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# Towards a generic agent-based vector-host model: effects of carrying capacity and host mobility

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## Abstract

The aim of our work is to develop a generic conceptual agent-based model to formalize the interaction of vector and host given climate change. The model consists in creating a hypothetical example of a vector-host system. It simulates the vector's life cycle while considering interactions with hosts and the temperature. It is presented following the ODD protocol and based on parameters and processes to conceptualize the vector-host complexity. It could accommodate a broad spectrum of vector species and different biogeographic regions. Our model can be extended to more ecologically complex systems with multiple species and real-world landscape complexity to test different host and / or vector-targeted control strategies and identify practical approaches to managing vector population and movement patterns.

**Keywords:** Agent based models, Vector-host system, ODD protocol, Tick

## Introduction

Ectoparasites are vectors of pathogens that cause vector-borne diseases. Most ectoparasites are hematophagous species, such as insects and acarids. Ectoparasitic acarids (*i.e.* ticks) of vertebrates (*e.g.* Cattle, sheep, etc.) are vectors of pathogens responsible for zoonoses and significant economic losses for livestock (Sonenshine and Roe 2014; Randolph 2004). Understanding the role of vectors in the transmission of pathogens involves studying their population dynamics (Ogden et al. 2004, 2005). In this regard, the study of vector population dynamics and their interactions with the environment seems essential to surveillance vector-borne diseases (Wikel 2018; Estrada-Peña and Fuente 2014; Estrada-Peña et al. 2023). The most important factor is climate change (Ogden et al. 2018, 2021). In fact, variations in climate and temperature induce great alterations in the distribution of vectors in nature and, in particular, in ticks (Ogden et al. 2021; Nolzen et al. 2022; Wu et al. 2010; Medlock et al. 2013; Eisen et al. 2016).

The use of computer simulations to address complex ecological systems with explicit details while implementing individual-level interactions and spatial structure is promising (Tracy et al. 2018). Moreover, mathematical and simulation models were developed to further understand the ecological mechanisms and processes underlying the

vector-host systems and had shown efficiency in answering problems that controlled experiments or field observations solely cannot fully address (Ogden et al. 2021; Ndongo et al. 2022). In fact, these models give a new degree of knowledge to support public health strategies for disease and vector control (e.g. Wu et al. (2010); Healy et al. (2020); Tosato et al. (2022)).

Simulation models as the Agent-Based Models (ABM) models are prominent tools to predict the relationships between biological processes, the environment, and ecological patterns across different scales, both for population dynamics and evolutionary scales (Tosato et al. 2022; Smajgl and Barreteau 2014; Mount and Haile 1989; Halsey and Miller 2018; Tyre et al. 2004; Gilbert et al. 2014).

Many ABM models have been developed to tackle whether host-vector (e.g. Healy et al. (2020); Yong et al. (2015)), host-vector-pathogen (e.g. Halsey and Miller (2018); Tardy et al. (2022); Gaff and Nadolny (2013); Nadolny and Gaff (2018)), or host-pathogen systems (refer to Mori et al. (2023)). Simulation models are increasingly being used to solve problems and aid in decision making in agricultural systems (Kremmydas et al. 2018) and veterinary epidemiological systems (Healy et al. 2020) as well as in public health systems (Tracy et al. 2018). Our work aims to develop a generic agent-based model to formalize the interaction of vector and host with explicit consideration of temperature when describing the vector's life cycle since ABMs can integrate several scales, unlike ODE mathematical models (e.g. Ndongo et al. (2022)). The distinguishing feature of our model is that it explicitly incorporates all the life stages of the vector, as well as temperature, as an environmental factor in the development of the vector's life cycle. In addition, the integration of host movement and interactions with the vectors. Our objectives are (1) to develop an agent-based model that simulates the host-vector relationships while considering vector development as a temperature-dependent process, (2) to study the effects of host movement patterns (random versus herd movement) on vector population dynamics, and (3) study the effect of carrying capacity of the host on vector population dynamics.

This paper is organized as follows: In Sect. 2.1, we describe the background knowledge and modeling assumptions we considered. In Sect. 2.2, we explain our model using the overview, design concepts, and details (ODD) protocol (Grimm et al. 2010, 2020). Then, in Sect. 3 we present our simulation's results by comparing two movement approaches of Cattle agents. Finally, in Sect. 4, we discuss our results and point out some limits and perspectives to generalize and promote our model to fill the gap between understanding the ecology of the vector and hosts on the one hand and the effects of host movement on the other hand.

## Materials and methods

### Background

Our model creates a hypothetical example of a semi-intensive livestock production system. This closed system comprises only three entities: ticks, Cattle and Rodents. We consider that Cattle are grazing and then return to a barn. We do not consider in our model the diurnal activity of ticks nor that of Rodents. The host population is closed, while the tick population is an open monospecific population whose recruitment is done through egg laying. It is stratified in cohorts of biological life stages: egg, larva, nymph and adult.

Interstadial development of ticks are temperature-dependent processes (Ogden et al. 2004, 2005). A blood meal is the only interaction between the hosts and the ticks.

The vector model in this study is a species of hard ticks. Ticks have four developmental stages: an egg and three active obligatory hematophagous ectoparasitic stages characterized by only one larval and nymphal stage before reaching the adult stage and discontinuous feeding, a single blood meal to get through the next life stage.

At the end of the embryo's development, the eggs hatch into larvae (Sonenshine and Roe 2014; Arthur 1948). The larva begins to search for a host. All instars can enter a behavioural quiescence state called "diapause" where development is paused. In our model, we consider diapause as a temperature-dependent state, which is activated when the temperature of the environment reaches a stage-dependent threshold (Gray et al. 2016; Belozarov and Naumov 2002; Dautel and Knülle 2010). Two known host-finding strategies are described in the literature (Lane et al. 2009; Mejlou and Jaenson 1997): a passive strategy called *questing* where the tick waits on vegetation for passing by of a possible host and an active seeking host strategy where the ticks move actively looking for a host.

### The conceptual model

The description of the model follows the "Overview, Design Concepts, and Details (ODD)" protocol developed by Grimm et al. (2020) to standardize the use of ABMs.

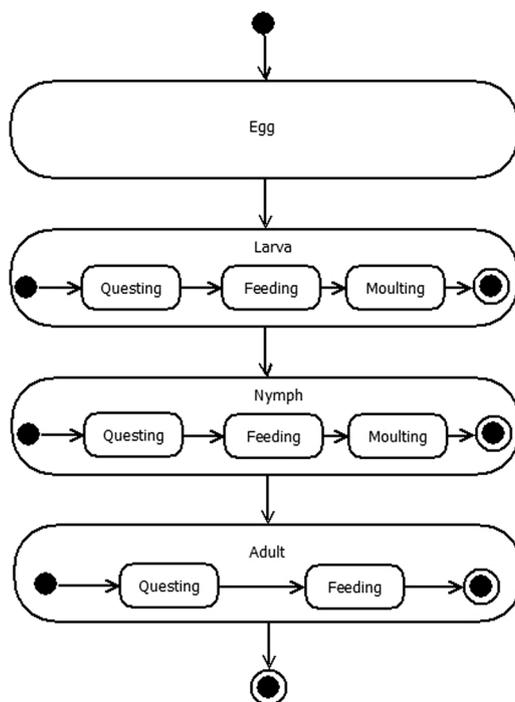
#### Overview

**Purpose and patterns** The purpose of the model is to reproduce the tick life cycle, considering temperature-dependent processes and host movement patterns.

**Entities, state variables, and scales:** The model is made up of two agent types: the vector agent and host agents. The vector agent represents the hard tick; the host is either a Cattle or a Rodent. The interactions between agents are ruled by two ecological processes: (1) vector-host interaction and (2) host movement.

**The Vector agent:** The *Vector* agents are characterized mainly by the life stage attribute *state* respectively: egg, larva, nymph, and adult. The activity status of the vector agents is characterized by three behavioural states (1) *questing*: This is a generic term to designate the activity of the vector before attaching to a possible host and while it waits for the passing of a host or the actively seeking of the host, (2) *feeding*: while the vector attaches to the host for taking the blood meal, and finally (3) *moulting*: the behavioral state after completing the blood meal and detaching from the host (Figs. 1 and 2).

**The host agent:** The *Host* agent includes two sub-agents (Fig. 2): *Cattle* and *Rodent* agents: Rodent agents have a random movement in the environment characterized by a velocity randomly fixed at the beginning of the simulation. The Cattle agent moves following two behaviours. In the first movement behavior, the cattle agents are endowed with random movements. In the second movement behaviour, Cattle agents abide by a herd movement pattern and follow a dominant Cattle agent considered a leader. In both behaviors, cattle are characterized by diurnal activity, whether active or resting, by regaining the barn.



**Fig. 1** Conceptual view of the vector life stages (*state*) and behavioural states *BehState* attributes. In every *state*, the vector agent can have, at one time, a sole behavioural state. The egg state has no behavior. The adult state has only two behavioural states. The larva and the nymph state can have the behavioural state, respectively, questing, feeding and moulting

*The environment* The environment is set up as a hypothetical square world with a dimension of 1 km x 1 km with unwrapping boundaries movement and does not cause Host agents to jump to the other side of the world.

The environment is considered a grazing area where all Host agents can move around. In the centre of the environment, a hypothetical barn of square geometric shape and a dimension of 50 m x 50 m (refer to Fig. 3). As for the climatic parameters, only the temperature is considered a climatic factor influencing the vector agents.

*Process overview and scheduling* The model simulates the interactions between the vector (tick) and the hosts (Cattle and Rodents) agents on the one hand and between environmental (temperature) and vector agents on the other hand. We consider six submodels (Fig. 4):

Host agents (Cattle and Rodents) move according to the *move\_host* submodel every hour. Questing vector (tick) agents are stationary, waiting for the passing-by of a possible host within a specific distance *PERCEPTION\_DISTANCE*. When finding a host (Rodent or Cattle), vector (tick) attach to the host based on the *attach* submodel and start a blood meal. Each day, vectors detach from hosts following the *detach* submodel after completing the blood meal. Furthermore, the life cycle processes of the vector population are the result of the *development* submodel compiled of the following five submodels that occur every day: *preoviposition*, *incubation*, *moulting*, and finally the *diapause*

submodel. The *death* submodel is also composed of two submodels: *natural\_mortality* and *environment\_induced\_mortality*.

The temperature is updated every day based on the *SetEnvCdt* submodel.

### **Design concepts**

**Basic principles** The model considers that the life cycle of ticks consists of four stages, the duration of which depends on temperature. Moulting between stages depends on blood meals and is, therefore, closely linked to the presence of hosts. Adult vectors are all females and would give offspring, and mating is implicitly included in our model. We have considered the host population a closed system with a constant host population. Both scenarios do not include trophic resources for *Host* agents.

**Emergence** Abundance and stage distribution emerge from the properties of the relationships between temperature and moulting duration and also from host location and probability of attaching to a possible host, permitting the fulfilment of the transition into the next behavioural stage and life state. The host agents' and vector's combined actions and states in response to the environment produce the total number of vectors questing, feeding, or moulting in any particular location at any given moment.

**Sensing** Moulting and diapause behaviours are temperature-dependent processes, *vector* agents sense the temperature variation and enter diapause when the daily temperature reaches a stage-dependent threshold. *larva* and *nymph* states sense the temperature when moulting. *Egg* state of vector agents sense the temperature when incubating, as for *Adult* state sense it when either in preoviposition or oviposition phase. Intraspecific interactions are not taken into account in our model; *Vector* agents perceive the *host* agent within the range of their distance of perception (refer to tab 2) and do not sense each other or communicate. Both *Cattle* and *Rodent* agents do not sense the temperature. Rodents do not sense each other nor sense *Cattle* agents. In the first scenario (S1), Cattle do not sense each other; meanwhile, in the second scenario (S2), they sense the movement of each other and move in a herd pattern while following a leader *Cattle* agent.

**Interaction** *Vector* agents interact with both *Cattle* and *Rodent* agents through blood meals, the result of the *attach* submodel. *host* agent, through a blood meal, can be a limiting factor as it is necessary for the moulting from one stage to another.

The *larva* state of the *vector* agent can only attach and have a blood meal from a *Rodent* agent. *Nymph* and *adult* state can attach to both *Rodent* and *Cattle* agents.

**Stochasticity** Stochasticity plays a crucial role in three submodels within the system. Firstly, in scenario (S1), the movement of Rodents and Cattle is governed by randomness. Their velocity direction is randomly determined at each time step.

Additionally, the environmental-induced mortality is a stochastic process. At every time step, a probability of death is computed based on the life state and the temperature, both of which contribute to the stochastic nature of the model.

Moreover, the *attach* submodel relies on the probability of attachment, and the selection of the host is determined randomly at each time step. The probability of attachment is influenced by the number of hosts within the perception distance of the vector agents.

**Observation** The main target observations are the vector's population and per-stage abundance. Additionally, we tracked the life-stage behavioural state (questing, feeding, moulting, and diapause).

We denote the total abundance of the tick population, at time  $t$ ,  $N(t)$  and  $\bar{N}(t)$  the mean over the replication of the population abundance and  $\bar{N}_{state(i)}(t)$ , the life stage population abundance, where  $i$  is, respectively to “egg”, “larva”, “nymph” and “adult” stage.

$$\bar{N}(t) = \sum_i \bar{N}_{state(i)}(t) \quad (1)$$

### Details

**Initialization** Each simulation starts with an environment wherein *Cattle* are situated in the centre of the barn. In the second scenario (S2), the leader *Cattle* agent is selected randomly. *Rodent* agents are located randomly in the environment. All *Vector* agents are adults on day zero of the preoviposition stage. The initial date of the simulation is October 1<sup>st</sup>, 1990. The initial daily temperature corresponds to that of the initialization date. The initial values of all parameters are in table 2.

**Input data** The model is parameterized for the species *Ixodes scapularis*. Climate data used in this model are the Climatic Research Unit (CRU) TS Time Series datasets 4.04 (Harris et al. 2020). This dataset is monthly estimates of Temperature recorded between the years 1990 and 2000 with a spatial resolution of (0.5x0.5 degree) grids for the region of Wisconsin. Fitting data points generate the daily estimates to a polynomial function of the order 3.

The parameters used in this model come from bibliographic data and/or the modeler's expertise, as detailed in table 2.

### Submodels

#### *Host's agent submodels* *move\_my\_parasite submodel*

We assume that the hosts will move the attached hosts on themselves following their position according to the *move\_my\_parasite* submodel. This submodel is common for both *Rodent* and *Cattle* agents. *Vector* agents attached to a *host* agent change their location as per the host they are fixed on until they detach.

***move\_Cattle submodel*** The *move\_Cattle* sub-model simulates the movement and activity patterns of *Cattle* sub-agents. Two movement behaviours are considered in the *Cattle* and *Rodent* agents move randomly according to the *move\_host\_random* submodel. Unlike the first scenario, *Cattle* agents follow a leader agent according to the *follow\_leader* process, which itself follows a predefined path according to the *follow\_path sub-model* starting from the centre of the barn and returning to it. *Cattle* agents, besides the leader, are moving in a herd cohesion according to a boid movement composed of the “separation”, “alignment”, and “cohesion” processes as described by Reynolds (1987), *Cattle* agents flocks to the centre of a mass of agents within the *minimal\_distance*, and avoiding other agents while trying to match the position of other *Cattle* agent. If a current hour of the day is in the grazing time range, the *leader* will move with a random

speed following the path. Otherwise, the *leader Cattle* agent will move to the centre of the barn *BARN\_LOC*.

### Vector's agent submodels

*The attach submodel* The *attach* submodel describes the attachment of the vector to a host agent within the *PERCEPTION\_DISTANCE* when its behaviour stage is questing. Vectors which have their life state equal to “larva” attach to *Rodent* agent, *nymph* and *adult* attach both *Cattle* and *Rodent*. The *attach* submodel does not apply to *egg* since it is a free life stage.

The process of attachment has a probability *ProbIndAttach* dependent on the number of neighbouring hosts *NeighHosts* within the *PERCEPTION\_DISTANCE*, computed as follows:

$$ProbIndAttach = 1 - (0.8)^{NeighHosts} \quad (2)$$

Since the vector is more likely to attach to one of its hosts, the probability of attachment success “*ProbIndAttach*” is determined by the number of host in the range of the vector’s perception distance (refer to Eq. 2). When applying a carrying capacity for the host, we assume that every host agent (both *Cattle* and *Rodent* agents) have a maximum number of vectors that can be attached to them, *parasite\_max*. The *attach* submodel is modified in a way that if the attribute *VectorOfParasite* is more or equal *parasite\_max*, the *Vector* agent will not attach to the host.

*detach submodel* This sub-model describes the detachment of vectors from the host after a successful blood meal. A successful blood meal is controlled by a fixed duration of the blood meal: *AttachToDetach* (refer to table 1). When this occurs, the *Vector* detach from the *host* agent at a random proximate location, and its behaviour state, *BehState* updates to “*moulting*”.

*develop submodel* The *develop* submodel considers the life stages transitions and *diapause* process. In this submodel, we consider the development of the vectors as daily temperature functions (Fig. 5). Also, the *develop* submodel is itself organized into five processes, respectively, *diapause*, *moulting*, *preoviposition*, and finally *incubation*. The transition between each life state is the result of the success of the *attach*, *detach*, and *moult* submodels.

*moult, preoviposition and incubation submodels* Based on the work of Ogden et al. (2004), moult, preoviposition and incubation are temperature-dependant processes (refer to Figure 6). The development is incremented every day. We denote  $f(t)$  the duration function for every life state, respectively,  $m_{larva \rightarrow nymph}$ ,  $m_{nymph \rightarrow adult}$ , (Fig. 6 and equations 3) and each behaviour is structured by life state  $i$ , respectively  $i_{moult}$  and  $i_{preoviposition}$ .

We assume at every time step, the duration of moulting, respectively for larva into a nymph and nymph into an adult, the preoviposition and the incubation are computed according to, respectively, the equations 3, where  $m$  is, respectively, the moulting duration respectively for larva and nymph, preoviposition duration, and  $T_{current}$  is the daily temperature (Fig. 5, Eq. 3).

**Table 1** Summary of attributes and variables with definitions and periods of update

Attri.	Typ.	Dim.	Desc.	Peri.
<i>Vector</i>				
location	$\mathbb{R}^2$	–	Position	1 H
speed	$\mathbb{R}^2$	km/h	Speed of vector agent	1 H
BehState	Category	–	Behavioural state	1 D
State	Category	–	Life stages;egg, larva, nymph,adult	1 D
AttachDetachDate	Date	–	blood meal duration	1 D
LayDate	Date	–	Date of egg hatching	1 D
QuestDate	Date	–	Questing start date	1 D
NeighHosts	List	–	Neighbouring hosts	1 H
TargetHost	Host	–	Target host	1 H
LayingEgg	Boolean	–	Fitness of adults to lay eggs	1 H
Diapause	Boolean	–	Diapause	1 D
LaidToIncubation	$\mathbb{R}$	–	Incubation duration	1 D
PreoviToOvi	$\mathbb{R}$	–	Preoviposition duration	1 D
MoultingDuration	$\mathbb{R}$	–	Moulting duration	1 D
oviposition	Boolean	–	Oviposition	1 D
moulted	Boolean	–	True to change the life state	1 D
incubation	Boolean	–	incubation	1 D
ProblndAttach	$\mathbb{R}$	–	Probability of attachment	1 H
counter	$\mathbb{R}$	–	Counter for development rate	1 D
<i>Hosts</i>				
location	$\mathbb{R}^2$	–	Position of the agent	1 H
speed	$\mathbb{R}^2$	km/h	Speed of host agent	1 H
VectorOfParasite	$\mathbb{N}^n$	–	List of vectors	1 H

$$\begin{aligned}
 m_{j(state1 \rightarrow state2)} &= aT_{current}^{-b} \\
 i_{j(state1 \rightarrow state2)} &= i_{j(state1 \leftarrow state2)} + f(t)
 \end{aligned}
 \tag{3}$$

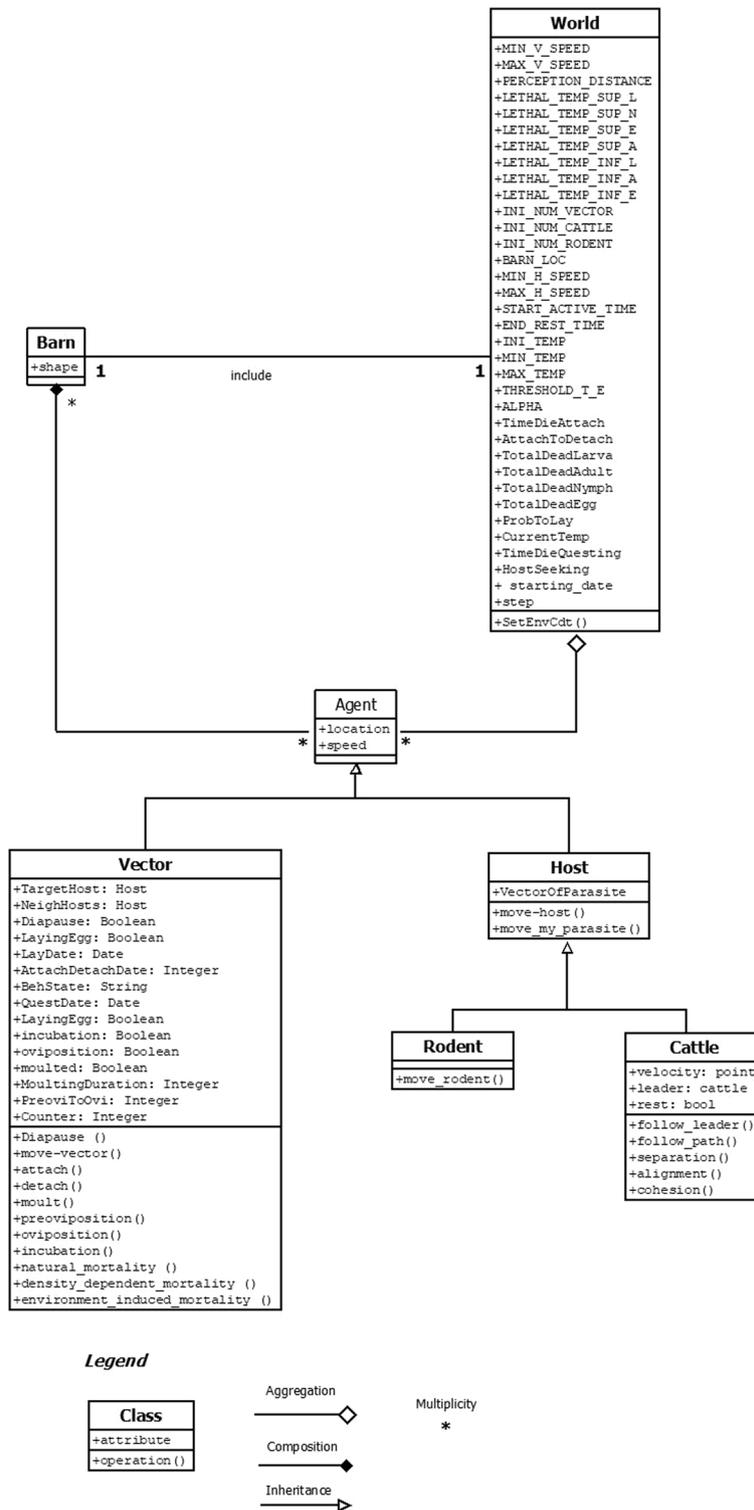
where

$$f(t) = 1/m_{j(state1 \rightarrow state2)}$$

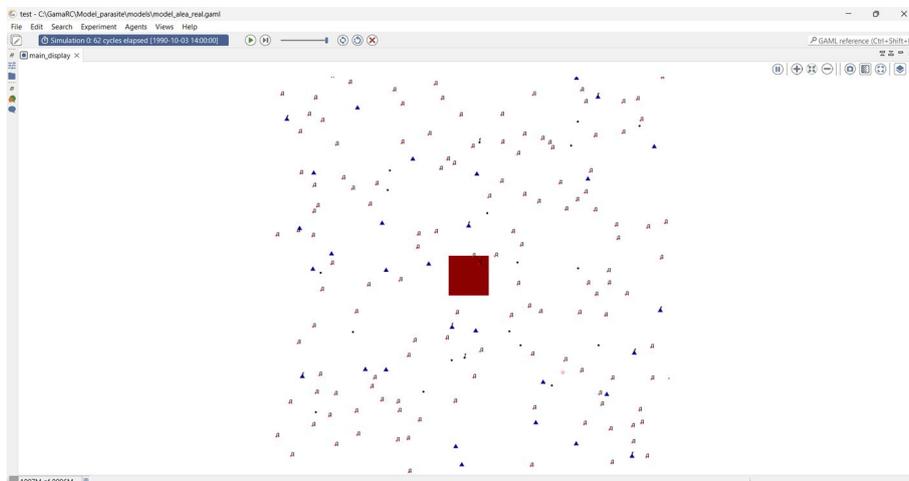
*diapause submodel* The *diapause* submodel describes the temperature-dependent process of the diapause. The diapause state is activated when the daily temperature reaches a life state-dependent threshold temperature (refer to table. 1). When the diapause state is activated, the development incremental function  $f$  approaches infinity  $f \rightarrow \infty$ , the *develop* submodel is paused until the daily temperature surpasses the diapause temperature threshold, then the *diapause* submodel is deactivated, and the *develop* submodel in its turn is activated.

*death submodel* The *death* submodel describes mortality processes. Two types of mortality are considered in this submodel *natural mortality*, *environment-induced mortality*.

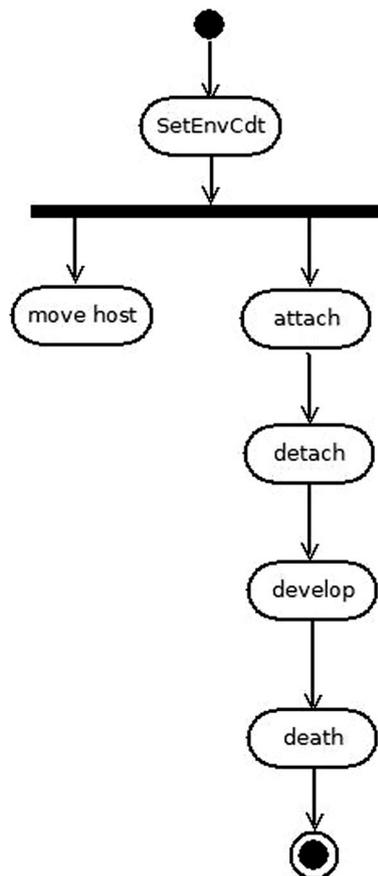
*Natural mortality* Every day at the end of the day, each *vector* agent had a daily probability of mortality for every life state (refer to table 1). Also, all adult agents die after laying eggs.



**Fig. 2** UML (unified modelling language) class diagram represents our ABM, with two types of agents: Vector agent and Host agent. Both agents are located in the World



**Fig. 3** Screenshot of the Environment on Gama Platform. The central cell ( in dark red) represents the barn. Triangles (in blue) represent the rodent agent. Circles (in red) represent the vector agents. The letter designs the behavioural state of every vector agent (q: questing, f: feeding,m: moulting)



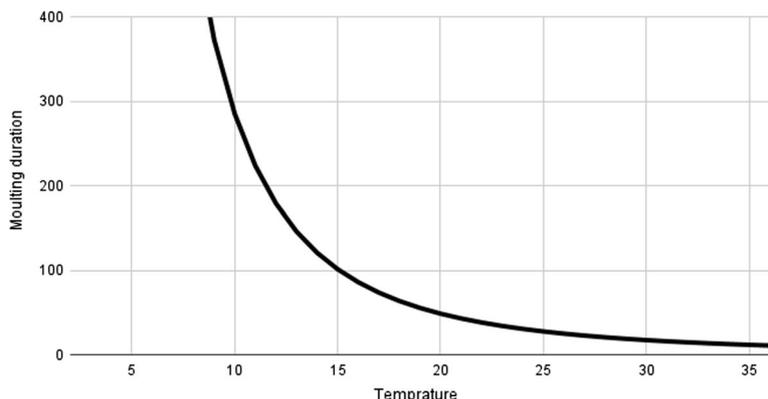
**Fig. 4** Conceptual view of the submodels: the diagram represents an outline of the sequence of processes and the schedule of interactions between *Vector* and *Host* agents at each discrete time step

**Table 2** Global Parameters and input values of the vector agent and host agent attributes. For the dimension, the following symbols are used: “-” indicates no dimensions

Param.	Sym.	Val.	Dim.	Uni.	Ref.
<i>World</i>					
The current daily value of T°	CurrentTemp	-	$\mathbb{R}$	°C	(Harris et al. 2020)
Maximum T°	MAX_TEMP	40	$\mathbb{R}$	°C	-
Minimum T°	MIN_TEMP	-30	$\mathbb{R}$	°C	-
Coeff.of Environment-induced mort.	ALPHA	0.2	$\mathbb{R}$	-	-
Time step	step	2	$\mathbb{R}$	hour	-
World size	shape	1	$\mathbb{R}$	km	-
Posi. of the barn	BARN_LOC	(500,500)	$\mathbb{R}^2$	m	-
<i>Vector</i>					
Initial num. of vectors	INI_NUM_VECTOR	150	$\mathbb{N}$	-	-
Distance of perception	PERCEPTION_DISTANCE	7	$\mathbb{N}$	m	-
Larva max. Lethal T°	LETHAL_TEMP_SUP_L	40	$\mathbb{R}$	°C	(Ogden et al. 2004)
Nymph max. Lethal T°	LETHAL_TEMP_SUP_N	45	$\mathbb{R}$	°C	(Ogden et al. 2004)
Egg max. Lethal T°	LETHAL_TEMP_SUP_E	32	$\mathbb{R}$	°C	(Ogden et al. 2004)
Adult max. Lethal T°	LETHAL_TEMP_SUP_A	35	$\mathbb{R}$	°C	(Vandyk et al. 1996)
Nymph min. Lethal T°	LETHAL_TEMP_INF_N	-18	$\mathbb{R}$	°C	(Brunner et al. 2012)
Adult min. Lethal T°	LETHAL_TEMP_INF_A	-20	$\mathbb{R}$	°C	(Brunner et al. 2012)
Larva min. Lethal T°	LETHAL_TEMP_INF_L	-18	$\mathbb{R}$	°C	(Daniels et al. 1996)
Egg min. Lethal T°	LETHAL_TEMP_INF_E	-30	$\mathbb{R}$	°C	(Dautel and Knülle 2010)
Threshold T° of diapause for L.	THRESHOLD_T_L	8	$\mathbb{R}$	°C	(Daniels et al. 1996)
Threshold T° of diapause for N.	THRESHOLD_T_N	11	$\mathbb{R}$	°C	(Brunner et al. 2012)
Threshold T° of diapause for E.	THRESHOLD_T_E	8	$\mathbb{R}$	°C	(Dautel and Knülle 2010)
Threshold T° of diapause for A.	THRESHOLD_T_A	8	$\mathbb{R}$	°C	(Vandyk et al. 1996)
Proba. to lay eggs	ProbToLay	1	[0, 1]	-	-
Larva Nat. Mortality Proba.	P_NAT_MOR_N	0.006	[0, 1]	-	-
Nymph Nat. Mortality Proba.	P_NAT_MOR_L	0.006	[0, 1]	-	-
Adult Nat. Mortality Proba.	P_NAT_MOR_A	0.006	[0, 1]	-	-
Egg Natural Mortality Proba.	P_NAT_MOR_E	0.006	[0, 1]	-	-
Proba. of attachment	P_ATTACH	0.9	[0, 1]	-	-
Duration of attachment	AttachToDetach	7	$\mathbb{R}$	day	(Kocan et al. 2015)
Time to die when questing	TimeDieQuesting	167	$\mathbb{R}$	day	-
<i>Host</i>					
Initial num. of Cattle	INI_NUM_Cattle	50	$\mathbb{N}$	-	-
Initial num.of Rodents	INI_NUM_Rodent	100	$\mathbb{N}$	-	-
Min. Host speed	MIN_H_SPEED	0.02	$\mathbb{R}^2$	km/h	-
Max. Host speed	MAX_H_SPEED	0.5	$\mathbb{R}^2$	km/h	-
Cattle's activity start time	START_ACTIVE_TIME	9	$\mathbb{R}$	hour	-
Cattle's activity end time	END_ACTIVE_TIME	16	$\mathbb{R}$	hour	-
New position of boid movement	velocity	(0,0)	$\mathbb{R}^2$	-	-
Resting status	rest	False	Boolean	-	-
Min. distance of perception	minimal_distance	50	$\mathbb{N}$	meter	-
Carrying capacity	parasite_max	-	$\mathbb{N}$	-	-
Movement behaviour	movement_beh	["R", "H"]	list	Cat.	-



**Fig. 5** A schematic diagram for the duration incremental function  $f$



**Fig. 6** The curve of the relationship of larva moulting duration with temperature variation

**Table 3** Experimental plan for the scenarios S1 and S2

Parameter-Scenario	Scenario 1 (S1)	Scenario 2 (S2)
Host movement behaviour	Random movement	Herd movement
Carrying Capacity	{2, 3, 4, 5, 6, 7, 8, 9, 10}	{2, 3, 4, 5, 6, 7, 8, 9, 10}

For both S1 and S2, we vary the carrying capacity parameter for these different values

*Environment-induced mortality process* the *Environment-induced mortality* process is temperature-dependent. Every life state has a daily  $\gamma$  probability of death if the current daily temperature reaches the state-dependent lethal temperature threshold (refer to table 1).

### Results

The objective of our simulations is to study the effects of host movement patterns on vector population dynamics as well as the effect of the carrying capacity of the host on vector population dynamics. Simulations were performed using the Gama 1.8.2 (Tailandier et al. 2019) platform. All simulations reproduce a duration of ten years from October 1st 1990 until September 30th 2000.

Two scenarios are tested for the movement behaviour of *Cattle* agent (refer to Table 3). First, we run the random movement scenario (S1) and then the Herd movement scenario (S2). Both simulation scenarios were run using the same parameter values and initial state. First, we run the simulations with no carrying capacity applied (thereafter, they are defined as, respectively, S1-NC and S2-NC), and then, we fix the carrying capacity for both S1 and S2 (refer to subsection 3.3). We analyze the total and per-stage population

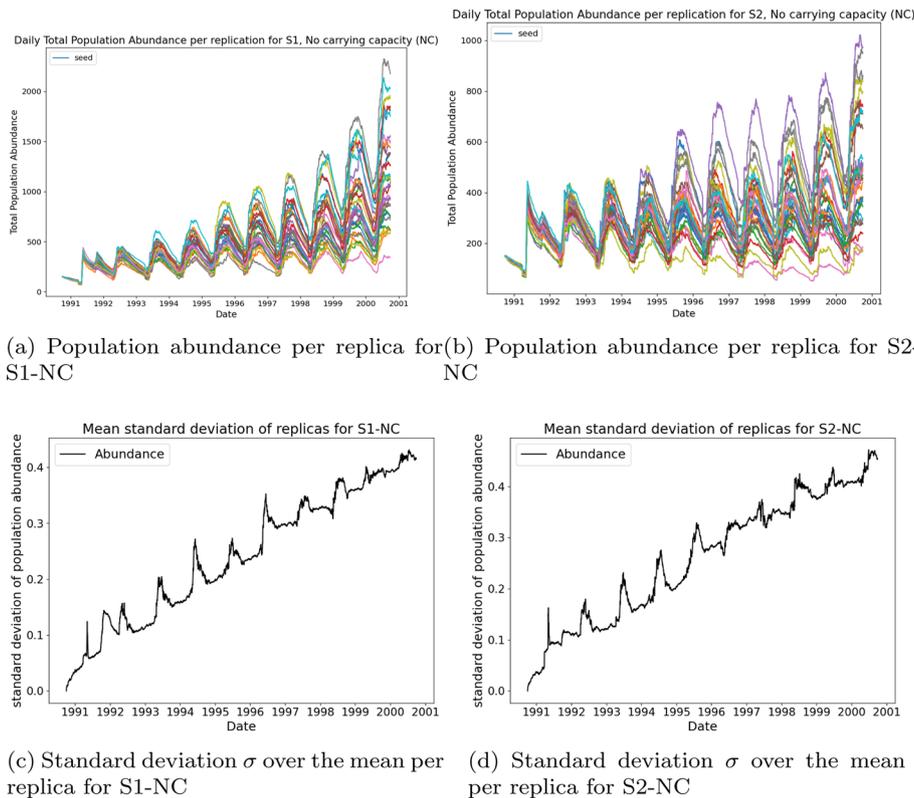
and the total population abundance for all simulation sets. We run 30 replicas per simulation set.

**Effect of simulations replication**

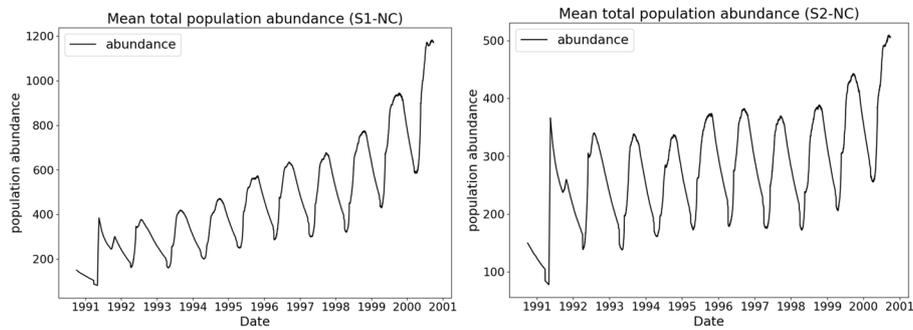
The replication effect is analyzed for both scenarios (S1 and S2) with no carrying capacity applied (S1-NC and S2-NC), we observe an annual fluctuation in the total population abundance per replication (refer to Figure 7a and 7b). Additionally, there is a noteworthy disparity in the magnitude of fluctuation between both scenarios and within the replications of each scenario, which becomes significant over the last four years of the simulation time. This is confirmed by computing the standard deviation  $\sigma_i$  over the mean between the replication for both S1-NC and S2-NC (Fig. 7c and Fig. 7d).

**Random movement Versus Herd movement patterns**

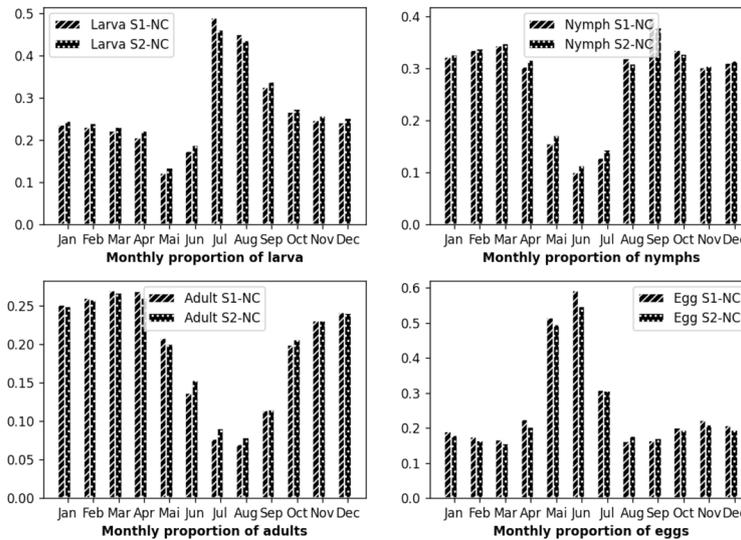
The total population abundance for both scenarios (S1 and S2) increases over time while no carrying capacity is fixed. Specifically in S1-NC (Fig. 8 and 8a).The mean population abundance  $\bar{N}(t)$  grows exponentially from an initial value of 150 until reaching roughly 1200. In the second scenario, S2-NC, the mean population abundance knows a significant peak in the first year of the simulation, then, it recognizes a slight fluctuation in



**Fig. 7** Total population abundance and standard deviation  $\sigma_i$ , where  $i$  is the replica index, over the mean, per replica respectively for the first scenario with no carrying capacity applied (S1-NC) and for the second scenario with no carrying capacity applied (S2-NC)



(a) Mean total population abundance (S1-NC) (b) Mean total population abundance (S2-NC)



(c) Monthly per-stage population abundance

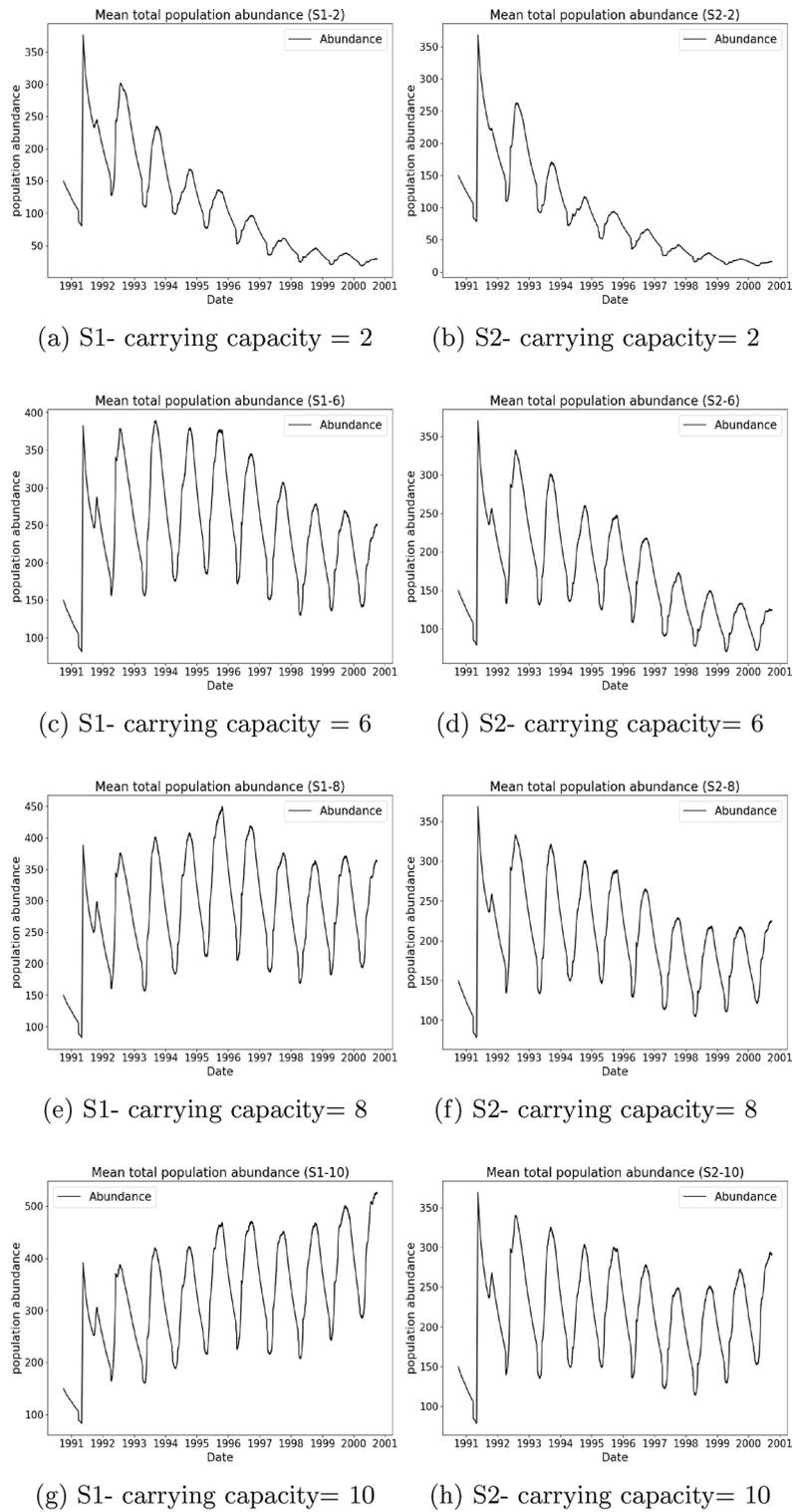
**Fig. 8** Mean total population with no carrying capacity (NC) and Monthly per-stage population, respectively, for the first scenario with no carrying capacity applied (S1-NC) and for the second scenario with no carrying capacity applied (S2-NC)

the yearly maximum, after which it reaches two new peaks, respectively, in the ninth and tenth year of the simulation (Fig. 8b). For the first set of simulations (S1-NC and S2-NC), the total population has an increasing trend based on the Mann-Kendall Trend test ( $p_{value} < 0.05$ ).

Both simulation sets have roughly the same per-stage population distribution (refer to Fig. 8c). The egg population knows a peak in early summer as expected (Ogden et al. 2004, 2005). Larva population emerged after the rise of the egg population in midsummer, followed by a peak of the nymph population in late summer. The adult population increases in early autumn and stays steadily high until late spring.

### Host carrying capacity effect

We varied the carrying capacity of the host agent for both S1 and S2 and analysed the mean total population abundance over 10 years (Fig. 9). For every simulation set, the carrying capacity of host values is fixed. For low values of the parameter (refer to Fig. 9a



**Fig. 9** Mean population abundance for both scenarios S1 and S2 for the different carrying capacity parameter values. The evolution of the mean population abundance is inversely proportional to the carrying capacity

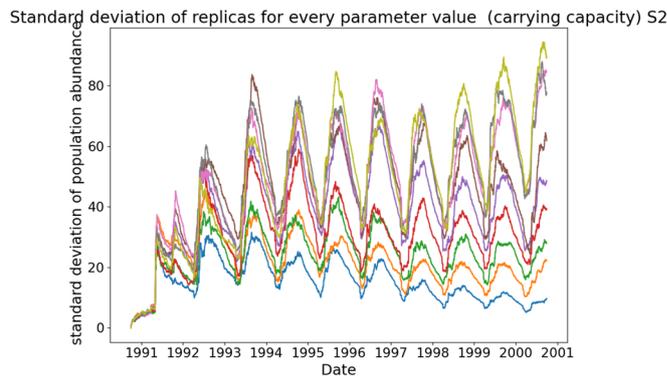
and 9b), representing a low number of vectors able to attach to the host, the average population decreases over the simulation time towards extinction. For higher values (refer to Fig. 9c and 9d), the population decreases less steeply. A stabilization begins to take hold for both scenarios when the carrying capacity is equal to 8 (refer to Fig. 9e and 9f). For the extreme value of the parameter, the population behaviour is similar to that of the scenario where the host’s capacity limit is not applied in the first scenario (refer to Fig. 7).

*Scenario 1: Random pattern*

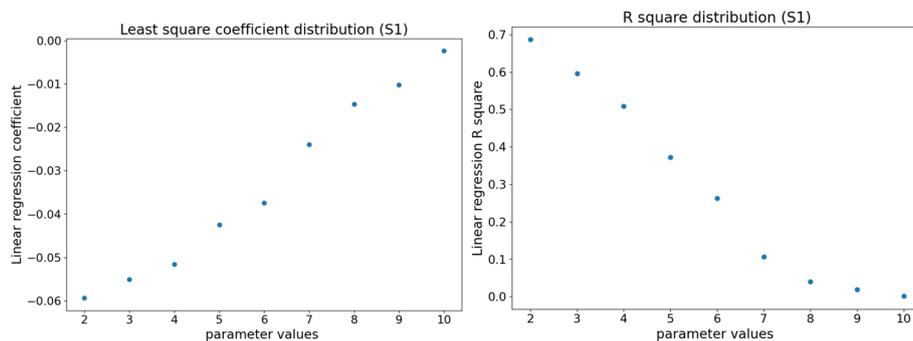
We notice, as expected that the mean population abundance increases as the *parasite\_max* values increase (Fig. 10). We fitted the output into a linear least square regression for the 30<sup>th</sup> replicas for every parameter value (refer to Figure 10a).

For S1, the least square coefficient increases gradually with the parameter value (refer to Figure 10b). Also, we notice the  $R^2$  is the highest for the simulation set S2, as well as for the minor square coefficient, is the lowest for the carrying capacity is equal to 7 ( $R^2 = 0.004$ ), then it is the value that best regulates our vector population (Figure 10c).

*Scenario 2: Herd movement pattern* The same approach used for the first scenario, S1, is followed in the second scenario (Fig. 10a and 11b). However, for the coefficient  $R^2$ , we notice the best value for the carrying capacity is equal to 10 (Figure 11c).



(a) Standard deviation of replicas for every parameter value

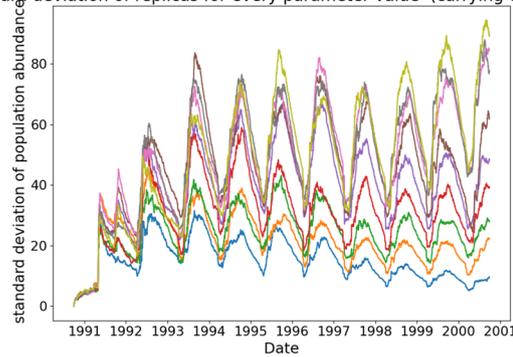


(b) Least square coefficient for S1

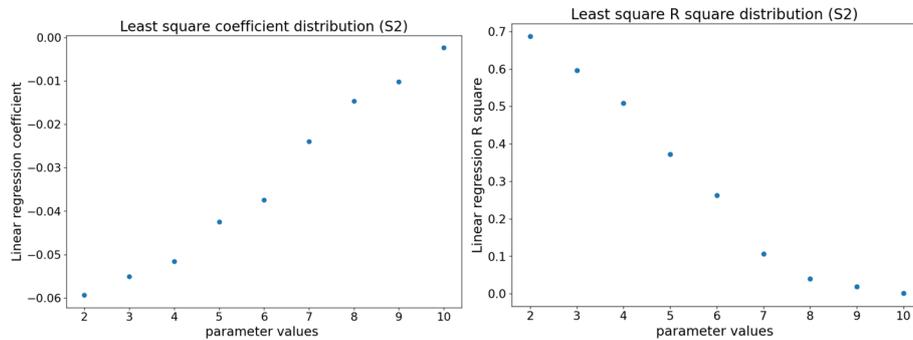
(c)  $R^2$  for S1

**Fig. 10** The figure shows the standard deviation and the fitting of replicas for the first scenario S1 **a** Standard deviation of replicas for each parameter value for S1. **b,c** Least square fitting of replicas for each parameter value for S1

Standard deviation of replicas for every parameter value (carrying capacity) S2



(a) Standard deviation of replicas for every parameter value



(b) Least square coefficient for S2

(c) Least square  $R^2$  for S2

**Fig. 11** The figure shows the standard deviation and the fitting of replicas for the second scenario S2. **a**) Standard deviation of replicas for each parameter value for S2. **b, c**) Least square fitting of replicas for each parameter value for the second scenario S2

**Discussion**

We developed an agent-based model to investigate the dynamics of tick populations. The model primarily aims to evaluate host movement patterns on tick population dynamics. We monitored annual and seasonal population fluctuations and population growth tendencies. We tested different host movement patterns while varying the carrying capacity of the host. The outcome of the different simulation scenarios suggests that the movement pattern of the host does not affect the seasonality of the vector agent, although it impacts its population abundance. Since the random movement pattern allows a higher likelihood for the host agent to be located within the perception distance of the vector agent, driving vectors, in a cascade effect, to execute the remaining processes and produce offspring. Furthermore, our model introduces an essential dimension by incorporating resource competition, mainly through host availability, as a significant regulatory factor influencing vector populations. This approach enhances the generalization and formalizes the intricate relationship between vectors and hosts, making our model adaptable to a broad spectrum of vector and host species across diverse biogeographic regions. The most obvious finding to emerge from analyzing the carrying capacity of the host, on the one hand, is the exponential growth of the population when increasing the capacity of the host to

attach vectors approaching the results of S1, and on the other hand, the extinction of the population when low carrying capacity is fixed, limiting the vector agents to continue other processes and fulfill the next life state. Over ten years of simulations, we note that the population abundance shows a decreasing behaviour for both S1 and S2 while applying low carrying capacity parameter values. While the carrying capacity of the host increases, the population knows a gradual increase and tends to stabilize over time for both S1 and S2 until reaching a turning point for the simulation, where the population behaves as the one in S1 when no carrying capacity is applied.

So far, our work has focused on host movement patterns' effect on vector population on the one hand, and on the other hand, it focused on the grooming effect of the host illustrated in our model by the carrying capacity parameter.

This model complements studies *e.g.* Watts et al. (2018); Chen et al. (2022); O'Neill et al. (2023) by incorporating temperature-dependent vector developmental stages, host-vector interactions, and the influence of host movement on tick species characterized by passive host-seeking behaviour, exemplified by *Ixodes ricinus*. Our model's uniqueness lies in its ability to encompass the entire tick life cycle, representing development as a temperature-dependent process and the sole interaction between vector and host through blood meals. Our model's hypotheses exhibit a robust capacity to replicate the seasonal dynamics of the vector population. Remarkably, this is achieved by considering only temperature as the regulating factor governing transitions between developmental stages as Randolph (2004); Ogden et al. (2004) highlighted. While our model's assumptions are straightforward, they have proved essential in reproducing the tick's whole life cycle. Moreover, our model affords us a comprehensive descriptive framework for understanding the tick's life cycle, integrating physiological processes (illustrated by vector life state transitions and behavioural states of each instar) and ecological processes (captured through host availability for blood meals).

Also, our model seeks to explore the tangled mesh between ecological interactions at the individual level and their impact on physiological processes, particularly the development time of each life stage; the individual dependence on the temperature to develop will create a seasonality. This objective aligns with the distinction of various scales in ecology, as the scale of matter, from cellular processes to ecosystems, with individuals as the key link. This illustration of ecological scales facilitates the subsequent delineation of other dimensions, such as temporal and spatial scales ... (Maâroufi et al. (2014); Louati (2017); Ellison and Gotelli (2021)).

The issues related to changes in scale levels are relevant, and coupling different scales in modelling is a challenge. Prior studies have underscored the importance of agent-based modelling in elucidating the complexities of vector-host systems (*e.g.* Nolzen et al. (2022); Halsey and Miller (2018); Tardy et al. (2022)). These studies have predominantly focused on landscape characteristics, particular tick species, and host-specific models. Unlike its counterparts, our model does not rely on actual landscapes or the real movement of hosts; instead, it delves into a theoretical exploration. In doing so, it allows to examine intriguing ecological phenomena, such as the impact of temperature on developmental processes, in a controlled and hypothetical environment.

Our work utilizes empirical data outlined in Table 1 to enhance its adaptability across a diverse range of case studies and contexts. We take a comprehensive approach to

understanding the life cycle of tick species, considering their wide geographical distribution and varied phenological patterns. A key highlight of our contribution is its implicit recognition of the role of host presence in influencing tick population dynamics, particularly in species with significant geographical expansion and diverse phenological patterns. Our contribution underscores the significant role of host presence in shaping tick population dynamics. This aspect is seamlessly integrated into our model through the parameter of host carrying capacity, showcasing its adaptability in simulating the complexities of tick populations and their interactions with hosts. This understanding leads to another valuable application of our model: evaluating the capacity of hosts to sustain tick populations. Such evaluations are particularly pertinent when considering various control methods, both on-host and off-host, such as the application of acaricides or host population management. These methods are aimed at reducing tick numbers, especially nymphs and adult ticks that may pose risks to livestock. In addition, the possibility of extending the model to other tick species, it also has a potential for generalization to include other vector species, such as the *Anopheles* mosquitoes responsible for malaria transmission. The fundamental interactions between anopheles and their hosts closely resemble those observed with ticks. However, a distinctive challenge arises when selecting an appropriate scale representing mosquito movement. When addressing mosquitoes, we can describe them as individual clusters exhibiting synchronous movement, collectively representing a single agent. Alternatively, we can model them as individual mosquitoes acting as individual agents, a concept already outlined in our model.

Furthermore, a compelling application of our model is its capacity to assess the impact of temperature variations as a primary driver influencing tick life cycles (see Sect. 2.2). This includes predicting population densities and conducting comparative analyses between outbreeding and inbreeding scenarios within stable livestock populations.

## Conclusion

This work introduces an initial model designed to conceptualize the dynamics of the vector-host system, specifically focusing on investigating the impact of both host movement patterns and host carrying capacity on short-term vector population dynamics. The model's hypotheses are aligned within the framework of a hypothetical landscape encompassing host and vector populations while considering the vector physiological development as a temperature-dependent process. The simulation experiments carried out in our work substantiate the importance of host-carrying capacity in the dynamics of the vector population and contribute to our understanding of these complex interactions. One of the more significant conclusions to emerge from this work is that the temperature can regulate vectors' life cycle and keep the vector population dynamics seasonality. Moreover, the host movement behavior has no effect on the vector dynamics. A natural progression of this model is to validate the findings with empirical data and extend it to cover more environmental factors and include vector-borne diseases, since our model possesses the versatility to explore a variety of host- and environment-targeted control strategies, facilitating the identification of practical approaches for managing vector population dynamics in a broader ecological context.

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### Author contributions

C.C. co-conceived the conceptualization and methodology and co-performed the computation, writing and the original draft preparation. N.M.: co-performed the computation, the validation and the reviewing and co-supervised the work. S.B.M.: co-conceived conceptualization and methodology, co-performed the writing, reviewing and editing and co-supervised the work. All authors discussed the results and contributed to the final manuscript. All authors reviewed the manuscript.

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### Availability of data and materials

Not applicable.

### Declarations

#### Conflict of interest

All authors declare no Conflict of interest.

#### Ethics approval and consent to participate

Not applicable.

#### Consent to participate

Not applicable.

#### Consent for publication

All authors consent to the publication of the manuscript.

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### References

- Sonenshine DE, Roe RM (eds) (2014) *Biology of Ticks* volume 1, 2nd edn. Oxford University Press, Oxford
- Randolph SE (2004) Tick ecology: processes and patterns behind the epidemiological risk posed by ixodid ticks as vectors. *Parasitology* 129:537. <https://doi.org/10.1017/S0031182004004925>
- Ogden NH, Lindsay LR, Beauchamp G, Charron D, Maarouf A, O'Callaghan CJ, Waltner-Toews D, Barker IK (2004) Investigation of relationships between temperature and developmental rates of tick *Ixodes scapularis* (acari: ixodidae) in the laboratory and field. *J Med Entomol* 41:622. <https://doi.org/10.1603/0022-2585-41.4.622>
- Ogden NH, Bigras-Poulin M, O'Callaghan CJ, Barker IK, Lindsay LR, Maarouf A, Smoyer-Tomic KE, Waltner-Toews D, Charron D (2005) A dynamic population model to investigate effects of climate on geographic range and seasonality of the tick *Ixodes scapularis*. *Int J Parasitol* 35:375. <https://doi.org/10.1016/j.ijpara.2004.12.013>
- Wikel SK (2018) Ticks and tick-borne infections: complex ecology, agents, and host interactions. *Veterinary sciences*. <https://doi.org/10.3390/vetsci5020060>
- Estrada-Peña A, Fuente JDL (2014) The ecology of ticks and epidemiology of tick-borne viral diseases. *Antiviral Res* 108:104. <https://doi.org/10.1016/j.antiviral.2014.05.016>
- Estrada-Peña A, Guglielmine AA, Nava S (2023) Worldwide host associations of the tick genus *Ixodes* suggest relationships based on environmental sharing rather than on co-phylogenetic events. *Parasites & Vectors* 16:75. <https://doi.org/10.1186/s13071-022-05641-9>
- Ogden NH, Pang G, Ginsberg HS, Hickling GJ, Burke RL, Beati L, Tsao JI (2018) Evidence for geographic variation in life-cycle processes affecting phenology of the Lyme disease vector *Ixodes scapularis* (acari: ixodidae) in the United States. *J Med Entomol* 55:1386. <https://doi.org/10.1093/JME/TJY104>
- Ogden NH, Beard CB, Ginsberg HS, Tsao JI (2021) Possible effects of climate change on ixodid ticks and the pathogens they transmit: predictions and observations. *J Med Entomol* 58:1536. <https://doi.org/10.1093/JME/TJAA220>
- Nolzen H, Brugger K, Reichold A, Brock J, Lange M, Thulke HH (2022) Model-based extrapolation of ecological systems under future climate scenarios: The example of *Ixodes ricinus* ticks. *PLoS ONE* 17:e0267196. <https://doi.org/10.1371/journal.pone.0267196>
- Wu X, Duvvuri VR, ab JW (2010) Modeling dynamical temperature influence on tick *Ixodes scapularis* population, Modelling for Environment's Sake. In: *Proceedings of the 5th Biennial Conference of the International Environmental Modelling and Software Society, iEMSs 2010* 3, 2272
- Medlock JM, Hansford KM, Bormane A, Derdakova M, Estrada-Peña A, George JC, Golovljova I, Jaenson TGT, Jensen JK, Jensen PM, Kazimirova M, Oteo JA, Papa A, Pfister K, Plantard O, Randolph SE, Rizzoli A, Santos-Silva MM, Sprong H, Vial L, Hendrickx G, Zeller H, Bortel WV (2013) Driving forces for changes in geographical distribution of *Ixodes ricinus* ticks in Europe. *Parasites & Vectors* 6:1. <https://doi.org/10.1186/1756-3305-6-1>

- Eisen RJ, Eisen L, Ogden NH, Beard CB (2016) Linkages of weather and climate with *Ixodes scapularis* and *Ixodes pacificus* (Acari: Ixodidae), enzootic transmission of *Borrelia burgdorferi*, and Lyme disease in North America. *J Med Entomol* 53:250. <https://doi.org/10.1093/jme/tjv199>
- Tracy M, Cerdáí M, Keyes KM (2018) Agent-Based Modeling in Public Health: Current Applications and Future Directions. *Annu Rev Public Health* 39:77. <https://doi.org/10.1146/annurev-publhealth-040617-014317>
- Ndongo MS, Ndiaye PI, Gharbi M, Rekik M, BenMiled S, Darghouth MA (2022) A climate-based model for tick life cycle: positive semigroup theory on Cauchy problem approach. *J Math Biol* 84:1. <https://doi.org/10.1007/S00285-022-01755-X/FIGURES/7>
- Healy C, Pekins PJ, Atallah S, Congalton RG (2020) Using agent-based models to inform the dynamics of winter tick parasitism of moose. *Ecol Complex* 41:100813. <https://doi.org/10.1016/j.ecocom.2020.100813>
- Tosato M, Zhang X, Wu J (2022) A patchy model for tick population dynamics with patch-specific developmental delays. *Mathematical biosciences and engineering* : MBE 19:5329. <https://doi.org/10.3934/mbe.2022250>
- Smajgl A, Barreteau O. Empiricism and Agent-Based Modelling. *Empiricism and Agent-Based Modelling* (Springer New York, 2014), pp. 1–26. [https://doi.org/10.1007/978-1-4614-6134-0\\_1](https://doi.org/10.1007/978-1-4614-6134-0_1)
- Mount GA, Haile DG (1989) Computer simulation of population dynamics of the American dog tick (Acari: Ixodidae). *J Med Entomol* 26:60. <https://doi.org/10.1093/JMEDENT/26.1.60>
- Halsey SJ, Miller JR (2018) A spatial agent-based model of the disease vector *Ixodes scapularis* to explore host-tick associations. *Ecol Model* 387:96. <https://doi.org/10.1016/j.ecolmodel.2018.09.005>
- Tyre AJ, Tenhumberg B, Bull CM. in *Transactions of the 2nd Biennial Meeting of the International Environmental Modelling and Software Society*, vol. 2, ed. by C. Pahl-Wostl, S. Schmidt, A. Rizzoli, A. Jakeman (Complexity and Integrated Resources Management, Transactions of the 2nd Biennial Meeting of the International Environmental Modelling and Software Society, 2004), vol. 2, pp. 895–901. <https://digitalcommons.unl.edu/bioscifacpub/185>
- Gilbert L, Aungier J, Tomkins JL (2014) Climate of origin affects tick (*Ixodes ricinus*) host-seeking behavior in response to temperature: Implications for resilience to climate change? *Ecol Evol* 4:1186. <https://doi.org/10.1002/ece3.1014>
- Yong KE, Mubayi A, Kribs CM (2015) Agent-based mathematical modeling as a tool for estimating *Trypanosoma cruzi* vector-host contact rates. *Acta Trop* 151:21. <https://doi.org/10.1016/j.actatropica.2015.06.025>
- Tardy O, Vincenot CE, Bouchard C, Ogden NH, Leighton PA (2022) Context-dependent host dispersal and habitat fragmentation determine heterogeneity in infected tick burdens: an agent-based modelling study. *Royal Society Open Science*. <https://doi.org/10.1098/rsos.220245>
- Gaff H, Nadolny R (2013) Identifying requirements for the invasion of a tick species and tick-borne pathogen through ticksim. *Math Biosci Eng* 10:625. <https://doi.org/10.3934/mbe.2013.10.625>
- Nadolny RM, Gaff HD (2018) Modelling the effects of habitat and hosts on tick invasions. *Letters in Biomathematics* 5:2. <https://doi.org/10.1080/23737867.2017.1412811>
- Mori K, Massolo A, Marceau D, Stefanakis E (2023) Modelling the epidemiology of zoonotic parasites transmitted through a predator-prey system in urban landscapes: The Calgary *Echinococcus multilocularis* Coyote Agent-based model (CEmCA). *Ecol Model* 475:110177. <https://doi.org/10.1016/J.ECOLMODEL.2022.110177>
- Kremmydas D, Athanasiadis IN, Rozakis S (2018) A review of Agent Based Modeling for agricultural policy evaluation. *Agric Syst* 164:95. <https://doi.org/10.1016/j.agry.2018.03.010>
- Grimm V, Berger U, DeAngelis DL, Polhill JG, Giske J, Railsback SF (2010) The ODD protocol: a review and first update. *Ecol Model* 221:2760. <https://doi.org/10.1016/j.ecolmodel.2010.08.019>
- Grimm V, Railsback SF, Vincenot CE, Berger U, Gallagher C, DeAngelis DL, Edmonds B, Ge J, Giske J, Groeneveld J, Johnston AS, Milles A, Nabe-Nielsen J, Polhill JG, Radchuk V, Rohwäder MS, Stillman RA, Thiele JC, Ayllón D (2020) The ODD protocol for describing agent-based and other simulation models: A second update to improve clarity, replication, and structural realism. *Journal of Artificial Societies and Social Simulation*. <https://doi.org/10.18564/jasss.4259>. <https://www.jasss.org/23/2/7.html>
- Arthur DR (1948) On the egg of the tick, *Ixodes ricinus* L. *Parasitology* 39:53. <https://doi.org/10.1017/S0031182000083554>
- Gray JS, Kahl O, Lane RS, Levin ML, Tsao JI (2016) Diapause in ticks of the medically important *Ixodes ricinus* species complex. *Ticks and Tick-borne Diseases*. <https://doi.org/10.1016/j.ttbdis.2016.05.006>
- VN Belozero, RL. Naumov (2002) Nymphal diapause and its photoperiodic control in the tick *Ixodes scapularis* (Acari: Ixodidae). *Folia Parasitologica* 49: 314. <https://doi.org/10.14411/fp.2002.058>
- Dautel H, Knülle W. in *Proceedings of the 12th International Congress*, ed. by M.W. Sabelis, J. Bruin (Springer Dordrecht, 2010). [https://doi.org/10.1007/978-90-481-9837-5\\_52](https://doi.org/10.1007/978-90-481-9837-5_52)
- Lane RS, Mun J, Stubbs HA (2009) Horizontal and vertical movements of host-seeking *Ixodes pacificus* (Acari: Ixodidae) nymphs in a hardwood forest. *Journal of vector ecology* : journal of the Society for Vector Ecology 34:252. <https://doi.org/10.1111/j.1948-7134.2009.00034.x>
- Mejlon HA, Jaenson TGT (1997) Questing behaviour of *Ixodes ricinus* ticks (Acari: Ixodidae). *Exp Appl Acarol* 21:747. <https://doi.org/10.1023/A:1018421105231>
- Harris I, Osborn TJ, Jones P, Lister D (2020) Version 4 of the CRU TS monthly high-resolution gridded multivariate climate dataset. *Scientific Data* 7:1. <https://doi.org/10.1038/s41597-020-0453-3>
- Vandyk JK, Bartholomew DM, Rowley WA, Platt KB (1996) Survival of *Ixodes scapularis* (Acari: Ixodidae) Exposed to Cold. *J Med Entomol* 33:6. <https://doi.org/10.1093/jmedent/33.1.6>
- Brunner JL, Killilea M, Ostfeld RS (2012) Overwintering survival of nymphal *Ixodes scapularis* (Acari: Ixodidae) under natural conditions. *J Med Entomol* 49:981. <https://doi.org/10.1603/ME12060>
- Daniels TJ, Falco RC, Curran KL, Fish D (1996) Timing of *Ixodes scapularis* (Acari: Ixodidae) Oviposition and Larval Activity in Southern New York. *J Med Entomol* 33:140. <https://doi.org/10.1093/jmedent/33.1.140>
- Kocan KM, Fuente JDL, Coburn LA (2015) Insights into the development of *Ixodes scapularis*: a resource for research on a medically important tick species. *Parasit Vectors*. <https://doi.org/10.1186/s13071-015-1185-7>
- Reynolds CW (1987) Flocks, herds and schools: a distributed behavioral model. *ACM SIGGRAPH Computer Graphics* 21:25. <https://doi.org/10.1145/37402.37406>

- Taillandier P, Gaudou B, Grignard A, Huynh QN, Marilleau N, Caillou P, Philippon D, Drogoul A (2019) Building, composing and experimenting complex spatial models with the GAMA platform. *Geoinformatica* 23:299. <https://doi.org/10.1007/S10707-018-00339-6/FIGURES/6>
- Watts AG, Saura S, Jardine C, Leighton P, Werden L, Fortin MJ (2018) Host functional connectivity and the spread potential of Lyme disease. *Landscape Ecol.* <https://doi.org/10.1007/s10980-018-0715-z>
- Chen L, Chen S, Kong P, Zhou L (2022) A regression-based calibration method for agent-based models. *Front Ecol Evol.* <https://doi.org/10.3389/fevo.2022.993844>
- O'Neill X, White A, Gortázar C, Ruiz-Fons F (2023) The impact of host abundance on the epidemiology of tick-borne infection. *Bull Math Biol.* <https://doi.org/10.1007/s11538-023-01133-8>
- Maâroufi DL, BenMiled S, Saoud NBB (2014) HermaDEB an evolutionary individual based model for energy allocation in hermaphrodite, *lccsa* 2014 175–182
- Louati D (2017) Couplage de modèles multi-niveau de systèmes complexes: application aux systèmes biologiques, Université Pierre et Marie Curie - Paris VI; École Nationale des Sciences de l'Informatique (La Manouba, Tunisie). Français
- Ellison AM, Gotelli NJ (2021) *Scaling in ecology with a model system*. Princeton

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