the south to the north for a couple of months following the northward progression of rain, cowpea cultivation and the flowering pattern of alternative hosts (Bottenberg et al., 1997). For example, when looking at the inter year variability of temporal development in Maradi 2008 and 2009, it looks like in 2008 there are less *M. vitrata* adult females immigrating and as if the immigration starts earlier (because it peaks earlier). However the light trap catches from the area show that in fact adults start flying later in 2008 than in 2009 (Figure 34). Possible explanation as to why *M. vitrata* does not establish in the cowpea field in 2008 is that the big portion of the immigrating adults are late for the cowpea flowering. In the model the pest immigration is coupled with flowering, which is a possible reason as to why the model fails to simulate population dynamics of 2008. However it is not reported as to why immigration starts when it does.

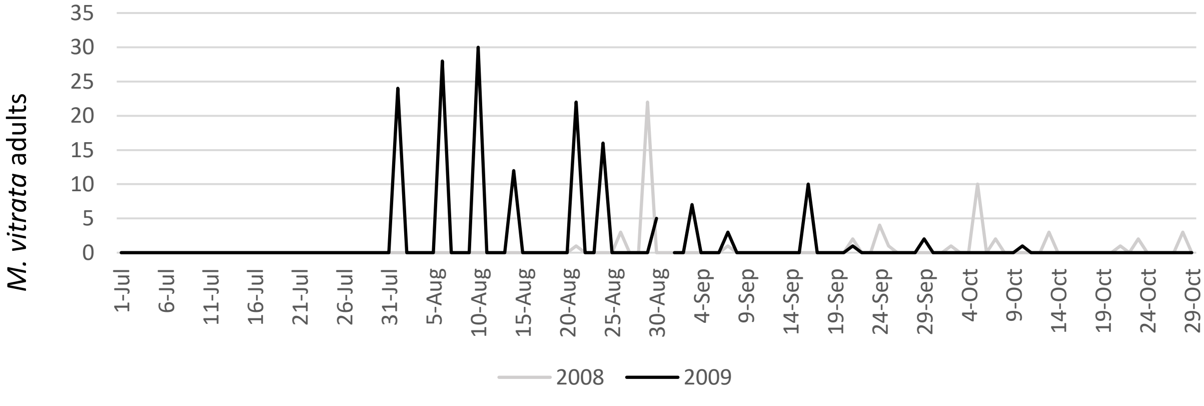

Figure 34 Adult *M. vitrata* catches in light trap in Maradi, Niger in 2008 and 2009

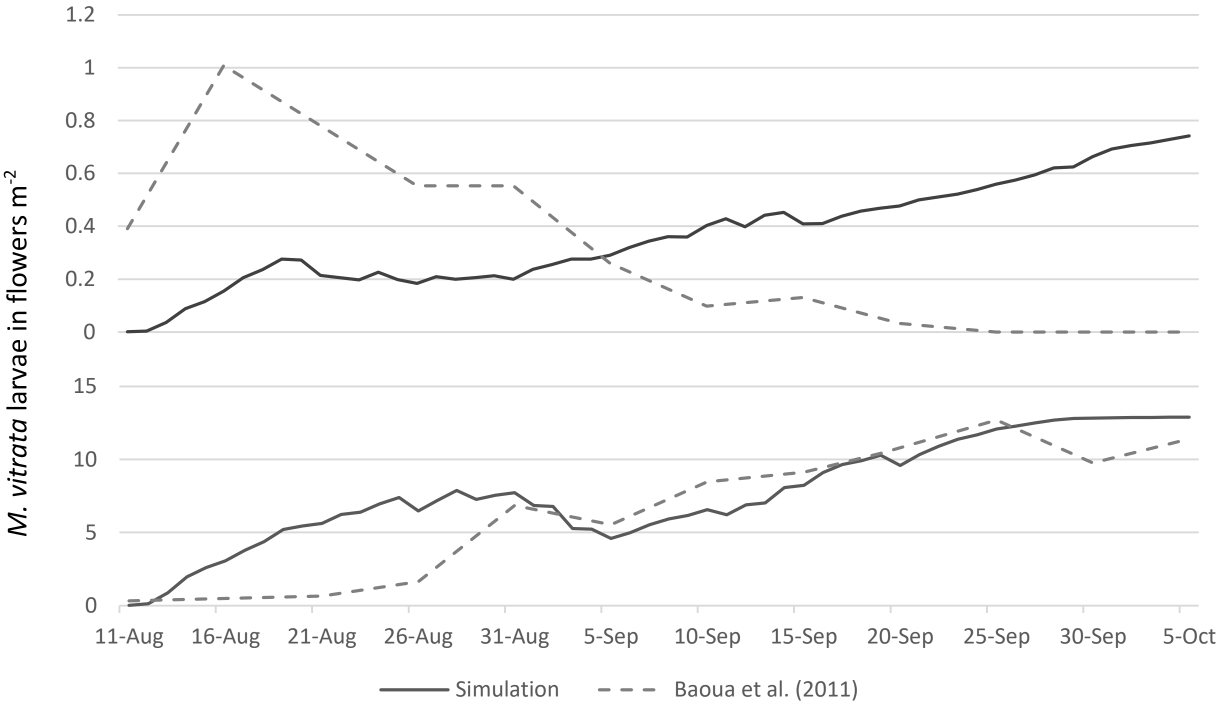

Figure 35 Population of young *M. vitrata* larvae in cowpea flowers in the period of August to October (2008 top chart; 2009 bottom chart) according to the simulation (solid line) and Baoua et al. (2011) (dashed line). Simulation is tuned in accordance to the Baoua et al. (2011) reported peak infestation density values of 0.716 larvae per m^2 for 2008 and 12.9 larvae per m^2 for 2009 in Maradi, Niger, resulting respectively in immigration rate of 0.004 (2008) and 0.0835 (2009) adult *M. vitrata* females per day per m^2. Simulation runs with planting date set to 16th of July for 2008 and 17th of July for 2009 at a planting density of cowpea of 7.16 per m^2 with *M.* vitrata life cycle demand of 3 flowers per larva. Temperature data is used for Niamey, a city located nearby Maradi on the same latitude.

In addition to the parasitoids *M. vitrata* is also attacked by a number of predator species, which can occasionally reduce *M. vitrata* populations (Figure 36) (Srinivasan, Tamò, & Malini, 2021). Predators that attack larvae and adults are spiders, ants and mantis (Adati et al., 2007; Usua & Singh, 1979). However, because generalist predators such as spiders attack beneficial , pest and insects of neutral economic importance, their importance on the crop is hard to estimate (Nyffeler, Sterling, & Dean, 1994). In addition, there is a number of pathogens such as protozoa (*Mettesia* sp., *Nosema marucae* sp. n.), bacteria (*Bacillus* sp., *Colostridium* sp.) and virus (CPV, Granulovirus, *Mavi*MNPV) (Ba et al., 2019). The only reported beneficial is a parasitoid *Gryon fulviventris* of the pod bug *Clavigralla tomentosicollis* (Asante, Jackal, & Tamó, 2000). While there is one report about pathogens being most significant factor in regulating *M. vitrata* inducing a 37% mortality in the field conditions information on pathogen role in regulating *M. vitrata* is largely unavailable (Sharma et al., 1999).

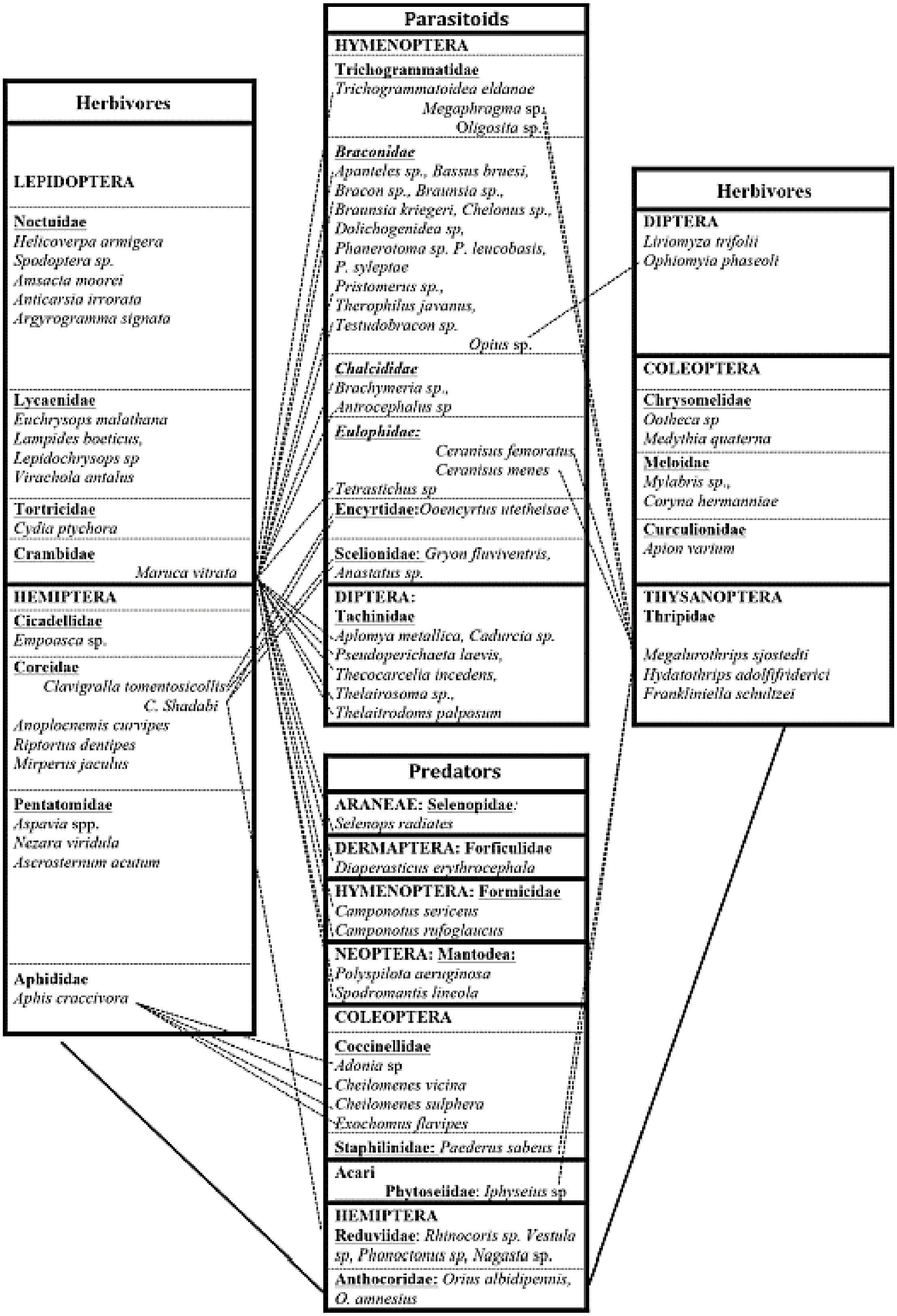

Figure 36 Food web of herbivores feeding on cowpea in West Africa. Source: Ba et al., (2018).

5.3. The simulation experiment

The effect of *T. javanus* is the strongest compared to *A. taragamae* or combined effect of the two parasitoids, when looking at the effect on *M. vitrata* young larvae produced per m^2. Overall, when looking at the impact of the RCP 4.5 temperature increase on the effect of parasitoids on *M. vitrata* young larvae density per m^2 (both combined and separate immigrations) it seems that there is no impact. It is important to keep in mind that the RCP 4.5 trajectories are based on an intermediate mitigation scenario of increasing temperature with a likely temperature change of 1.5 °C in 2081 – 2100 relative to the 1850 -1900 (Pachauri & Mayer, 2015).

On the other hand, in 2030 the effect on *M. vitrata* young larvae population produced per m^2 is notably stronger for either *T. javanus*, *A. taragamae* or them immigrating together in all immigrating rate scenarios (except for *T. javanus* immigrating at 50% of *M. vitrata* immigration rate, where reduction of *M. vitrata* young larvae population is over 90% throughout 2020-2050). The average temperatures in 2030 are above the upper thermal development threshold of *M. vitrata* young larvae (Figure 37). Consequently, young M. vitrata larvae population density per m^2 is the highest and lasts the longest (Figure 38), because the upper thermal development threshold of *M. vitrata* eggs is higher than its young larvae (34.3 °C compared to 29.3 °C), meaning that the inflow of new young larvae is restricted only by the availability of cowpea flowers, whose upper thermal development threshold is even higher at 36 °C. This results in no-outflow of young *M. vitrata* population as they cannot complete their development, when daily average temperature is above their upper thermal development threshold, while at the same time the inflow is unaffected by the increased temperatures.

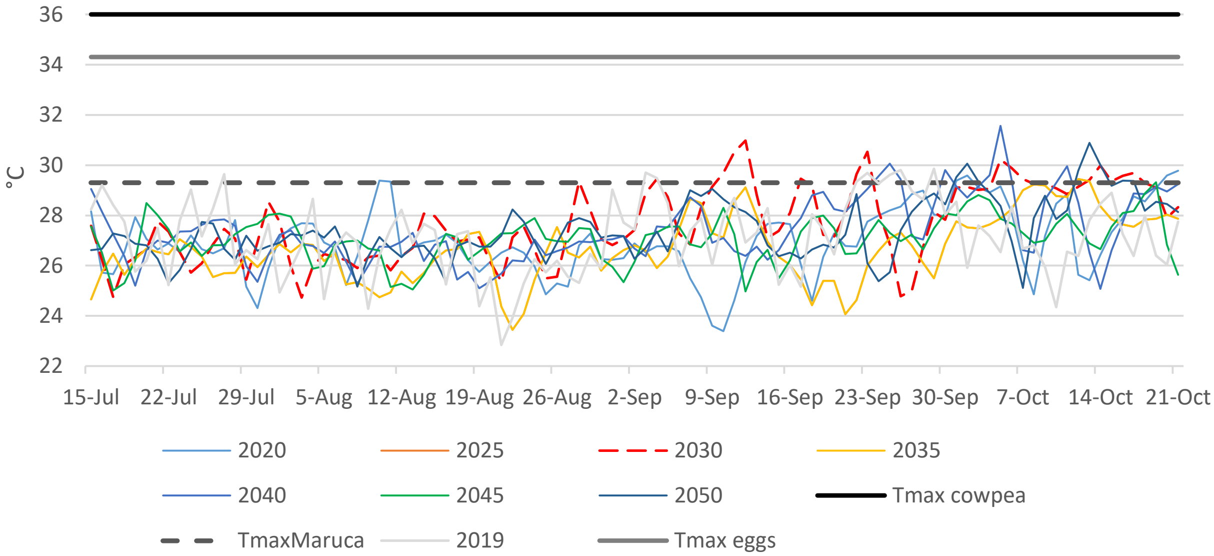

Figure 37 Average daily temperature in Sokoto, Nigeria according to the temperatures from NorESM1-M (NCC, Norway) model adopted to RCP 4.5 trajectories and thermal development thresholds of *M. vitrata* young larvae and eggs and cowpea flowers. Temperature data source: The Copernicus Climate Change Service (2022).

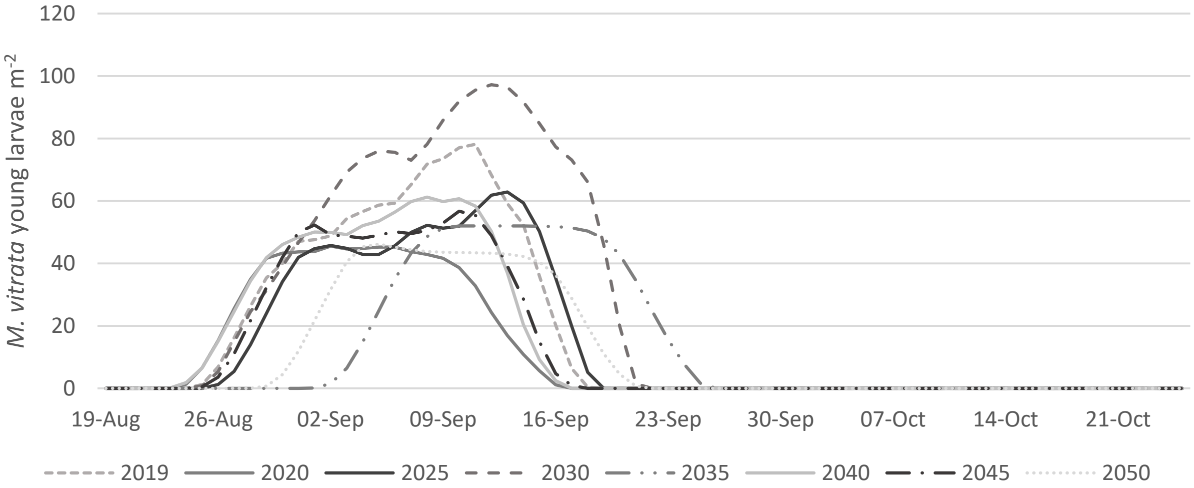

Figure 38 *M. vitrata* young larvae population density in Sokoto, Nigeria, when *T. javanus* adult females immigrate at 10% of *M. vitrata* immigration rate.

Ultimately, a better synchrony between the parasitoid and the pest is observed (Figure 39). In the example of *T. javanus* immigrating at 10% of the *M. vitrata* immigration in the year 2030 (strongest effect year) the overlap of the attacking and prey populations lasts 31 days with 49.6 young larvae of *M. vitrata* and 123.7 cocoons of *T. javanus* produced per m^2 in comparison to the year 2045 (weakest effect year), where overlap lasts 27 with 112.8 young larvae and 60.4 cocoons per m^2. It can be said that if pest development gets longer, while parasitoid is unaffected, then it is a good long term prospect for the control. However, it is important to bear in mind the physiological effect of temperatures above the upper thermal threshold are not considered, which might include reduced fecundity, different sex ratio of the progeny and overall increased mortality (Y. Huang et al., 2020). Another important point is that the longevity of the parasitoids is simulated without temperature dependence.

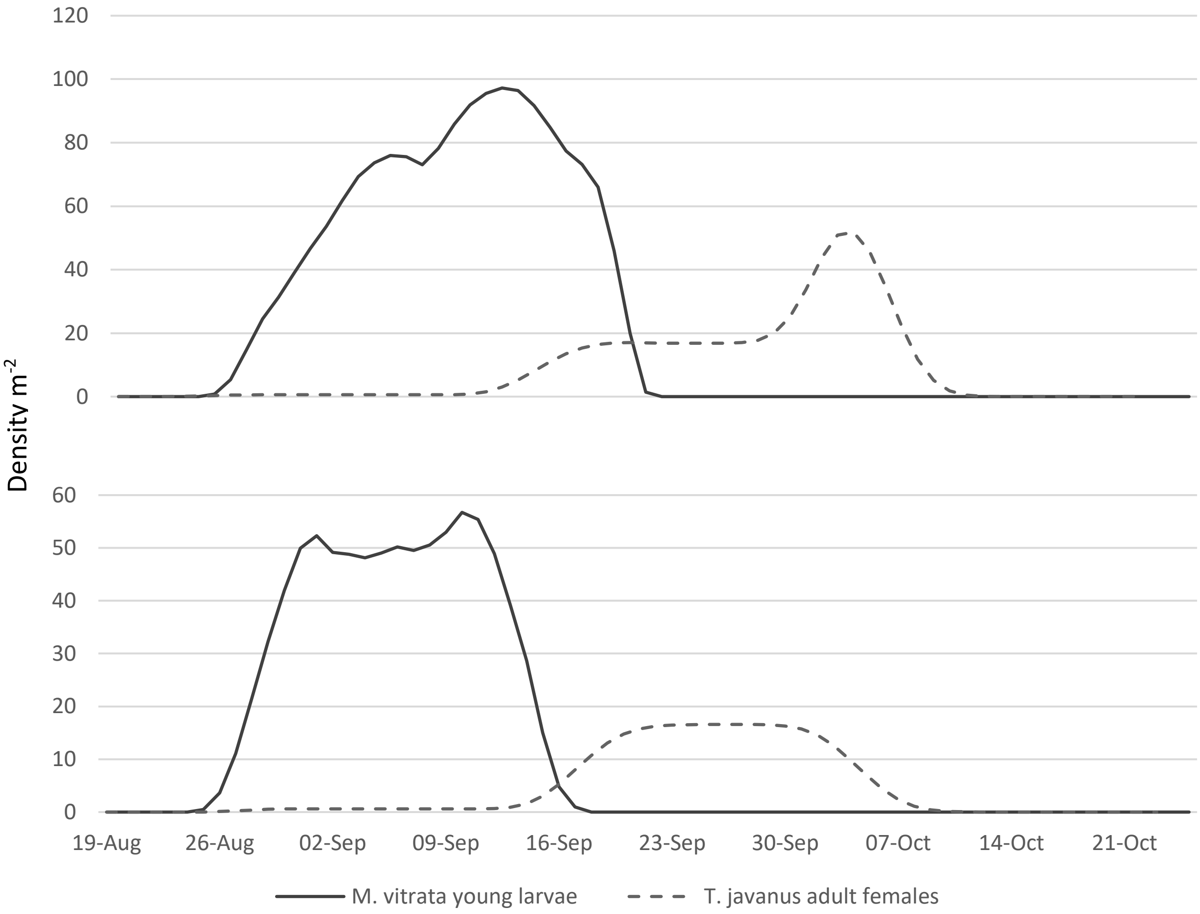

Figure 39 Temporal development of *M. vitrata* young larvae and *T. javanus* adult females in 2030 (upper graph) and 2045 (lower graph) in Sokoto, Nigeria.

6. Conclusion

System analysis of the agro-ecosystem surrounding cowpea and *M.vitrata* in West Africa identifies over 20 components and multiple model drivers. However, quantifiable data in terms of what effect does a model driver has on the model components is available only for the daily temperature, which is used to simulate cowpea and *M. vitrata* development based on day-degrees. Major disadvantage of the model is that the development of *A. taragamae* and *T. javanus* is not simulated based on day-degrees, because their thermal requirements are not found in the scientific literature. The model also behaves in a way that might overestimate the duration and the density of any developmental stages (e.g. young larvae of *M. vitrata*), if daily temperature exceeds the upper developmental thermal threshold. Rainfall and wind direction are the other potential model drivers, which together with *M.vitrata* populations on alternative host plants are responsible for the migration pattern of *M. vitrata* from the south to the north of West Africa. Hence, a more complete set of interactions of the cowpea and *M. vitrata* agro-ecosystem would be highly relevant. As a result, the current model assesses the impact of exotic parasitoids *A. taragamae* and *T. javanus* on *M. vitrata* young larvae (1st and 2nd instars) population in cowpea flowers in the northern part of Western Africa in Sokoto, Nigeria in a scenario, where *M. vitrata* is perfectly timed with the flowering of cowpea fields. In such a scenario using the peak infestation value as a target for adjusting the immigration rate of *M. vitrata* is capable of giving a close to field simulation of *M. vitrata* young larvae temporal development.

In all three experimental rates at which the parasitoids immigrate the field (10%, 20% and 50% of the immigration rate of *M. vitrata*) throughout the years of 2019-2050, *T. javanus* has a stronger reduction effect on the young *M. vitrata* larvae produced per m^2 compared to just *A. taragamae* or the combination of both parasitoids. The shorter life cycle of *T. javanus* and especially the shorter egg development time determines the success of *T. javanus*, despite the longer oviposition period of *A. taragamae*. In turn, it can be said that *A. taragamae* reduces the effectiveness of *T. javanus*. The latter reduces young *M. vitrata* larvae per m^2 by 40% even, when *T. javanus* immigrates at a 10% of *M. vitrata* immigration rate as opposed to 30%, when both of the parasitoids immigrate together. The immigration rate of *M. vitrata* is set to represent heavy infestation to elicit potential effect of the parasitoids, hence, the chosen immigration rate of *M. vitrata* might be overestimated. Future temperatures are based on RCP 4.5 trajectories and pose no risk to the effectiveness of *T.*

javanus and *A. taragamae*. However, RCP 4.5 trajectories assume lower temperature increase compared for example to RCP 8.5.

Management of *M. vitrata* in West Africa still relies largely on the application of chemical insecticides with all their unintended side effects (Agyekum, Donovan, & Lupi, 2016; M. Tamò et al., 2019). A number of reasons suggest this is not the best practice: (1) *M. vitrata* evolved to resist some of the synthetic pesticides (Ekesi, 1999), (2) majority of the farmers cannot even afford them (Harry Bottenberg, 1995), (3) synthetic pesticides can wipe out natural enemies of the pest resulting in pest outbreaks during yield formation (Onstad et al., 2012; M. Tamò et al., 2019) and (4) safety of the farmers is at stake, because they have no access to proper safety equipment and if they do their low literacy makes it challenging to understand instructions for safe and effective use (Diabate et al., 2002; Onstad et al., 2012; M. Tamò et al., 2019). Classical biological control is a feasible alternative. It is based on ecological theories related to the invasive insect flourishing due to the absence of its enemies from the original area. It makes sense then to look for a potentially effective biological control agent from the geographical area of origin and import it. At the same time, assessment of classical biological control releases is complex with multiple interactions on various levels *viz.* direct effects and indirect effects of released organisms, dispersal of released organism to new areas and climate change-induced effect on relationship between the released organisms and their target (Jennings, Duan, & Follett, 2017; Simberloff, 2012). Currently, classical biological control of *M. vitrata* in West Africa operates on a three trophic levels framework approach, meaning that there is no research in terms of the impact natural enemies have on the efficacy of the native and introduced exotic parasitoids. At the same time all of the life table parameters and feeding behavior of the exotic parasitoids are laboratory derived, hence the actual behavior in the field might be different. However, the current model helps to explore population dynamics in the context of rising temperatures and highlights long-term feasibility of *T. javanus* as a classical biological control agent of *M. vitrata*.

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