

**Development of a population dynamics model to
investigate the displacement of *Rhipicephalus decoloratus*
by *Rhipicephalus microplus***

By

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DECLARATION

I (Johannes L. Kotzé) hereby declare that this dissertation submitted to the University of Pretoria for the degree of Master of Science (Veterinary Epidemiology) is my own work and has not been submitted by me or anyone else for a degree at any other university.

Signature:

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Professor Frans Jongejan started making me curious about the interplay between *R. microplus* and *R. decoloratus*, and I am very thankful for that. Professor Geoff Fosgate made me push myself to produce better and better work, and I am very thankful for that. Thanks to God for giving me a curious mind to start and the determination to finish. A big thank you to my wife and sons for accepting the temporary neglect I exposed them to while I worked on this project. I look forward to spending more time with you!

ABBREVIATIONS

AIC	Akaike Information Criterion.
cdf	Cumulative distribution function.
E	Euler's number, approximately equal to 2.71828.
pdf	Probability density function.
<i>R.</i>	The genus <i>Rhipicephalus</i> .
RH	Relative humidity.
REI	Reproductive efficiency index.
S	Saturation deficit.
T	Temperature in degrees Celsius (unless otherwise noted).

DEFINITIONS

Akaike Information Criterion	An index used to compare the fit of different regression models of the same dataset whilst penalising for complexity. A lower AIC
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indicates a better fit with the lowest number of independent variable terms.

Boophilid	A sub-genus within <i>Rhipicephalus</i> containing the single-host cattle ticks formerly named <i>Boophilus spp.</i>
Cumulative distribution function	A method to describe the distribution of values for a random variable (X). The cumulative probability for the random variable to take on values less than or equal to x .
Ecdysis	The process of shedding the outer cuticle in arthropods (also referred to as moulting).
Pangamy	Random mating among individuals of a species without selection. In ticks specifically, it often refers to sufficiently random mating that is not favouring matings with siblings (as would be expected with large egg clutches hatching together).
Parthenogenesis	A form of asexual reproduction where the unfertilized egg develops without fertilization.
PERT distribution	A probability density function defined by the minimum, the most likely (the mode) and the maximum values.
Probability density function	A mathematical function that gives the probability for a random variable (X) to be equal to x .
Refugium	An area where a population can survive when conditions are unfavourable. In parasites it specifically refers to surviving away from hosts that are normally treated with parasiticides.
Reproductive efficiency index	The number of eggs laid divided by the weight of the engorged female at the time of detachment.

Saturation deficit The difference between the actual vapour pressure of air and the saturation vapour pressure (at that specific temperature). The greater the difference the greater the potential for air to absorb moisture and therefore the faster the expected evaporation rate.

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SUMMARY

**Development of a population dynamics model to
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Rhipicephalus microplus is displacing *Rhipicephalus decoloratus* at an alarming rate. Besides being invasive, *R. microplus* is the only tick that can act as a vector for the substantially more virulent form of Babesiosis caused by *Babesia bovis*. There is no cross-immunity between the indigenous *Babesia bigemina* and *Babesia bovis*. There is a need to understand better the reasons for the success of *R. microplus* at the cost of *R. decoloratus*. To address this need, we developed a stochastic population dynamics model with daily time steps. The model was cohort-based for the eggs and questing larvae and individual-based for all later life stages.

The model parameters have been specified using the best available knowledge of the two competing species of ticks. Seven sensitivity parameters were identified that could influence the success of *R. microplus*. Different model simulations with varying values of the seven sensitivity parameters allowed the creation of a dataset of outcomes linked to the different sensitivity parameter combinations. The result measured was the proportion of *R. microplus* in the population after two years of simulation following an initial introduction comprising 30% of the total tick population. The sensitivity parameters assessed were (1) the development threshold for egg development, (2) the required degree-days to complete egg development, (3) the delay of the development of the parasitic lifecycle of *R. decoloratus*, (4) the length of time males survived on the host, (5) the number of male partners of each female tick, and, finally, (6) the starting date of the simulation and (7) a slight change in the mean environmental temperature.

R. microplus can displace *R. decoloratus* primarily due to its relatively faster development rate. In warm sub-tropical climates, the stage of development that provides *R. microplus* with the most significant advantage is the development of the eggs, followed by the parasitic life stages. This effect is likely to diminish substantially in colder climates and winter since *R. microplus* has a higher temperature requirement to start egg development (specified as the development threshold).

Although introductions of *R. microplus* into a herd are usually accidental, introductions just before winter will have a lower chance of establishing itself. There is a potential opportunity to eliminate already established *R. microplus* from mixed populations by aggressive dipping

in autumn, followed by artificial infestations of *R. decoloratus* after the efficacy of the acaricide has waned. This may lead to disproportionately high numbers of *R. decoloratus* males in spring which could sterilize a high proportion of the *R. microplus* females tipping the balance in favour of *R. decoloratus*.

1. JUSTIFICATION

Cattle ticks cause considerable economic losses worldwide, especially the one-host *Rhipicephalus* ticks (grouped under the sub-genus *Boophilus*). *Rhipicephalus microplus* (also known as the Asiatic Blue tick) is the most important and widespread species. The range of this tick continues to expand in Africa at the expense of indigenous ticks (*R. decoloratus* in southern Africa) (Horak et al., 2018; Madder et al., 2012). *Boophilus* ticks act as vectors for two important cattle blood parasites causing babesiosis and anaplasmosis; however, only *R. microplus* can transmit the significantly more virulent *Babesia bovis* (Aubry & Geale, 2011; Bock et al., 2004). An additional concern is that *R. microplus* might develop resistance to acaricides faster than *R. decoloratus* (Nyangiwe et al., 2013a).

There is a need to understand the biological drivers of the relative success of *R. microplus*. A population model allows one to compare the impact of different theories under the same modelling assumptions. This could assist in determining the most important causes for the success of *R. microplus*, which in turn could help to control it more effectively.

2. LITERATURE REVIEW

2.1. One-host ticks

One-host ticks remain on the same host as they moult from larvae to nymphs to adults. Some examples of one-host ticks include *Dermacentor spp.*, *Hyalomma dromedarii*, *Hyalomma*

scupense and *Margaropus spp.*, all of which can potentially infest cattle (Guglielmone et al., 2013). However, the most important one-host ticks of cattle are all from the subgenus *Boophilus* (Murrell & Barker, 2003). In 2003, *Boophilus* was reclassified from genus to subgenus when it was noted that some *Rhipicephalus* ticks are more closely related to *Boophilus* ticks than with other *Rhipicephalus* ticks (Murrell & Barker, 2003).

A one-host life cycle is important because it is completed faster, thereby having shorter generation times leading to a faster spread of beneficial mutations throughout a population (Alphey et al., 2020). When livestock are treated with acaricides, the one-host tick larvae, nymphs and adults are all exposed meaning fewer ticks in the environment escaping treatment (fewer ticks in refugia) and faster development of resistance (Mekonnen et al., 2002).

Rhipicephalus microplus and *R. decoloratus* typify the single-host ticks in the southern-African region by completing fast life cycles (2 months when conditions are favourable) and quickly developing resistance (Horak et al., 2018). *Rhipicephalus microplus* has been steadily extending its range, displacing other boophilid ticks in the process (*R. decoloratus* in East and Southern Africa (Nyangiwe et al., 2013a) and *R. geigy* and *R. annulatus* in West Africa (Madder et al., 2012)). Although the boophilid group share remarkably similar life cycles, the displacements have been occurring at surprisingly rapid rates suggesting that minor differences in the life cycles and ecological interactions can be critically important (Horak et al., 2009). Subtle morphological differences between *R. microplus* and *R. decoloratus* have

been described (Heyne, 1987). Most notably, *R. decoloratus* females have three rows of teeth on each side of the hypostome, whereas *R. microplus* has four rows on each side. *R. decoloratus* females have a protuberance on the 1st palpal segment that *R. microplus* females lack (the absence of which contributes to the concave shape of the medial aspect of palpal segment one in *R. microplus*). The shape of the adanal plates most easily distinguishes males. In *R. decoloratus*, the internal spur is more prolonged, extending beyond the posterior body margin. The length of the two spurs of the adanal plates is more pronounced in *R. decoloratus* than in *R. microplus* (Heyne, 1987). No morphological differences can currently assist to explain the observed ecological differences between the two species.

Rhipicephalus australis was first described as a one-host tick from Australia (Fuller, 1899) but was soon after considered conspecific with *R. microplus* (Ali et al., 2016). More recently, genetic divergence, sub-fertile crosses and minor morphological differences led to the reinstatement of *R. australis* (Estrada-Peña et al., 2012; Labruna et al., 2009). During the previous century, Australian scientists have researched the life cycle of what they considered to be *R. microplus* (most notably Hitchcock (1955a, 1955b)). More recent work on *R. microplus* proper, has failed to demonstrate significant differences from the work now attributed to *R. australis* (Mastropaolo et al., 2017; Senbill et al., 2018). Indeed the two species are very closely related, so clear differentiation on morphological features alone remains challenging (Barker & Walker, 2014; Berry, 2017).

R. australis is genetically closer to some genetic clades of *R. microplus* than they are to one another, leading to speculation that further work on *R. microplus* might reveal more species (Baron et al., 2018; Burger et al., 2014; Roy et al., 2018). For these reasons, we accept the

past work done in Australia under the name *R. microplus* as representative for *R. microplus* proper. We avoid throughout this paper making unnecessary, repetitive distinctions between work labelled *R. microplus* in Australia versus work performed elsewhere.

2.1.1. The economic and health importance of one-host ticks

Together, *R. microplus* and *R. decoloratus* present the most critical ticks on cattle in South Africa. Their impact is derived from blood loss, tick worry, hide damage (given their preference for feeding at sites that are important for leather production) and by transmitting the agents that cause Gallsickness and Redwater (Graf et al., 2004; Jongejan & Uilenberg, 2004). Gallsickness is caused by infection with *Anaplasma marginale*, a blood parasite that causes parasitised red cells to be phagocytosed within the animal leading to anaemia and icterus. Other biting insects can also transmit *Anaplasma marginale* but one-host ticks remain the principal vector (Aubry & Geale, 2011). Redwater derives its name from the red urine produced by affected cattle following the intravascular haemolysis of parasitised red blood cells (Bock et al., 2004). Two distinct types of Redwater exist caused by *Babesia bovis* (a severe form transmitted only by *R. microplus*) and *Babesia bigemina* (a milder form transmitted by both tick species) (Sivakumar et al., 2020). Immunity against the two *Babesia* spp. is not cross-protective (Bock et al., 2004). The range expansion of *R. microplus* (De Clercq et al., 2012; Lynen et al., 2008; Madder et al., 2012; Nyangiwe et al., 2013b) has subsequently extended the range of *Babesia bovis*, causing substantial losses in some naïve herds (Kamani et al., 2017).

The extent of the economic losses ascribed to boophilid ticks alone was estimated in 1997 to be around US\$13.9–18.7 billion per annum (de Castro, 1997). Nearly twenty years later the estimate was revised for inflation and cattle numbers to US\$22-30 billion per annum (Lew-Tabor & Rodriguez Valle, 2016).

2.1.2. Theories for the displacement of autochthonous ticks by *R. microplus*

Different theories have been put forward to explain the superiority of *R. microplus* over *R. decoloratus*. These include:

1. Slight differences in the life cycle lengths (Horak et al., 2009; Sutherst, 1987). As the lifecycle of the single-host ticks is completed relatively fast, small differences in lifecycle lengths can summate over time to substantial advantages.
2. Slight differences in the number of eggs produced (Horak et al., 2009). Assuming all other lifecycle parameters are similar, the species that produces more eggs per batch would eventually outcompete the other.
3. Earlier sexual maturity of *R. microplus* males and subsequent sterile matings with *R. decoloratus* (Horak et al., 2009; Sutherst, 1987). Given that the matings between the two species are sterile, sterile matings would negatively impact the occurrence of both species. However, whichever species can produce the largest number of surplus males would ensure relatively more successful, conspecific matings. In this way, earlier sexual maturity would benefit *R. microplus*, but only if earlier sexual maturity equates to a longer time spent on the host. If earlier maturing males also leave the host earlier, the advantage would be nullified.
4. Different adaptations to micro-climate conditions (Lynen et al., 2008; Yawa et al., 2019). Invasive species are very often adapted to the local climatic conditions equally well (or even better), when compared to the native species. A possible explanation for the

success of *R. microplus* may simply be that it is well adapted to the condition where it has been introduced.

5. *R. decoloratus* is more vulnerable to immune responses from cattle against ticks (Zeman & Lynen, 2010). Feeding ticks evoke an adaptive immune response in cattle (Tabor et al., 2017). Should *R. decoloratus* be more susceptible to these immune responses its relative breeding success would be impacted negatively.
6. Different rates of development of resistance to acaricides (Nyangiwe et al., 2013b). Field experiments have found higher levels of acaricide resistance in *R. microplus* compared to *R. microplus* (Baker et al., 1981), but it is unclear whether this is a widespread phenomenon and responsible for the success of *R. microplus*.

No single theory has gained prominence in the literature and the relative importance of each is currently unknown.

2.2. MATHEMATICAL MODELS FOR TICKS

2.2.1. Introduction

A quantitative model's intended purpose determines the appropriate methodology to employ. The vast range of possible research questions and the multiple means to address them has led to a confusing assortment of quantitative models that are complex to classify. Researchers typically call their models only by what they view as either their model's distinctive or critical features. Therefore, the classification of models can vary greatly depending on the point of reference. Wang et al. (2017) thoroughly reviewed models on single-host *Rhipicephalus* ticks. The study considered 113 different models developed from the 1970s up to the date of the study in 2017. This is an impressive number for such a restricted niche such as single-host *Rhipicephalus* ticks and stresses both the importance and

the complexity of one-host tick biology and its interactions with the environment. They distinguished between population dynamics and bio-climatic envelope models.

2.2.2. Bio-climatic envelope models

Bio-climatic envelope models evaluate the geo-spatial occurrence of a species as a factor of bio-climatic conditions (Araújo & Peterson, 2012). This approach has been popular in investigating single-host tick ranges (De Clercq et al., 2012; Estrada-Peña, 2003; Sutherst & Maywald, 1985; Zannou et al., 2021). The researcher collects geospatial information on tick prevalence and seeks the factors determining occurrence as a binary outcome linked to a location (Wang et al., 2017). Sungirai et al. (2018) followed this approach with particular reference to the displacement of *R. decoloratus* by *R. microplus* in Zimbabwe. They developed two separate logistic regression models setting the response variable as the presence or absence of the particular tick species. The predictor variables included 19 climate indicators and three vegetation indexes, and most climate indicators were highly significant. Their study confirmed both laboratory and field experiments that the two tick species have different sensitivities to changes in relative humidity (RH%) and temperature and that the ranges of *R. decoloratus* and *R. microplus* are dependent on these (Horak et al., 2018; Nava et al., 2013; Sutherst & Bourne, 2006). The model did not consider which species-specific life cycle factor led to the observed differences or how they compete. Indeed, some have argued that bio-climatic envelope models might lack the complexity required to fully understand the dynamics of species interactions (Araújo & Peterson, 2012; Zeman & Lynen, 2010).

Another limitation of bio-climatic envelope models for boophilid ticks involves the discrepancy between modelled distributions and observations. Ticks have either successfully spread to areas previously identified as unsuitable habitats (Adakal et al., 2013) or modelled distribution maps have been more extensive than observations (Olwoch et al., 2003). Regardless of the predictive limitations, geospatial models offer valuable insight into the drivers of range expansions.

2.2.3. Population dynamics models

The definitive feature of population dynamics models is that they all use growth rates (Frisman et al., 2021; Wang et al., 2017). When the model simulates dynamics between compartments such as the life stages in insects, it is known as a compartmental model. However, this term is more frequently applied to infectious diseases and pharmacokinetic systems (Enderle, 2012; Fitri et al., 2021). The rates of movement between the compartments can be modelled either by difference equations with set parameter values (deterministic) or by algorithms that assign values to the parameters by drawing randomly from a defined probability density function (stochastic) (Bertoin, 2016). By the nature of deterministic models, the model's output presents the estimated means, whereas stochastic model outputs show a distribution of possible results. Utilizing stochastic variables for tick models is preferable because parameters typically have inherent variability and there is often uncertainty about the true parameter value (Wang et al., 2017).

Estrada-Peña (2002) developed a deterministic model for the distribution of *R. decoloratus* across sub-Saharan Africa. He incorporated population dynamics into a bio-climatic envelope model, thus creating a hybrid model. This enabled the model to represent not only the geographic distribution of the tick, but also its seasonal abundance.

3.1 PROBLEM STATEMENT

The ability of *R. microplus* to rapidly displace *R. decoloratus* in some ecological niches has not been adequately explained. Different theories have been put forward that are hard to compare for their relative importance. Previous models were not designed with sufficient population dynamics complexity (including stochasticity) to investigate the reasons for this displacement.

3.2 BENEFITS

Creating a population model that can reproduce the life cycle of *R. decoloratus* and *R. microplus* ticks in a mixed population will allow further study of the life cycle differences.

3.3 AIMS/OBJECTIVES

3.3.1 Aim

The study aims to develop a stochastic population model to describe the life cycle of the one-host cattle ticks *R. microplus* and *R. decoloratus*.

3.3.2 Objectives

- Adjust model parameter inputs representing differences between *R. microplus* and *R. decoloratus* to obtain an extensive set of predicted outcomes.
- Assess the relative importance of model parameter values by analyzing predicted outcomes via sensitivity analysis.

4 ETHICAL CONSIDERATION

The ethics committee at the Faculty of Veterinary Science at the University of Pretoria approved the study protocol (Reference number REC014-21).

5 METHODOLOGY

5.1 Study location

The model was constructed basing the model parameters on the ecology of single-host ticks at the Malelane Research Unit in Mpumalanga, South Africa. The parameters included that are unique to this facility include the cattle movements between grazing camps and the climatic variables consisting of relative humidity (RH%) and temperature.

To simulate the Malelane Research Unit (located in Malelane, Mpumalanga Province of South Africa), the tick hosts are modelled as 60 cattle that move between 18 grazing camps spending two weeks in each. The grazing schedule is fixed such that no camp is rested, and all camps have equal stocking rates. The life stages of the ticks are modelled as either present on one of the 60 cattle or in any of the 18 camps.

No data from any animal experiments conducted at MRU were used in the development of this model.

5.2 Population dynamics model structure

The model has a compartmental structure with ticks moving through the compartments using algorithms coded in R-Studio (RStudio Team, 2021). Ticks move through each compartment of the model with the possibility of suffering mortality (Table 1). A daily time step is utilized, as is common for single-host tick models (Wang et al., 2017).

Table 1: The high-level structure of the population dynamics model. The compartments correspond to the different life stages of the ticks. The time spent in each compartment is determined by the function that drives movement to the next compartment and by the rate of mortalities. The table indicates the nature of the functions used whether a stochastic element is involved.

Compartment	Next compartment	Time spent in compartment		Mortalities	
		Nature of function	Stochastic element	Nature of function	Stochastic element
Egg	To questing larvae	Hyperbolic. Decreases with higher temperatures.	Yes	Exponential. Increases with desiccation and cold stress.	Yes
Questing larvae	To attached larvae	Exponential. Time is not modelled but rather the probability of questing success. Increases with cattle density.	Yes.	Log-linear. Increases with desiccation.	Yes.
Attached larvae	To nymphs	Linear. <i>R. decoloratus</i> is delayed at low saturation deficits.	No.	PERT distribution.	Yes.

Nymphs	To infertile male or fertile female	Linear. <i>R. decoloratus</i> is delayed at low saturation deficits.	No.	None.	NA
Infertile male	To fertile male	Linear.	No.	None.	NA
Fertile male	To mating male	Linear.	No.	None.	NA
Mating male	To fertile male	Linear.	No.	None.	NA
Fertile female	To mating female.	Determined by encounters with males.	Yes (potential mate presence is modelled stochastically.	None.	NA
Mating female	To pre-ovipositing female.	Determined by the life cycle length.	No.	None.	NA
Pre-ovipositing female	To ovipositing female	Log-linear.	No.	Beta distribution.	Yes.

Ovipositing female	To eggs	Quadratic. Increases with high temperatures up to inflection point at 27°C.	Yes. Temperature dependant.	None.	NA
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The climate data recorded at the Malelane Research Unit for the calendar year of 2020 were sourced from the facility (Figure 1). This included the daily average temperature and relative humidity taken at a three-meter height in the shade. However, the off-host tick life stages are found in microclimates near the ground that can be very different (Corson et al., 2004; Nava et al., 2013). At an hourly rate, temperature differences between microclimates can be as much as 15°C at temperature extremes. At longer time scales, the extremes average out to a maximum difference between microclimates of nearly 2°C (Haider et al., 2017). To simulate the microclimate variation found in the environment, the effect of temperature was modelled by adding a stochastically derived increase or decrease taken from a uniform distribution with a minimum of -1.3 and maximum of +1.3 to reflect the findings of Haider et al. (2017).

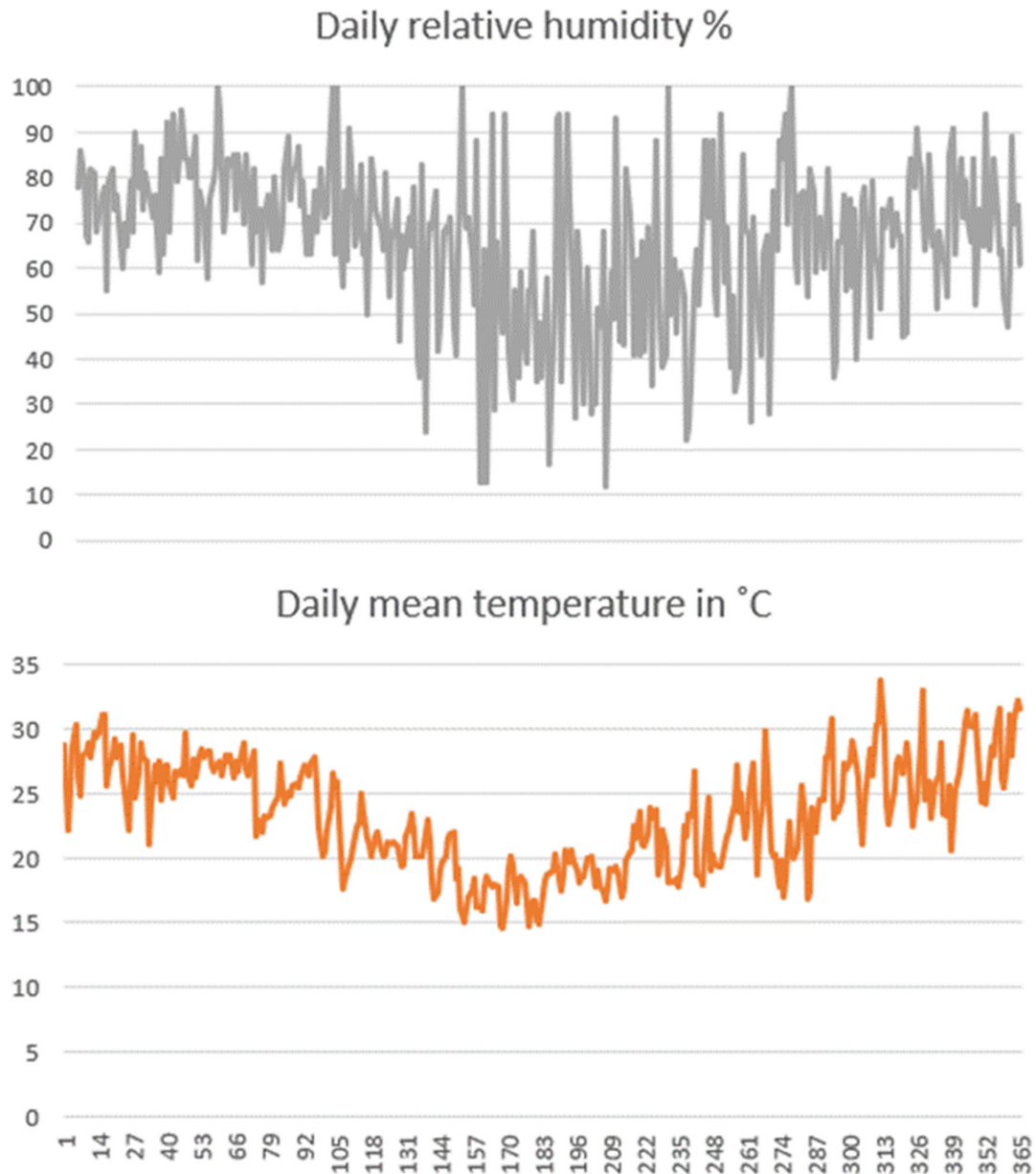


Figure 1: The daily average temperature relative humidity measured at the Malelane Research unit in 2020.

The relative humidity is often higher at ground level compared to measurements some distance above the ground (Hendy et al., 2020). However, when there is good vegetation cover, the relative humidity is relatively constant across habitats (Nava et al., 2013). Conversely, where habitats have open patches of soil, the relative humidity is much reduced

in those exposed patches (Lozano-Parra et al., 2018). The savannah habitat at the Malelane Research Unit is densely covered with grass, similar to the savannah habitat of Nava et al. (2013). We therefore do not add additional stochastic variability to the relative humidity recorded for each day.

The output of the model was the absolute number of ticks from each species, from which the relative proportions were calculated.

5.3 Population Model parameterisation

5.3.1 Egg incubation and egg hatching success

The time taken for eggs to reach maturity is independent of relative humidity (RH) but relies heavily on temperature (Hitchcock, 1955a; J. G. Londt, 1977). A simple mathematical formula to express egg development in terms of temperature involves first defining a minimum threshold temperature (T_0) below which no development occurs. Subsequently, the degree-days required (above the threshold temperature) to reach maturity is then defined (Estrada-Peña, 2002; Short et al., 1989; Sutherst & Bourne, 2006). Egg maturity is then modelled as the cumulative degree-days accumulated as a proportion of the degree-days required (D). Degree-days are only accumulated by the eggs when the temperature exceeds the minimum threshold (T_0). Maturity can be calculated using the following formula where *time* is measured in days spent at temperatures above the threshold temperature.

$$Maturity = ((T - T_0) \times time) / D$$

Maturation is important because proportional development drastically changes the susceptibility of eggs to stress (Sutherst & Bourne, 2006). Four previous studies provided data that could be used to estimate egg incubation periods (Table 2).

Table 2: The sources of data to estimate egg incubation periods

Author	Data source	Species	Temperature range	Calculated by	Threshold (T ₀)	Degree-days required (D)
Hitchcock, 1955	Laboratory	<i>microplus</i>	15.5 to 35°C	Sutherst & Bourne, 2006	15.5 °C	264
Nava et al., 2013	Field	<i>microplus</i>	6 to 30°C	Present author*	15.5 °C	248
Short et al., 1989	Field	<i>microplus</i>	5 to 30°C	Short et al., 1989	11.8 °C	490
Short et al., 1989	Laboratory	<i>microplus</i>	25°C	Short et al., 1989	11.8 °C	422
Spickett & Heyne, 1990	Field	<i>decoloratus</i>	7 to 21°C	Estrada-Peña, 2002	13.2 °C	457
Short et al., 1989	Field	<i>decoloratus</i>	5 to 30°C	Short et al., 1989	10.5 °C	633
Short et al., 1989	Laboratory	<i>decoloratus</i>	25°C	Short et al., 1989	10.5 °C	464

*The average required degree-days was calculated from the published dataset assuming a threshold temperature equal to that found in the laboratory by Hitchcock (1955a).

Although the degree-days required from the different sources might appear substantially different, when the respective threshold temperatures are included in calculating the

predicted incubation periods, they deliver reasonably similar results (see Figures 2 and 3). The R-Studio script to produce the Figures is attached as Appendix 1.

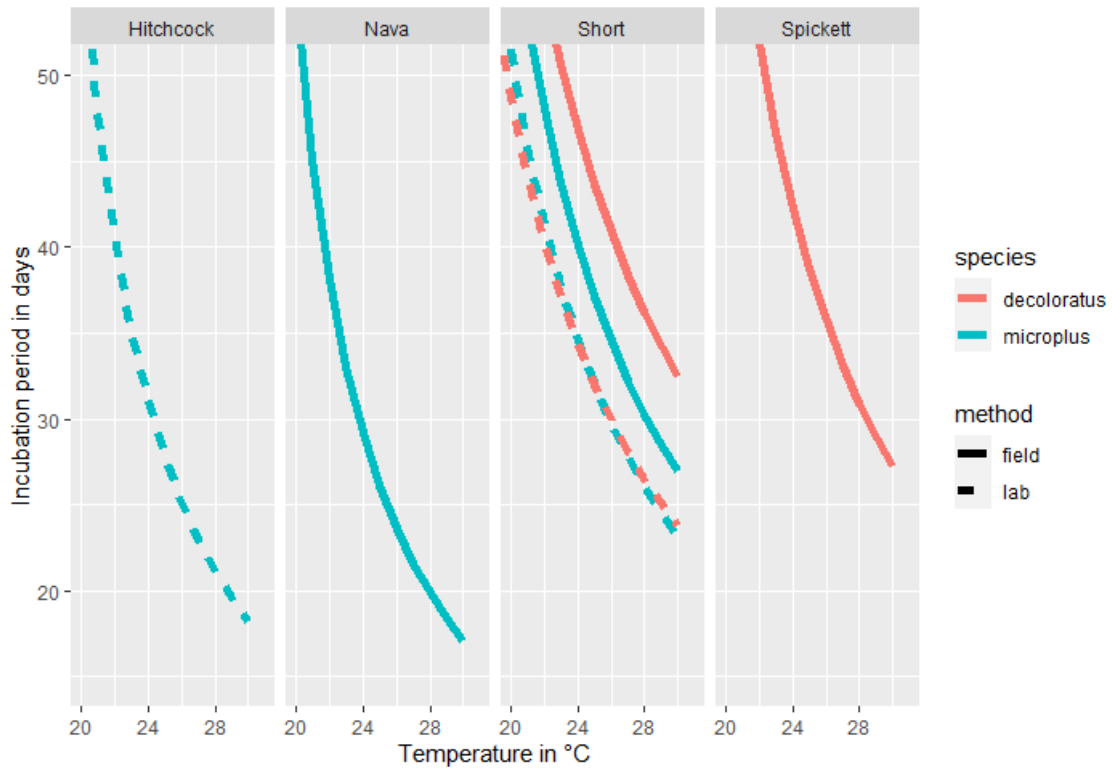


Figure 2: The predicted egg incubation periods by the different data sources (at warm temperatures).

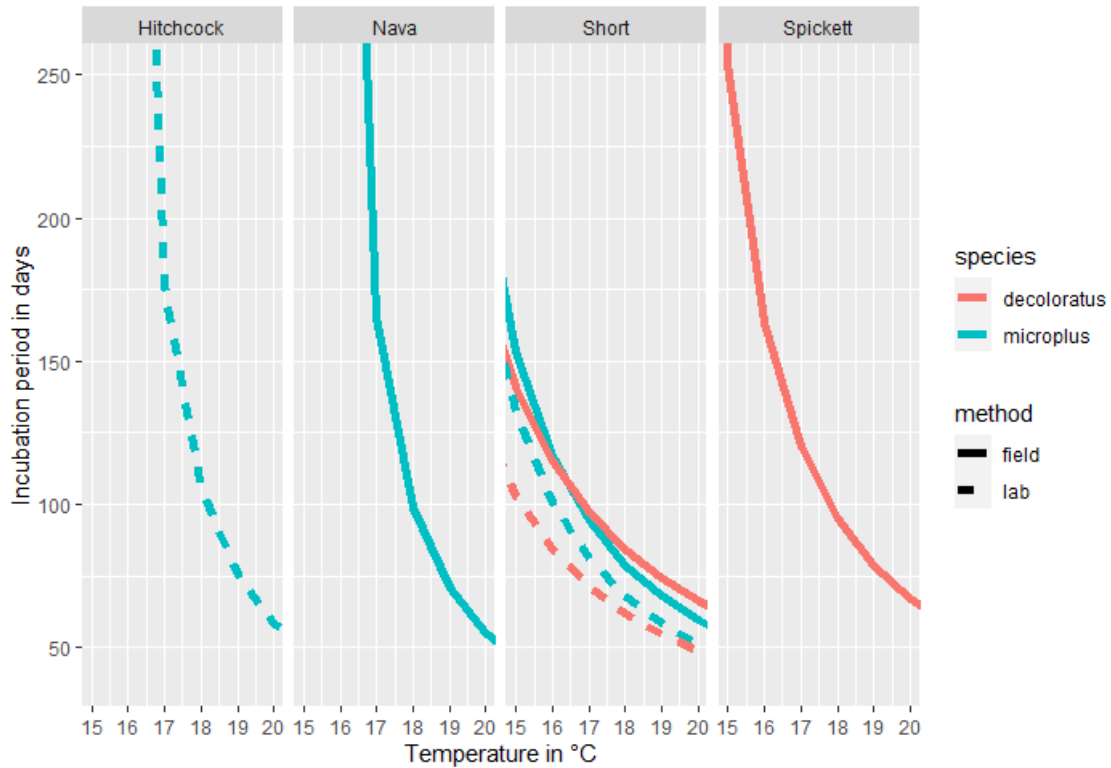


Figure 3: The predicted egg incubation periods by the different data sources (at cold temperatures).

At high temperatures (above 20°C, Fig 2), the development of *R. microplus* eggs is distinctly faster compared to *R. decoloratus* leading to shorter incubation periods. In contrast, the reverse is true at lower temperatures (Figures 2 and 3). The reasonably good agreement between laboratory and environmentally collected data presented in Figures 2 and 2 also confirms the findings of Hitchcock (1955a) that fluctuating temperatures predict the rate of development equally as well as the mean temperatures. Therefore, laboratory experiments that keep a constant temperature can be used to predict egg incubation periods under field conditions where temperatures fluctuate around a mean. The data of Short et al. (1989) is the only identified dataset that compared both *R. decoloratus* and *R. microplus* over a wide temperature range. This study was used to model parameter values for the threshold temperature and the required degree-days to reach maturity (Table 3).

Table 3: The population model parameters adopted in the population model to estimate egg incubation periods

Variable name	Description	Value(s)	Source	Notes
<i>dev_threshold_mic</i>	The developmental threshold temperature in Celsius for <i>R. microplus</i> .	11.8	(Short et al., 1989)	
<i>dev_threshold_dec_adapt</i>	A sensitivity parameter. Added to <i>dev_threshold_mic</i> to adapt for <i>R. decoloratus</i> . It is varied to facilitate the sensitivity analysis.	{-1.3; -0.87; -0.43; 0}	(Short et al., 1989)	The development threshold value for <i>R. decoloratus</i> determined by Short et al. is 10.5 and 11.8 for <i>R. microplus</i> (a difference of 1.3). Therefore, the maximum difference of 1.3 and a minimum of 0 was accepted. Two values were chosen in between the extremes at equal intervals.
<i>degree_days_mic</i>	The number of degree-days required above the threshold temperature to achieve full development.	422	(Short et al., 1989)	
<i>degree_days_dec_adapt</i>	A sensitivity parameter. Added to the <i>degree_days_mic</i> to adapt for <i>R.</i>	{0; 21; 42}	(Short et al., 1989)	The value for <i>R. decoloratus</i> determined by Short et al. is 464 (which is 422+42). Therefore, the

	<i>decoloratus</i> . It is varied to facilitate the sensitivity analysis.			maximum difference between the two species was chosen as 42, the minimum as 0 with one value in between (21).
<i>max_incubation_period</i>	A cut-off value to censor all calculated periods that are longer.	200	Informed estimate.	The theoretical maximum development time for <i>R. microplus</i> at 11.9°C is 4220 days (assuming above constants). This is certainly not realistic. The true cut-off is not known although it is known to be longer than 4 months (Canevari et al., 2017).

Tick egg mortalities are driven by two main factors, cold stress and desiccation (J. G. Londt, 1977; Sutherst & Bourne, 2006). Eggs dry out rapidly at high temperatures and low RH% leading to reduced hatchability. The evaporation ability of the air is proportional to the saturation deficit, so it is customary in the literature to refer to the saturation deficit (S) rather than the RH% (Perret et al., 2000; Teel, 1984; Theiler, 1964). Different equations for conversion between RH% and S are available with slightly varying results. The equation used by Perret et al. (2000) was chosen for this study to convert between RH% and S. Cold exposure primarily delays development. However, it also causes low mortalities through a poorly understood mechanism. Three previous studies provided data that could be used to estimate egg mortality due to either cold or desiccation stress (Table 5 and Figures 4-6-). A logistic regression model was specified from each dataset using temperature and saturation deficit as predictive variables. A maximum model was specified including the two variables, their squares, and all possible interactions. The optimal model was selected by minimizing the Akaike Information Criterion (AIC) through a backward and forward selection process using the R function step AIC from the package MASS (Zhang, 2016).

Table 4: The sources of data to estimate egg hatching success using logistic regression models

Data source	Species	Dataset details	Model details
Hitchcock, 1955	<i>Microplus</i>	T: 15.5 to 35°C SD: 0.1 to 13 mmHg # observations: 36	$\text{logit}(p) = 79.762 - 12.428T + 0.592T^2 - 0.927S^2 - 0.009T \cdot T^2 + 0.024T \cdot S^2$ Pseudo-R ² (Nagelkerke): 0.89
Londt, 1977	<i>Decoloratus</i>	T: 10 to 38°C SD: 0.9 to 24.7 mmHg # observations: 25#	$\text{logit}(p) = -68.11 + 5.750T - 3.756S - 0.108T^2 + 0.100T \cdot S$ Pseudo-R ² (Nagelkerke): 0.85
Nava et al., 2013	<i>Microplus</i>	T: 15.8 to 26°C SD: 1.9 to 7.3 mmHg # observations: 23#	$\text{logit}(p) = 373.774 - 53.449T + 3.712S + 2.489T^2 - 0.174T \cdot S - 0.038TT^2$ Pseudo-R ² (Nagelkerke): 0.19

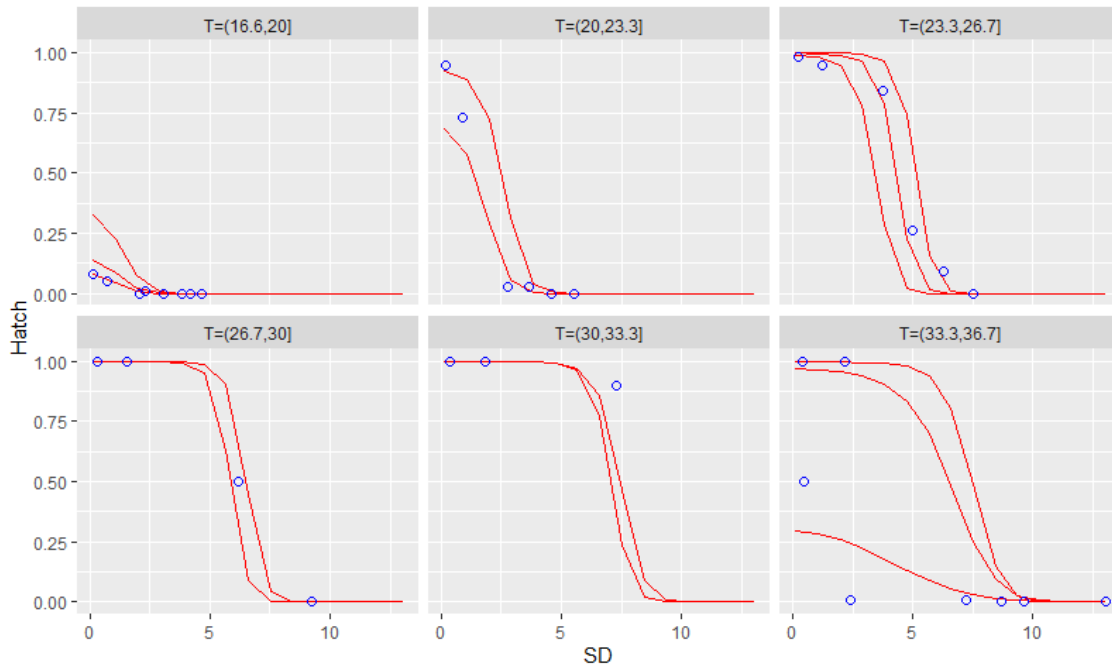


Figure 4: The observed (blue circle) and predicted (red line) hatching success at different saturation deficits and temperatures. Produced using a logistical regression model of the Hitchcock data (1955a)

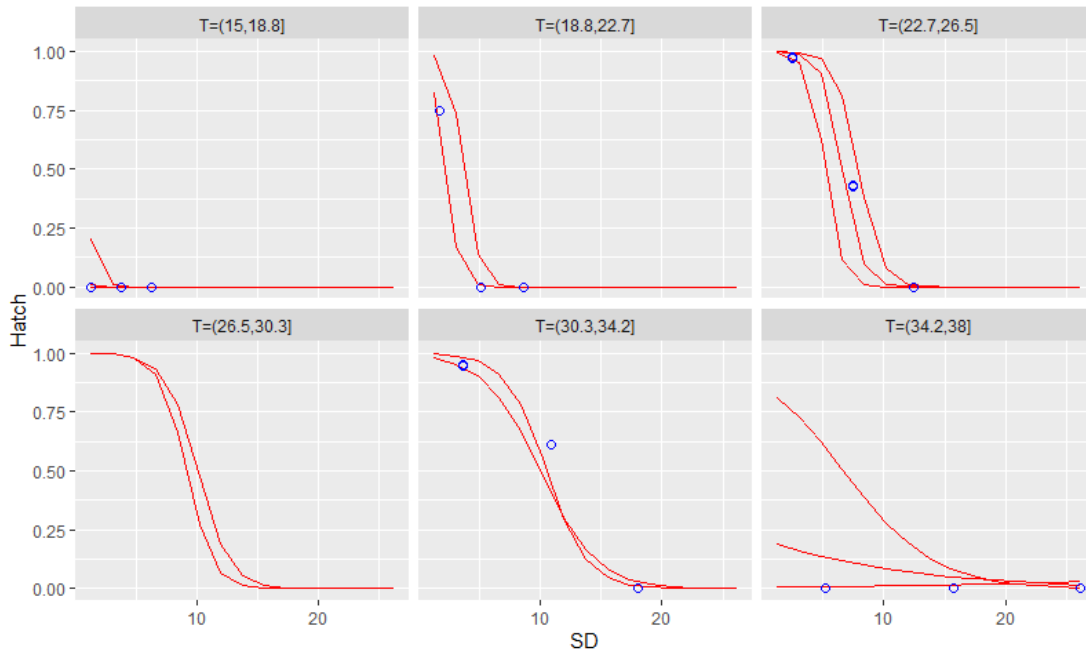


Figure 5: The observed (blue circle) and predicted (red line) hatching success at different saturation deficits and temperatures. Produced using a logistical regression model of the Londt data (1977).

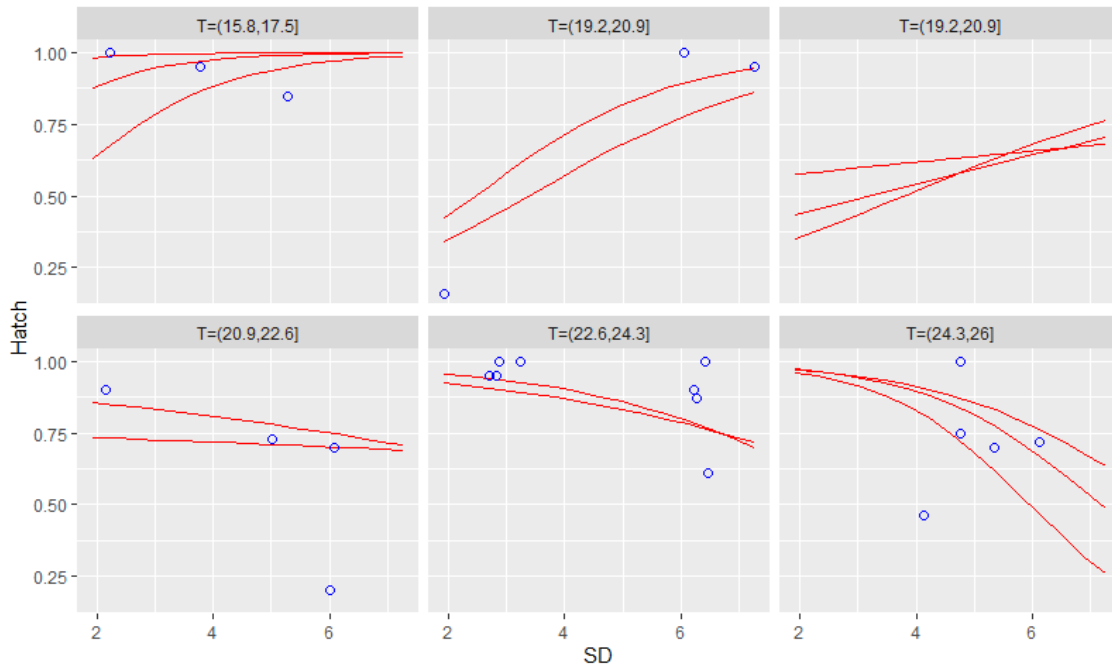


Figure 6: The observed (blue circle) and predicted (red line) hatching success at different saturation deficits and temperatures. Produced using a logistical regression model of the Nava data (2013).

A model for the dataset of Nava could not be specified with high accuracy (Pseudo- $R^2 = 0.19$). The predicted values from the model also did not produce the familiar reverse sigmoidal shape (see Figure 6). This might be because the dataset was compiled from 4 different ecological locations (Nava et al., 2013) or because lower values of hatching success were poorly represented in the dataset (see Figure 7). Good agreement between the observed and predicted values was seen for the datasets of Hitchcock (1955a) and Londt (1977). Using the method of Nagelkerke, Pseudo- R^2 's were 0.89 and 0.85 respectively (see Table 4). The same reverse sigmoidal shape was seen when plotting the hatching success against saturation deficit.

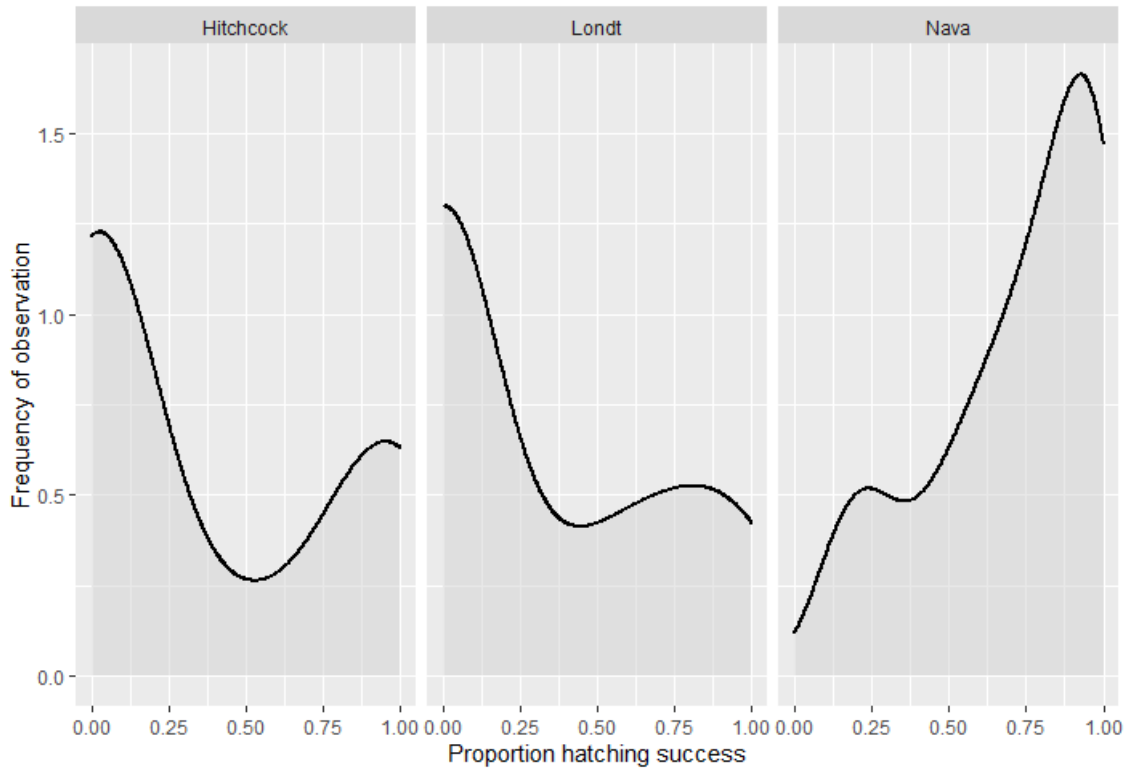


Figure 7: The frequency distributions for the three different datasets of hatching success. The frequency distribution of the underlying data gives an impression at what values for hatching success the model may be expected to be most accurate.

To inspect if a difference in hatching success between *R. decoloratus* and *R. microplus* exists, the models developed from Londt (for *R. decoloratus*) and Hitchcock (for *R. microplus*) were plotted together (Figure 8). It appeared that *R. decoloratus* was less sensitive to desiccation generally except at very high temperatures (35°C). Spickett and Malan (1978) reported similar mean hatching success rates for *R. decoloratus* and *R. microplus* incubated at 90% RH and 26°C (90.2% and 87.7% respectively). Unfortunately, they did not report the spread around the means. However, the small observed difference along with the small sample size of 20 each is not enough to conclude that an important difference exists under those climatic conditions.

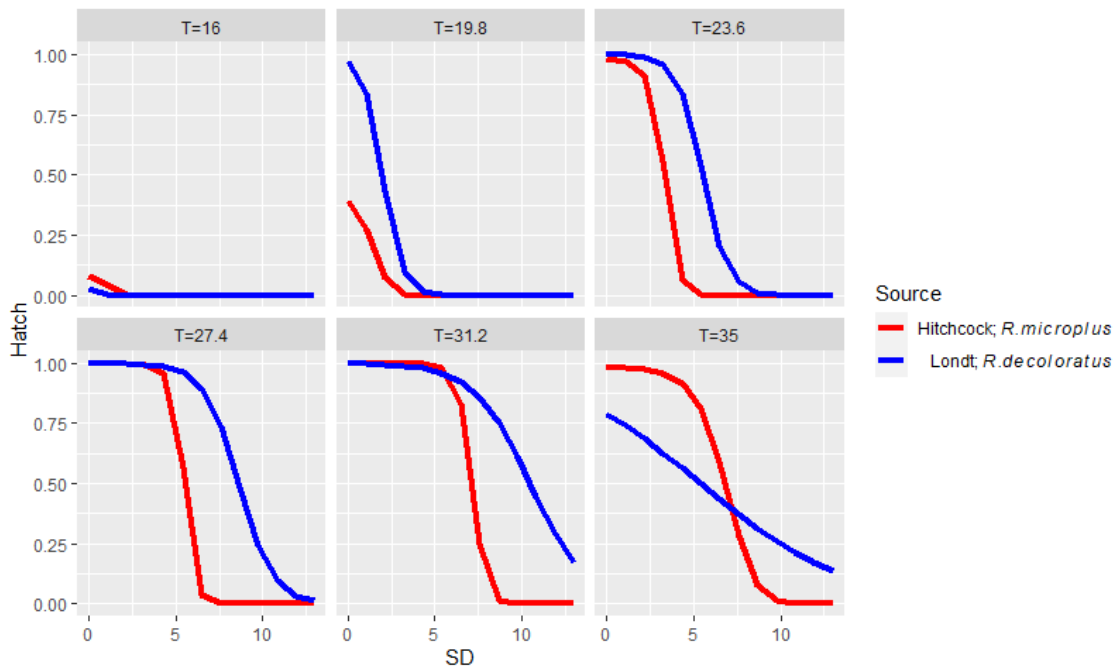


Figure 8: The predicted hatching success of models developed from the data of Londt and Hitchcock respectively.

Two sets of published functions to model egg mortality are presented in Table 5. Corson et al. (2004) produced an ecological model that included equations for egg mortality that were based on Teel's laboratory work. The dataset used to develop the equations only had two different temperature points (27 and 37°C). For this reason, their equations extrapolate poorly beyond the limits of the underlying data (see panel 1 of Fig. 9). The equations also do not deliver the reverse sigmoidal shape observed in Figs 4 and 5. The functions developed by Sutherst & Bourne (2006) to predict hatching success at different saturation deficit and temperature values give a reverse sigmoidal shape when plotting hatching success against saturation deficit (holding temperature constant) (see Fig 4). Two sets of equations predict either losses from desiccation stress or cold stress whilst controlling for temperature and the maturity of the eggs (see Table 5). The predictions above the maximum temperature limit of the underlying dataset (26°C) do not adequately show the increased desiccation effect at those temperatures.

Table 5: The sources of published formula to estimate egg hatching success

Author	Data source	Species	T and SD ranges	Formula described by
Sutherst & Bourne, 2006	Own laboratory	<i>microplus</i>	Cold stress: 5 to 14°C at 1 mmHg Desiccation stress: 0 to 20 mmHg at 20 to 26 °C	Sutherst & Bourne, 2006
Desiccation stress: $W = 0.0291T + T \times S(0.0146 + 0.1158)(1 - D)e^{0.3318-8.847D} + 0.0203S^2(D - 0.4015)^2$ $M = 100/(1 + e^{-0.31(W-30.58)})$ W = weight loss (%); T = temperature (°C); S = SD (mmHg); D = proportion of development as a fraction; M is the daily mortality given as a percentage. The term “$0.0203S^2(D - 0.4015)^2$” is only included when $D > 0.4015$. Cold stress: $M = 0.01476d(21 - T) + 2.55P(21 - T)(1 - D)(1 + P)^2$ $P = e^{-0.0255(1-D)(21-T)(d-1.55T+22.53T \times D)}$ D = the length of the exposure in days; e = Euler’s number = 2.7182818...; P = daily mortality probability; d = the number of days exposure (in our model this is always equal to 1).				
Corson et al., 2004	Laboratory data (Teel, 1984)	<i>annulatus</i> & <i>microplus</i>	Desiccation stress: 1.07 to 23.54 mmHg at 27 to 37°C#	Corson et al., 2004
$M = 0.0169 + 0.000086x - 2.1 \times 10^{-9}x^2$ $x = Time \times S$				

T = hours of exposure; S = SD (mmHg); M is the overall mortality given as a proportion.

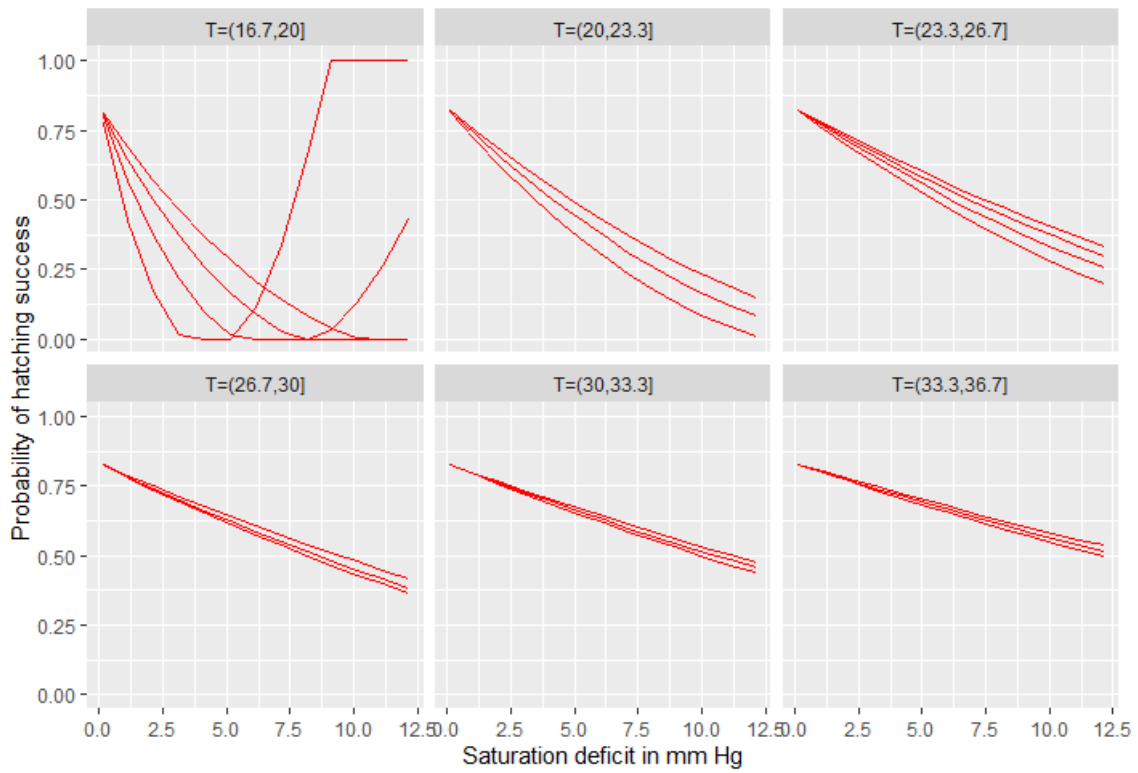


Figure 9: The predicted hatching success at different saturation deficits (mm Hg) and temperatures ($^{\circ}\text{C}$). Produced using Corson et al. (2006) equations. Each line presents a different temperature within the set.

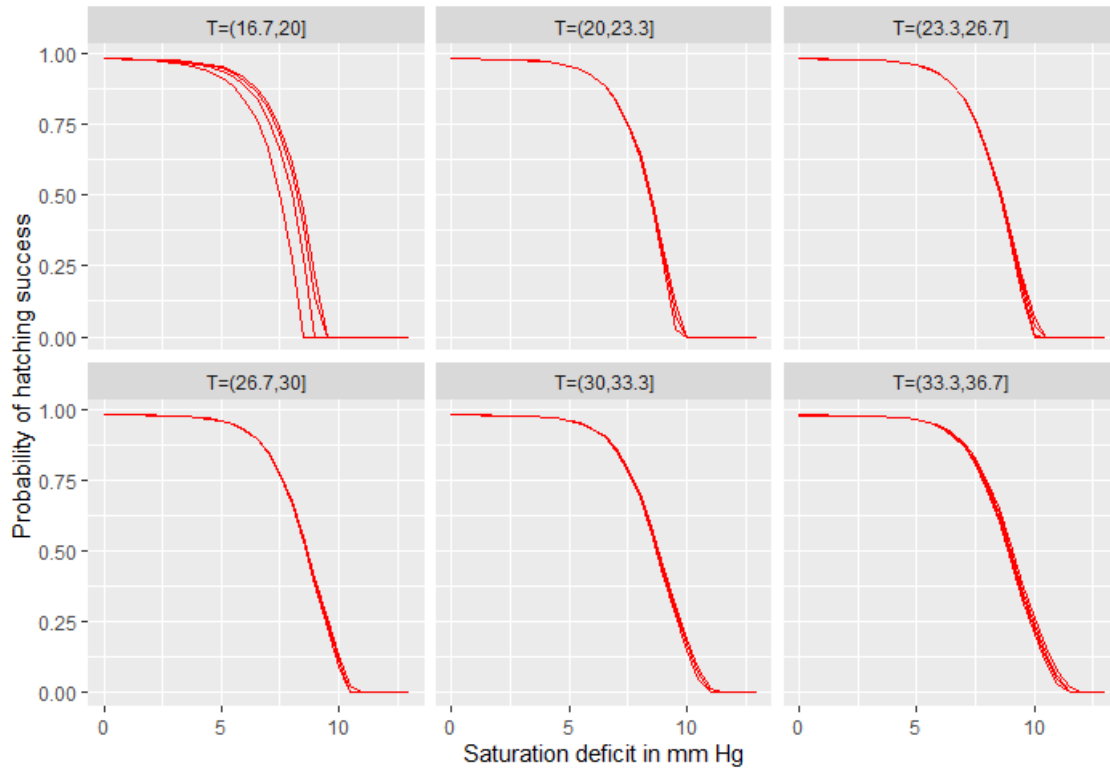


Figure 10: The predicted hatching success at different saturation deficits (mm Hg) and temperatures ($^{\circ}\text{C}$). Produced using Sutherst & Bourne (2006) equations. Each line presents a different temperature within the set.

We accept the formulas of Sutherst and Bourne (2006) as the best for use in the current population dynamics model. We do not have enough evidence to justify applying separate models for hatching success for *R. microplus* and *R. decoloratus*. The parameters and their values have already been described in Table 3.

The hatching rates and mortalities are subject to stochastic temperature variations. Different batches of eggs can be deposited in separate locations with different micro-climates. For this reason each batch of eggs was subjected to different temperatures selected stochastically from a uniform distribution (the nature of which has been described in section 5.2. In addition, tick eggs are subject to biological decay and predation from a wide range of organisms from fungi to arthropods to birds and small mammals (Samish & JA, 1999).

Predation on ticks appears to increase exponentially as tick density increases (Samish & Alekseev, 2001). This observation corresponds to the classically described Lotka-Volterra equations for the predator-prey cycle (Wangersky, 1978). However, serial observations of tick populations over different years have revealed remarkably stable population sizes despite the extremely high fecundity of female ticks (Randolph, 2004). Such stability can only be maintained if the density-dependent processes that control the tick populations are quick to adapt (unlike the Lotka-Volterra models, where predator numbers take some time to increase). Indeed, the range of simple organisms that feed on tick eggs would have short enough life cycles to enable swift responses to tick densities. Alternatively, the available tick predators respond to the available food, turning to tick eggs when the density rises (Hassan et al., 1991; Zingg et al., 2018). Regardless of the cause, the most appropriate model for predation on tick eggs would be one that responds quickly to a rise in tick eggs.

An exponential model is proposed to enable a predation effect that responds instantly to increased densities of tick eggs. The proportion of tick eggs consumed by predators increases exponentially with linear increases in the egg population (n).

$$predation_proportion = 0.001^{k/n}$$

The baseline predation proportion is 0.001 (or 0.1%). This number was chosen to bring the predation effect close to zero when tick numbers are exceedingly low. Having n in the exponent allows the rate of increase in predation to be proportional to the tick density. The constant k slows the rate at which the predation effect increases. The chosen value of 80 000 ensures that predation levels only start to exceed 0.001 when the population of tick eggs (n) exceeds 80 000 (the constant k). The value of n was iteratively selected during the model calibration process.

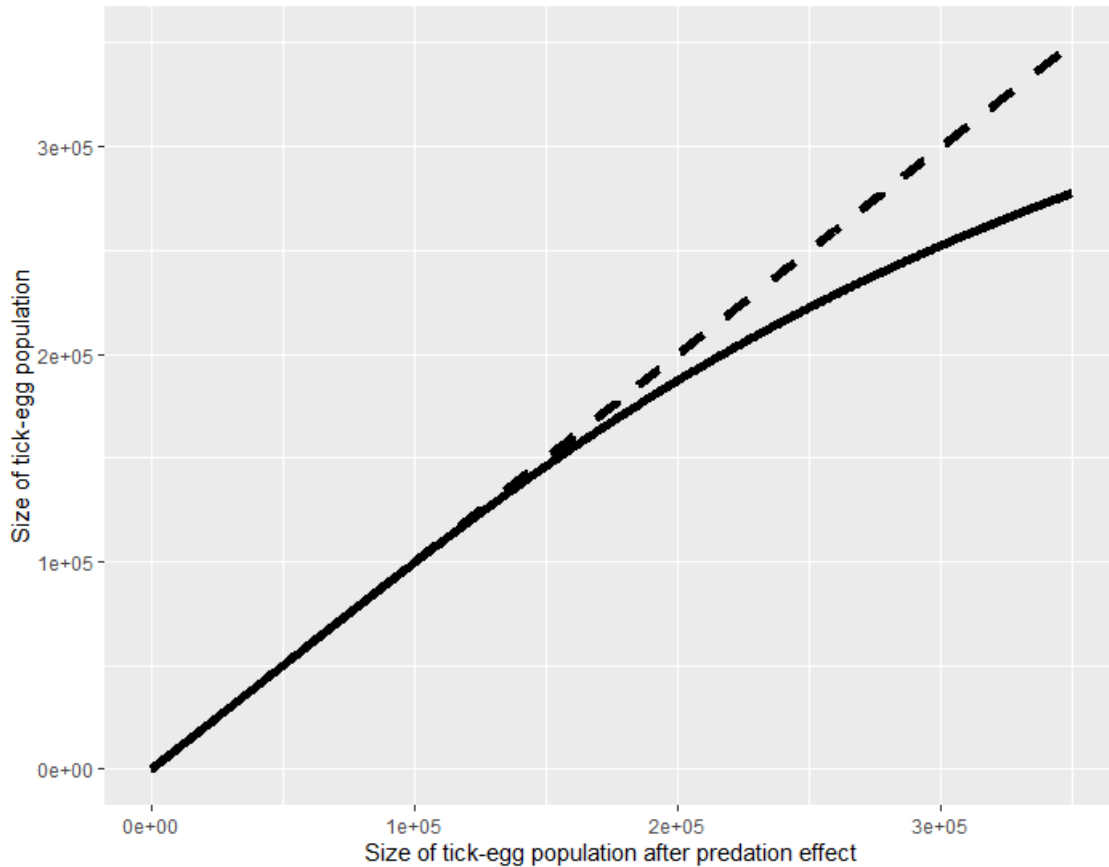


Figure 11: The effect of predation on egg mortalities. The dashed line is the baseline egg population without a predation effect. The solid line presents the egg population after applying a density dependent exponential function of egg mortalities.

5.3.2. Questing larvae

Hatched tick larvae actively seek out their hosts by ascending plant stalks and extending their front legs waiting for a host to pass. This process is known as questing (Leal et al., 2020). The survival time for larvae of both *R. decoloratus* and *R. microplus* typically has a mode of less than 50 days (Nava et al., 2013; M. Phalatsi et al., 2010), but long survivors contribute to a frequency distribution that is skewed to the right. Nava et al. (2013) provides a large set of observations ($n=47$) of *R. microplus* larval survival times taken over a wide range of climatic conditions in the field. A log-normal probability density function (pdf) was the best fit for the

frequency distribution of larval survival times (See Figure 12 and Table 6). The pdf provides a means for the population model to introduce stochasticity into the larval survival times.

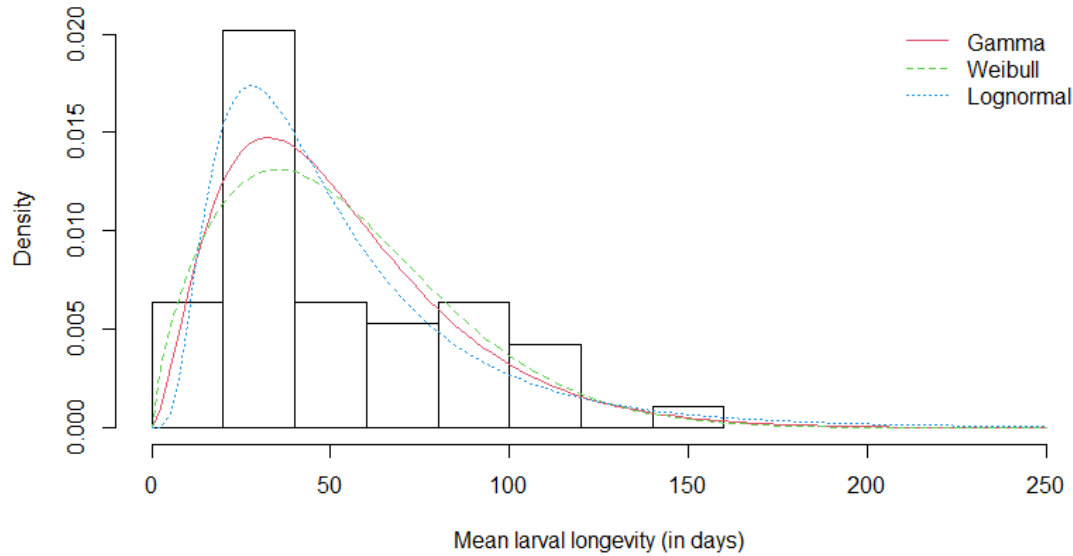


Figure 12: The frequency distribution (histogram) of larval longevity and attempts to fit a probability density function.

Table 6: Some goodness-of-fit statistics for the fitted probability density functions of larval longevity.

Statistic / Criteria	Gamma (MLE)	Weibull (MLE)	Log-normal (MLE)
Kolmogorov-Smirnov statistic	0.176	0.186	0.139
Cramer-von Mises statistic	0.156	0.182	0.108

Anderson-Darling statistic	0.800	0.938	0.622
Akaike's Information Criterion	452.084	453.573	452.670
Bayesian Information Criterion	455.784	457.274	456.370

Larval survival during questing depends on environment exposures and a carry-over effect of energy reserves from the egg phase. Sutherst & Bourne (2006) estimated that up to 67% of the larval longevity can be predicted using the hatchability as a proxy for the energy reserves of the larvae at hatching. They developed a cubic model to predict larval survival percentage (L) from hatching success (H) when eggs were kept under various field conditions and the hatched larvae were housed under laboratory conditions at 26°C and 95% RH:

$$L = 29.1 + 2.296H - 0.031H^2 + 0.000148H^3$$

Their model could be made stochastic by combining it with a log-normal density function as obtained from the Nava data (see Fig. 12). This is done by letting L define the mean of the pdf. As the mean changes, the pdf is adjusted along the x-axis retaining its shape. An assumption is therefore, that the shape of the pdf of larval survival remains relatively constant as the mean larval survival is adjusted. This assumption was accepted as data on larval survival from the research of Nava et al. (2013) and Phalatsi et al. (2010) both assume a log-normal pdf. Adjusting the mean of the log-normal pdf whilst retaining the shape is achieved by calculating a new logmean (μ_{log}) from the arithmetic mean (whilst retaining the standard deviation of the logarithm) (Gustavsson et al., 2014).

$$\mu_{log} = -\frac{\sigma_{log}^2}{2} + \log(\mu_{arithmetic})$$

Besides the carry-over effect from egg survival, larval survival is most strongly affected by temperature and saturation deficit exposures (Leal et al., 2018). Four previous studies provided data that could be used to model survival of questing larvae (Table 7). One dataset had a model specified by the original authors, for two datasets models were specified by the present authors and one dataset couldn't be modelled (Table 7). The model specified by the present authors and trained by the data of Phalatsi (2002) performed the best based on the R^2 value and a visual assessment (Fig. 14).

Table 7: The data sources evaluated that inform questing larva survival due to environmental stresses.

Data source	Species	Dataset details	Model details
Mastropaolo et al., 2017	<i>microplus</i>	T: 12.3 to 27.8°C SD: 0.2 to 8 mmHg # observations: 96	$Y = 3.881 - 1.529T - 0.429S$ $R^2 = 0.74$ Model specified by original authors.
Nava et al., 2013	<i>microplus</i>	T: 15 to 27°C S: 1.4 to 7.3 mmHg Hatch success (H): 15-100% # observations: 47	$\ln(Y) = -22.088 + 1.400T + 8.513S + 45.639H + 13.300H^2 - 0.430T.S - 3.594T.H - 16.319S.H + 2.295T^2 - 34.243H.I^2 + 1.080T.S.H - 0.702T.S.H^2 + 8.400S.H.H^2$ $R^2 = 0.75$ Model specified by present authors.
M. S. Phalatsi, 2002	<i>decoloratus</i>	T: 10 to 30°C RH: 35% to 75% # T and RH combinations: 10	$\ln(Y) = 5.273 - 0.082T - 0.302S + 0.010T.S$ $R^2 = 0.94$ Model specified by present authors.
Solomon & Kaaya, 1998	<i>decoloratus</i>	T: 10 to 34°C RH: 45% to 80% # combinations: only plots	No model possible. Only visual plots published.

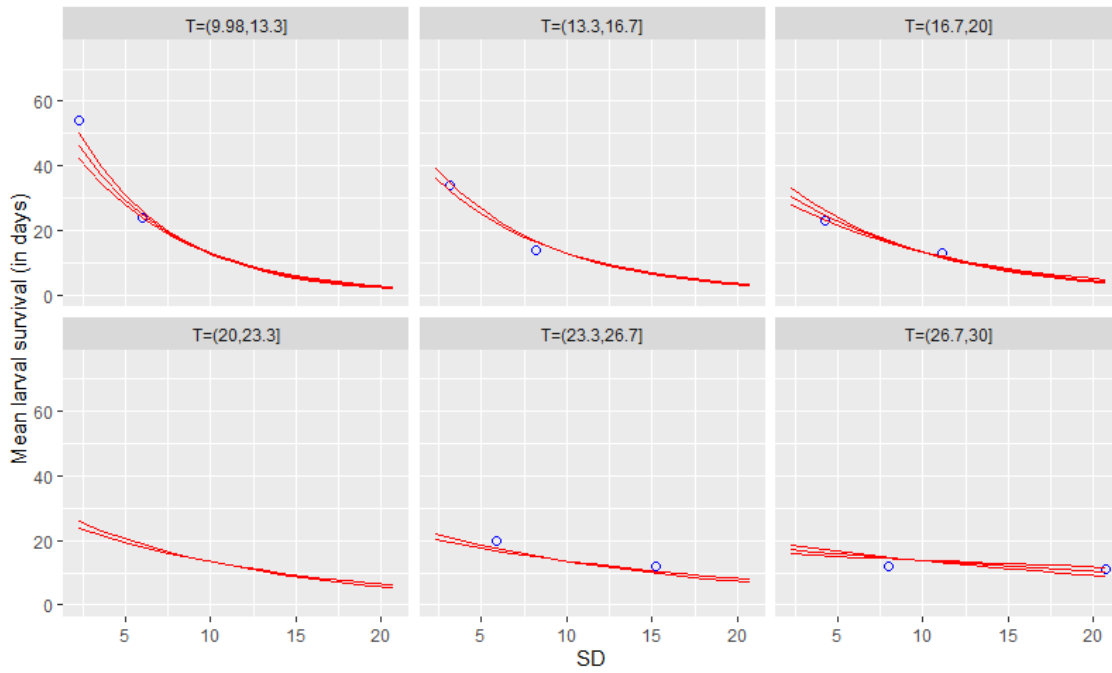


Figure 13: The observed (blue circle) and predicted (red line) larval survival at different SD's and temperatures. Produced from the Phalatsi data (2002) using a log-linear model.

To inspect for possible differences between *R. decoloratus* and *R. microplus*, the predicted data from the sources identified in Table 7 were plotted together (see Fig. 13). However, the graph should be interpreted with caution as there are potentially many unknown variables affecting the independent data sources. Yet, it does appear that *R. microplus* is more susceptible to desiccation (high S) but is able to survive longer under low S conditions. This would make sense given the wet, tropical conditions associated with the origin of the species in South-East Asia (Horak et al., 2018; Zeman & Lynen, 2010).

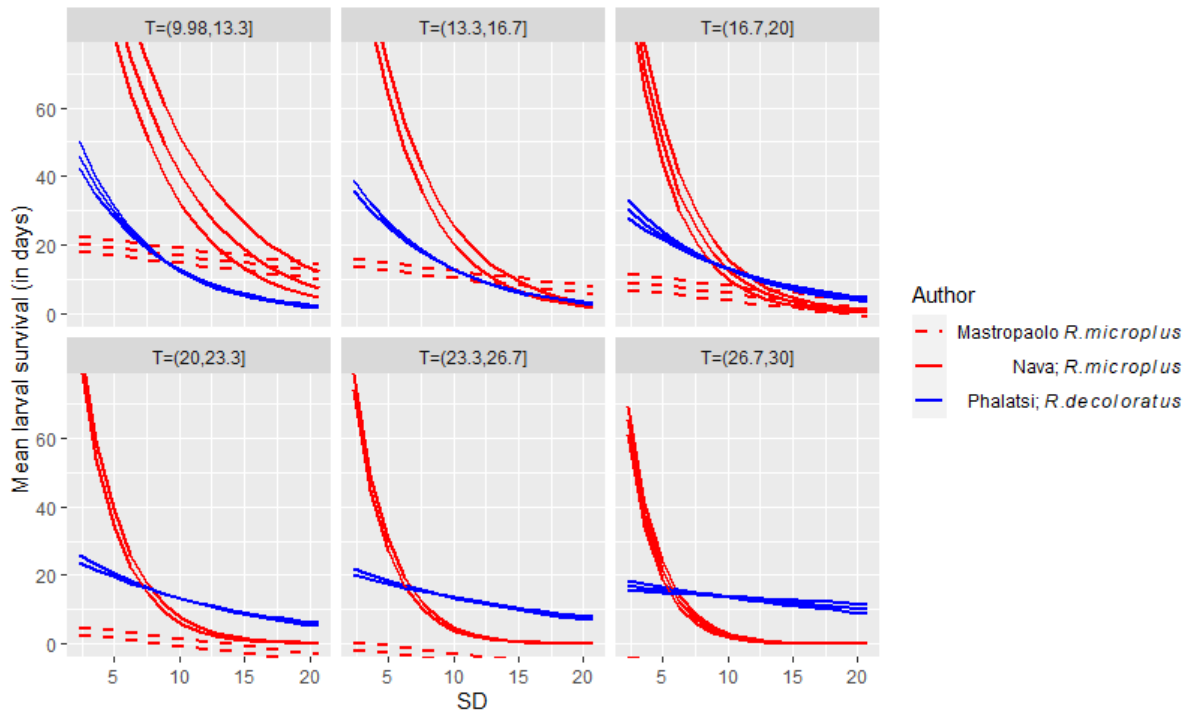


Figure 14: The predicted values for larval survival from three different models with three different data sources.

Larvae that survive in the environment, are further faced with the difficult task of successfully finding a host. The ability of the larvae to do this is dependent on three factors. The virility of the larvae, the rate of contact with cattle (i.e., the stocking rate of the cattle) and the competition between the larvae (i.e., the density of the larvae) (Floyd, 1986; Popham & Garriss, 1991). Quantitative assessments of questing success are limited to relative seasonal abundance measured by drag samples (Horak et al., 2011; Leal et al., 2020; Uys et al., 2015) and studies measuring the preferred height of questing larvae when waiting for a host to pass (Garriss & Popham, 1990; M. S. Phalatsi, 2002; Short et al., 1989). Drag sampling involves the pulling of a cloth across a paddock and counting the ticks that stick to it. The body of literature is therefore of little use to specify a quantitative model. Aware of the difficulties in quantifying questing success, Popham & Garriss proposed a function for questing success relying on host density (Popham & Garriss, 1991) where a represents an upper asymptote (equal to 1 since it

is a probability), r is a parameter that determines the rate of approaching the asymptote and d is the host density (number of animals per hectare):

$$P(\text{success}) = a(1 - e^{-rd})$$

The value for r is chosen arbitrarily. Popham & Garriss chose 0.05 based on their own expert opinion. Figure 15 provides three different relationships between questing success and cattle density based on three arbitrarily chosen values for r . The impact of the choice for r is clearly visible. The true value of r is likely to be dependent on vegetation type as boophilid ticks use tall grasses as ‘ambush’ sites while questing (Leal et al., 2020). Indeed, the questing phase has been described as the most poorly understood life stage of Ixodid ticks (Leal et al., 2020). The current study employed the formula of Popham & Garriss and their chosen value for r .

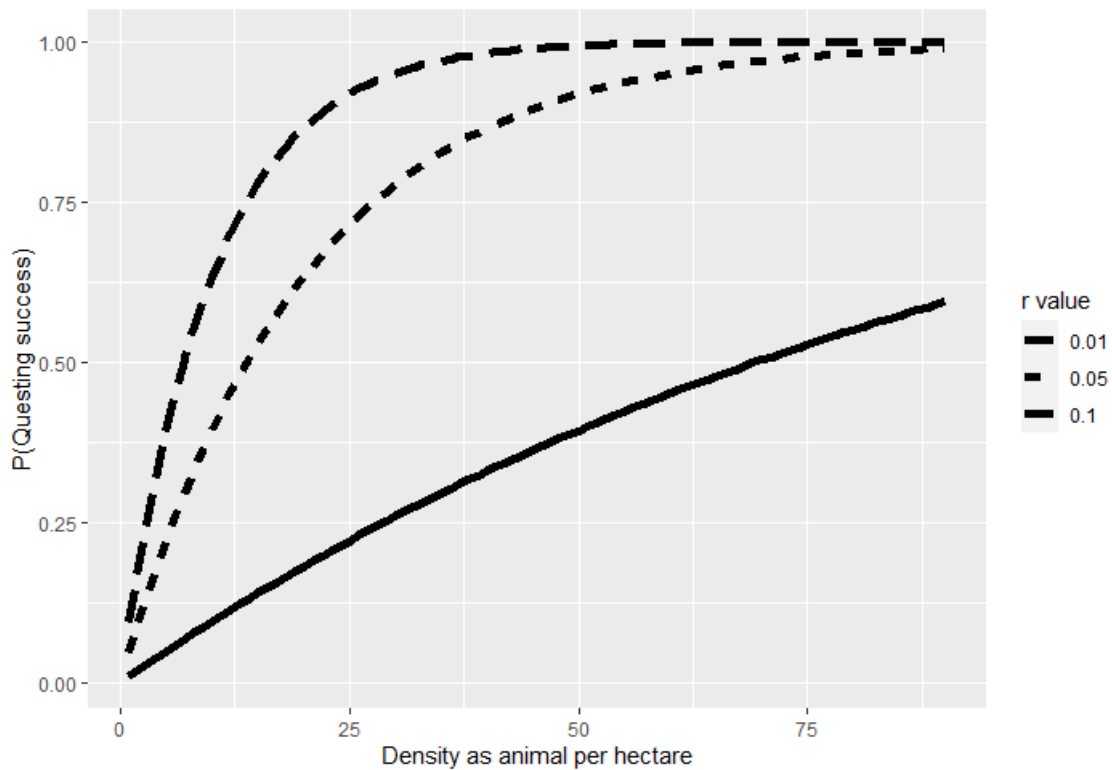


Figure 15: The probability for questing success by each larva by cattle density. Produced by formula from Popham & Garriss (1991). The r value is chosen arbitrarily.

Table 9 summarizes the parameters employed in the population model for questing. In the absence of convincing data, no differences were modelled between *R. decoloratus* and *R. microplus* for questing larvae survival and questing success.

Table 8: The population model parameters adopted in the population model to estimate survival of questing larvae and questing success.

Variable name	Description	Value(s)	Source	Notes
<i>SDlog_start</i>	The standard deviation of the natural logarithm for questing larvae survival times.	0.66387	(Nava et al., 2013)	Calculated by fitting a lognormal curve to the larval survival times.
<i>weight_larvae_survival_from_eggs</i>	The proportion of larval survival times attributed to the carry-over effect egg hatching success.	0.67	(Sutherst & Bourne, 2006)	The proportion of larval survival times is equal to the R^2 for the Sutherst & Bourne model that predicts larval survival based on hatchability.
<i>r_Popham</i>	A parameter that determines the rate at which the asymptote of a function is reached.	0.05	(Popham & Garris, 1991)	Expert opinion of the original authors.
<i>mdl_phal</i>	A multiple regression model for the mean age of questing larvae.	See Table 8.	(M. S. Phalatsi, 2002)	Model developed by present author.

5.3.3. Parasitic life stages

The parasitic life stages include larvae, nymphs, and adults. All three stages feed on the hosts with larvae and nymphs also completing a moulting phase on the host (Arthur & Londt, 1973). Once larvae have found a host, they need to attach to avoid being removed through grooming with the first 24 hours being most critical (Koudstaal et al., 1978). The proportion of larvae removed during grooming ranges from 9-54% and is dependent on host factors (Koudstaal et al., 1978). We assume in the model a larval removal probability following a PERT distribution based on the Koudstaal et al. parameters in addition to a mode for both species of ticks as 0.25.

Whereas wildlife hosts mount a response that disrupts larval progression to nymphs, this is not true for cattle, where most attached larvae proceed to the nymph and also to the adult stage (Arthur & Londt, 1973; Horak et al., 2018; Londt & Arthur, 1975).

Arthur and Londt (1973) and Londt and Arthur (1975) performed two separate studies to describe the parasitic life stages of *R. decoloratus* and *R. microplus*. Their results have been tabulated by Horak et al. (2018) and are reproduced in Table 9.

Table 9: The population model parameters from Arthur and Londt (1973; 1975) and tabulated in Horak et al. (2018).

Activity	<i>R. decoloratus</i> development time in days	<i>R. microplus</i> development time in days
Larvae feed	1-8	1-7
Nymphs pre-moult	5-8	5-9
Nymphs feed	6-17	6-20
Adults pre-moult	13-19	11-16
Females feed	15-31	14-20
Females detach	20-32	21-30

Although both studies (Arthur & Londt, 1973; Londt & Arthur, 1975) were conducted at the same facilities, they were conducted in different years, and only one study (that for *R. decoloratus*) recorded the environmental conditions. This makes interpretation of the environmental factors difficult. Yet, Hitchcock (1955b) concluded from their own work and a review of five more studies that climate has little effect on the duration of the parasitic stage of *R. microplus*. The present author's experience of breeding *R. microplus* confirms this statement, but not so for *R. decoloratus* (unpublished observations). Indeed, Solomon and Kaaya (1998) observed significant temperature and humidity dependant differences for *R. decoloratus* in their experiments conducted in Ethiopia. From their data (see Table 10) cold and wet weather delays both the larval and the nymphal moult stages. A possible explanation is therefore that *R. decoloratus* requires the tick cuticle to dry before ecdysis can be completed. This would require warm and dry weather (measurable as high saturation deficits).

*Table 10: The duration (in days) of the parasitic life stage of *R. decoloratus* (excluding adults) from experiments done by Solomon and Kaaya (1998).*

Season	Condition	Larval engorgement	Larval moult	Nymphal engorgement	Nymphal moult	Life cycle range	Life cycle mean
Dry	Shade	3	3-4 (3.5)	4	5-6 (5.5)	15-17	16
Dry	Open	3	3-5 (4)	4	5-6 (5.5)	15-18	16.5
Early rains	Shade	3	5-6 (5.5)	4	7-8 (7.5)	19-21	20
Early rains	Open	3	4-6 (5)	4	6-8 (7)	17-21	19
Heavy rains	Shade	3	6-7 (6.5)	4	6-8 (7)	19-22	20.5
Heavy rains	Open	3	6 (6)	4	7-11 (9)	20-24	22

Londt and Arthur (1975) reported that adult females drop six days after adult *R. microplus* emergence. In contrast, they reported 7 days for the same process in *R. decoloratus* in a different study (Arthur & Londt, 1973). Adding these numbers to the data of Solomon and Kaaya (1998) (who didn't include adult ticks in their study), we arrive at minimum life cycle durations comparable to the work of Arthur and Londt. These baseline periods correspond to 21 days for *R. microplus* and 22 days for *R. decoloratus*. Based on the work of Solomon and Kaaya (1998) we add to the baseline periods potential delays due to climate factors that affect

the moulting process of *R. decoloratus*. To make the estimates, we assume that the minimum mean life cycle duration (recorded in dry season shade) is representative of the coldest, wettest months in Addis Ababa, Ethiopia. Conversely, the maximum mean life cycle duration is 28 days and representative of the hottest, driest months. We further assume a linear trend between these two extremes that is solely dependent on saturation deficit (which combines the effects of relative humidity and temperature). See Table 11. The climate data for Addis Ababa was sourced from the internet (*Relative Humidity in Addis Ababa, Ethiopia*, n.d.) and (*Average Temperatures in Addis Ababa, Ethiopia Temperature*, n.d.). The dry season in Ethiopia from December to February is also the coldest season. The month with the warmest-driest combination is in May just before the start of rains and the coldest-wettest month would be at the peak of rains in July. See Table 11.

*Table 11: The climate data and resulting linear model to predict delays of the *R. decoloratus* life cycle due to slow cuticle drying.*

Description	Month	Conditions	Life cycle length incremented by
Warm and dry	May	T: 18°C RH: 52% S: 7.26 mmHg	0 days (baseline)
Cold and wet	July	T: 15°C RH: 82% S: 2.26 mmHg	6 days (28-22 =6)
Mathematical model:	$y = 8.712 - 1.2s ; (y > 0)$ y is the number of days by which the life cycle is delayed and s is the saturation deficit ($y > 0$)		

The population model parameters assumed in the population dynamics model are summarized in Table 12.

Table 12: The population model parameters adopted in the population model to estimate the length and success of the parasitic phases of the life cycle.

Variable name	Description	Value(s)	Source	Notes
<i>cycle_length_micro</i>	The baseline length of the parasitic life cycle	21	(J. G. H. Londt &	

	on the host for <i>R.microplus</i> females.		Arthur, 1975)	
<i>cycle_length_dec</i>	The baseline length of the parasitic life cycle on the host for <i>R.decoloratus</i> females.	22		
<i>cycle_delay</i>	The number of days by which the life cycle of <i>R. decoloratus</i> is delayed due to slow drying of the cuticle. A linear model with only SD as a predictor.	See Table 11.	(Arthur & Londt, 1973; J. G. H. Londt & Arthur, 1975; Solomon & Kaaya, 1998)	
<i>cycle_delay_factor</i>	A sensitivity parameter that determines how much of the Solomon and Kaaya observed delay is assumed.	{0; 0.5; 1}		A value of 1 would mean a full assumption of the delay for <i>R. decoloratus</i> observed in the Solomon and Kaaya data.
<i>cycle_prop_larvae</i>	The proportion of the total parasitic life cycle length that is larvae.	0.27	(Arthur & Londt, 1973; J. G. H. Londt & Arthur, 1975)	This value ignores long survival on the host of males.
<i>cycle_prop_nymphs</i>	The proportion of the total parasitic life cycle length that is nymphs.	0.41	(Arthur & Londt, 1973; J. G. H. Londt & Arthur, 1975)	This value ignores long survival on the host of males.

<i>cycle_prop_adults</i>	The proportion of the total parasitic life cycle length that is adults.	0.32	(Arthur & Londt, 1973; J. G. H. Londt & Arthur, 1975)	The value only applies to females.
<i>groomed_min</i> <i>groomed_max</i>	The proportion of larvae removed due to grooming.	min = 0.09; max = 0.54;	(Koudstaal et al., 1978)	Modelled as a PERT distribution to derive the proportion of larvae removed.
<i>groomed_mode</i>	The proportion of larvae removed due to grooming.	mode = 0.25;	Present authors' estimate.	Modelled as a PERT distribution to derive the proportion of larvae removed.

5.3.4. Reproductive physiology

Ixodid ticks have some interesting examples where reproduction in the absence of males regularly takes place in field conditions. For instance, in *Ixodes schulzei* (a tick of rodents in South America), parthenogenic reproduction is the norm as male ticks don't reach adulthood, and sexual reproduction has not been successfully documented (Soares et al., 2021). *Haemaphysalis longicornis* (an Asian tick of various mammals that has established itself in the eastern United States of America) is another interesting example, as it seems equally comfortable to reproduce sexually or parthenogenetically (Kiszewski et al., 2001; Matsuo et al., 2013). Whereas *R. microplus* achieves parthenogenesis in the strictest sense, the meagre hatching and survival rates render such reproduction irrelevant (Davey et al., 1983; Londt, 1976; Stone, 1963; Thompson et al., 1980). We, therefore, assume in the model that both *R. microplus* and *R. decoloratus* require the presence of males to reproduce. Unmated females also engorge and detach (Hilburn et al., 1991). Boophilid ticks mate solely on their

hosts (Kiszewski et al., 2001). Since boophilid larvae are not particularly motile and prefer to congregate in clumps, one would expect sibling larvae to attach to the same hosts (Goldsmid, 1967). This has led to an assumption that sibling matings would be common. Chevillon et al (2007) have shown this assumption to be false by studying gene transmission patterns. Instead, they propose pangamy (random matings across the population) enabled by a proportion of the population detaching and reattaching on a different host. Just like pangamy requires the detachment and reattachment of ticks, the transstadial transmission of *Anaplasma marginale* by *R. microplus* also does. Researchers found that although *R. microplus* is a single-host tick, *Anaplasma* is transmitted from stage to stage and not transovarially (Connell & Hall, 1972). This provides evidence from two different angles that single-host ticks do in fact detach and reattach on different hosts. We do not simulate ticks moving between hosts in the model, but the species of a male tick copulating with a female was performed by randomly selecting any sexually mature tick from the entire adult tick population. This equates to an assumption of pangamy.

Sexual maturation of Boophilid males is achieved in more or less two days following the emergence of adults (Thompson et al., 1980). Once mature, a complex series of pheromones assist the male ticks in finding females and direct their behaviour to achieve successful copulation (Bruyne & Guerin, 1998; Kiszewski et al., 2001). Mating will take around three days (J. G. H. Londt, 1976), after which the male will quickly move on to find another female. This process will repeat until the male has expended his semen reserves (Kiszewski et al., 2001).

Male ticks die after depleting their semen reserves (Kiszewski et al., 2001). Some male ticks can remain on the host for up to 70 days, but 42 days appears to be close to the meantime (Table 13) (Hitchcock, 1955b; Thompson et al., 1980). *R. microplus* males (and the closely related *B. australis*) are slow to attach, preferring to move around looking for females for mating. In contrast, there is evidence that *R. decoloratus* males prefer to first engorge for a few days before moving around seeking to mate (Arthur & Londt, 1973; Legg, 1930; J. G. H. Londt & Arthur, 1975). For this reason, there could be species differences in the survival time on the host, yet we could find no such evidence. Since this could have significant interactions with the parameters that determine sterile offspring from crosses, we chose to include a

sensitivity parameter that allows for *R. decoloratus* males to remain on the host either shorter or longer than *R. microplus*.

Table 13: The sources of reproductive parameters for male boophilid ticks (all time periods are in days).

Species	Premating period	Time spent mating with a female	Longevity	Females mated	Reference
<i>R. microplus</i>	3	-	-	-	(Falk-Vairant et al., 1994)
<i>R. microplus</i>	-	-	Up to 50 days	-	(Hitchcock, 1955b)
Type 1 hybrid: <i>R. microplus</i> ♂ × <i>B. annulatus</i> ♀	2.5 (1-4)	-	32.4 (14-59)	7.75 (3-14) †	(Davey et al., 1983)
Type 2 hybrid: <i>B. annulatus</i> ♂ × <i>R. microplus</i> ♀	3.1 (2-5)	-	71.2 (19-93)	22.65 (5-34) †	(Davey et al., 1983)
<i>R. decoloratus</i>	3.8 (3-6)	2.6 (1-10)	? (9-37) ††	5.2 (4-?) ††	(J. G. H. Londt, 1976)
<i>R. microplus</i>	3.3 (2.5-6.5) †††	-	42 (20.5-61.5) †††	10.8 (5-18) †††	(Thompson et al., 1980)
<i>B. annulatus</i>	2.6 (0.06-4.5) †††	-	36.9 (10-64) †††	7.5 (2-12) †††	(Thompson et al., 1980)

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†Males were housed with females at a ratio of 1:10. Mated females were replaced when they detached.

††Experiment terminated with 4 of 10 males still active.

†††The noted differences in the study of Thompson et al. were not statistically significant.

Hybrids between *R. microplus* and *R. annulatus* are known to occur in nature and have been extensively studied as a potential means to control *R. microplus* (Davey et al., 1994; Graham & Price, 1966; Osburn & Knippling, 1982). Interspecies crosses within the boophilid subgenus are either fully or partially sterile (Graham et al., 1972; A. M. Spickett & Malan, 1978). The extent of sterility and the virility of subsequent hybrids might differ with the direction of the cross (Davey, 1986). However in the case of *R. microplus* and *R. decoloratus*, it is believed that both directions cause completely sterile eggs (A. M. Spickett & Malan, 1978). This might cause a localised decrease in the density of boophilid ticks where hybridisation occurs (Baker et al., 1989; Lynen et al., 2008). The work done by Spickett & Malan (1978) conducted in containers suggested random mating. Subsequently, it has been claimed that on the animal hosts, significant assortative mating takes place (Hilburn & Davey, 1992; Norval & Sutherst, 1986). Norval & Sutherst (1986) placed larvae of *R. microplus* and *R. decoloratus* on Brahman steers. The number of observed hybrid matings versus the expected numbers were counted, assuming one male for each female, one mating per female and random mixing (see Table 15). Only 24% of the expected frequency of hybrids was observed. The experiments conducted by Hilburn & Davey (1992) on *R. microplus* and *R. annulatus* found less strong assortative mating (although still significant) – 83% of the expected frequency of hybrids were observed (see Tables 14 & 15).

Table 14: The observed versus expected hybrid matings of *R. microplus* and *R. decoloratus* from Norval & Sutherst (1986).

		Expected matings		Observed matings	
	Engorged females present	P(mate with own species)	Frequency	P(mate with own species)	Frequency
<i>R. decoloratus</i>	239	0.28	66	0.80	192
<i>R. microplus</i>	627	0.72	454	0.94	591
Hybrid mating		0.40	346	0.10	83
Totals	866		866		866
Ratio of observed hybrids to expected hybrids: 83:346= 0.24					

Table 15: The observed versus expected hybrid matings of *R. microplus* and *R. annulatus* from Hilburn & Davey (1992).

		Expected matings		Observed matings	
	Engorged females present	P(mate with own species)	Frequency	P(mate with own species)	Frequency
<i>B. annulatus</i>	568	0.51	258	0.43	246
<i>R. microplus</i>	553	0.49	300	0.74	410
Hybrid mating		0.50	563	0.41	465
Totals	1121		1121		1121
Ratio of observed hybrids to expected hybrids: 465:563= 0.83					

Instead of concluding that assortative behaviour of *R. microplus* is stronger with *R. decoloratus* compared to the assortative behaviour of *R. microplus* with *R. annulatus*, a possible explanation lies in one of the assumptions of the cited experiments. For the purpose of calculations, both experiments assumed one mating per female. However, it has been

reported that multiple *Rhipicephalus* males can fertilize the eggs of one female (Cutullé et al., 2009). Whilst the dynamics of inter-species competition of deposited spermatophores is not known for single-host *Rhipicephalus* ticks, the sequence of males in multiple matings is not important to determine paternity within the Ixodidae family (specifically *Ixodes arboricola* and *Ixodes dammini*) (Van Oosten et al., 2016; Yuval & Spielman, 1990). It is therefore likely also in *Rhipicephalus spp.* that after a sterile mating, conspecific matings could still fertilize eggs. In such a case one would expect that the higher the absolute number of males the more ‘sterile’ matings could be made to appear fertile if hybrid matings are followed with a conspecific mating (or vice versa). This would mean that the results of previous assortative mating experiments appear stronger than the reality. Hilburn & Davey’s experiment (1992) on *R. annulatus* crosses, used 6000 larvae per host per week whilst Norval & Sutherst’s experiment (1986) on *R. decoloratus* crosses, used 10 000 larvae per host per week. This key difference between the two experiments could account for the different observations from the two studies. Considering the evidence of the early container experiments and the more recent genetic research, we believe that multiple matings (polygamy) can better explain the differences between the expected and observed hybrid matings. The current model therefore assumed random matings and polygamy (no assortative mating).

The variables used in population model and their assumed values are summarized in Table 16.

Table 16: The population model parameters for mating behaviour.

Variable name	Description	Value(s)	Source	Notes
<i>male_maturation</i>	The number of days required for a male tick to mature before it can mate.	3 days	(Falk-Vairant et al., 1994; J. G. H. Londt, 1976)	
<i>mating_time</i>	The duration of mating.	3 days	(J. G. H. Londt, 1976)	

<i>male_survival_min</i> <i>male_survival_max</i>	The number of days male ticks remain on the host (including the time they take to mature through larval and nymphal stages).	min=0; max=70;	(Thompson et al., 1980)	The parameters are fed to a PERT distribution to derive the time spent on the host.
<i>male_survival_mode</i>	The number of days male ticks remain on the host (including the time they take to mature through larval and nymphal stages).	42	(Thompson et al., 1980)	The parameter is fed to a PERT distribution to derive the time spent on the host.
<i>male_survival_dec</i>	A sensitivity parameter that determines if <i>R. decoloratus</i> males remain on the host for shorter or longer periods compared to <i>R. microplus</i> .	{0.5; 1; 2}	(Arthur & Londt, 1973; Legg, 1930; J. G. H. Londt & Arthur, 1975).	A factor of 0.5 would mean that <i>R. decoloratus</i> males remain on the host for only 50% of the time that <i>R. microplus</i> males do.
<i>females_mated</i>	The maximum number of females that 1 male can mate before semen reserves are depleted.	11	(Thompson et al., 1980)	The actual number of females mated depends also on availability and longevity.
<i>males_mated</i>	The maximum number of male partners 1 female can have.	{1;2;3}	(Cutullé et al., 2009)	A sensitivity parameter.

<i>female_detachment_unmated</i>	Unfertilised females extend their baseline life cycle by this many days to wait for potential males.	1	(Hilburn et al., 1991)	The female time spend on host is determined by the cycle length. See Table 12.
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5.3.5. Preovipositing

Female ticks become positively geotropic and negatively phototactic once feeding and mating is complete (Oliver Jr., 1989). This guides their behaviour to drop to the ground and find a suitable spot for ovipositing. During this time female ticks are vulnerable to predation being slow to move. The proportion of females predated is highly variable ranging from zero to 100%, and specific to the local ecology (Samish & Rehacek, 1999; Sutherst et al., 2000). The data of Sutherst et al. (2000) allows an inspection of the nature of the frequency distribution of different probabilities for predation (see Figure 16). A beta distribution was fit to the 102 observation as it produces values between 0 and 1 only – appropriate for a probability (Bolker, 2008).

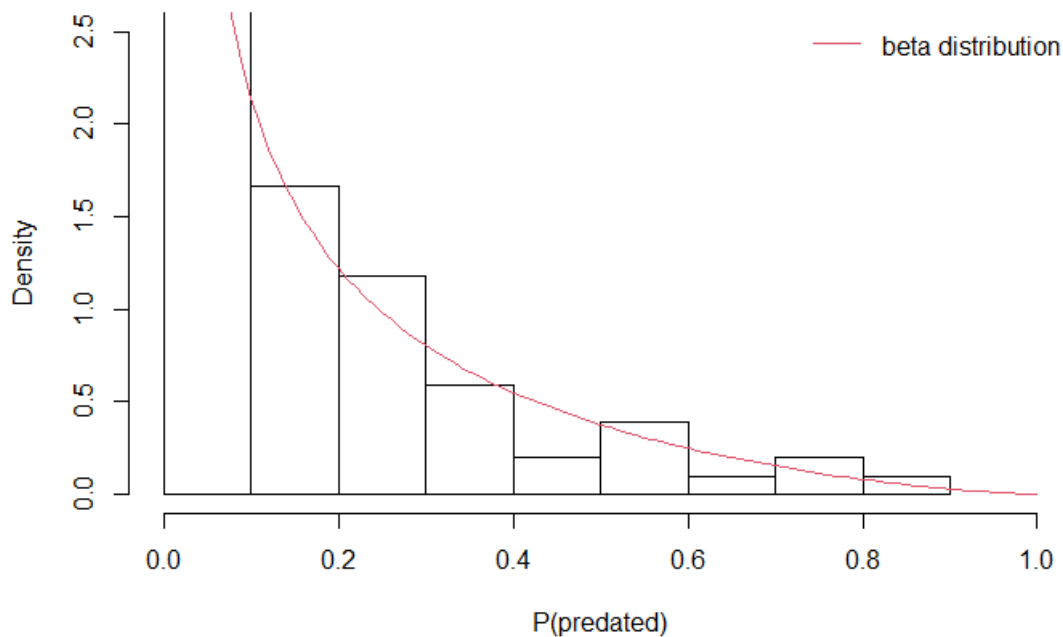


Figure 16: The frequency distribution (histogram) of the Sutherst et al. (2000) data for the probability of engorged females to fall victim to predation. A beta distribution is superimposed.

The stochastic mortality probability was modelled as a beta distribution with shape parameters $\alpha = 0.392$ and $\beta = 2.245$.

Under optimum laboratory conditions (high temperature), preovipositing can be as short 3 to 4 days and is not significantly different between *R. microplus* and *R. decoloratus* (Short et al., 1989; Thompson et al., 1980). Relative humidity has little to no impact on the pre-ovipositing period (Snowball, 1957; Solomon & Kaaya, 1998; Souza et al., 1988). Yet, excessively dry and hot conditions might still cause death of *R. microplus* females during this time (Short et al., 1989).

Three datasets are presented in Table 17 that contain a series of different temperatures with corresponding preovipositing times. The same data are represented graphically in Figure 17.

Table 17: The data sources evaluated that inform the preovipositing period.

Data source	Species	Dataset details	Model details
(Hitchcock, 1955a)	<i>Rhipicephalus microplus</i>	T: 15.5 to 36.1°C RH: 45 to 99% laboratory observations: 14	$\ln(Y) = 10.125 - 0.584T + 0.009T^2$ R ² : 0.90 Model specified by current author.
(Snowball, 1957)	<i>Rhipicephalus microplus</i>	T: 15.6 to 25.5°C RH: >90% field observations: 17	$\ln(Y) = 16.761 - 1.233T - 0.025T^2$ R ² : 0.85. Model specified by current author.
(M. Phalatsi et al., 2010)	<i>Rhipicephalusdecoloratus</i>	T: 5.5to 21.0°C RH: NA field observations: 15	$\ln(Y) = 4.133 - 0.029T + 0.003T^2$ R ² : 0.61 Model specified by current author.

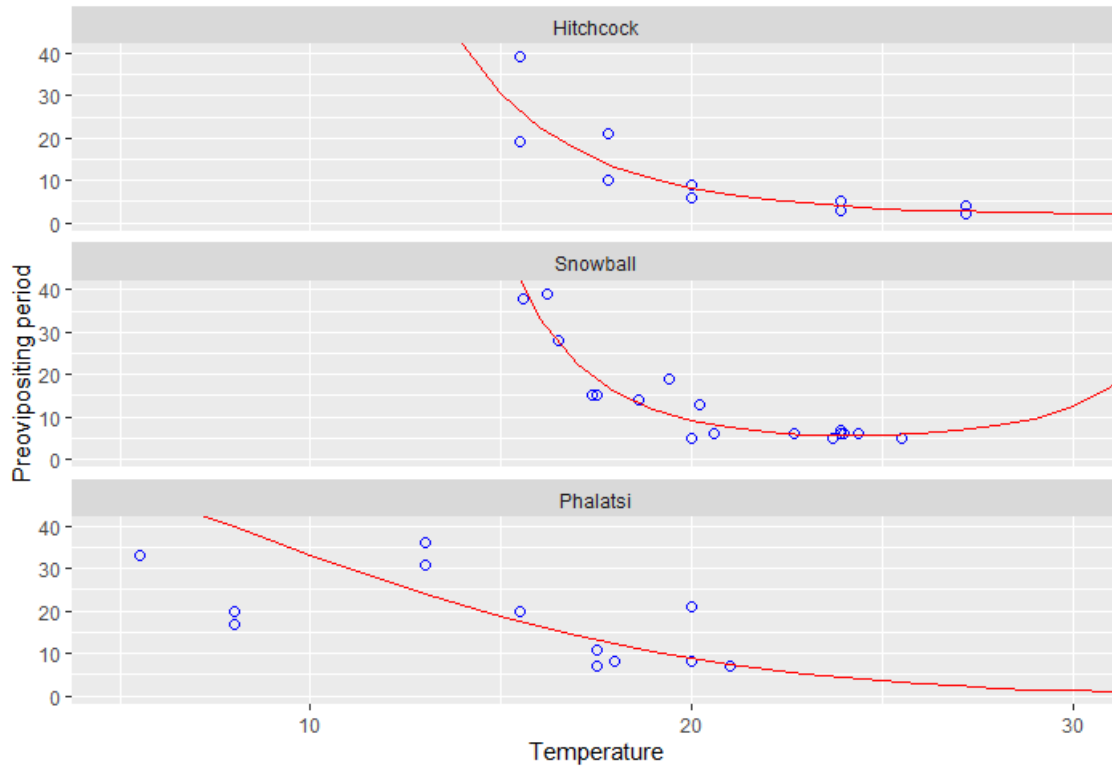


Figure 17: The observed (blue circle) and predicted (red line) preovipositing periods by using a log-linear models of three different datasets. The Hitchcock and Snowball datasets are based on *R. microplus* and the Phalatsi dataset on *R. decoloratus*.

Below 15°C, *R. microplus* has delayed preovipositing times suggestive of a lower limit temperature beyond which ovipositing might not occur at all. An experiment conducted at 4°C using *R. microplus* found no ovipositing to occur (Oshiro et al., 2021). In the same study, the ideal temperature to minimize the preovipositing period was 28°C, which is congruent with Hitchcock's (1955a) findings. Both Hitchcock and Oshiro reported that preovipositing development could be delayed by placing ticks in cold temperatures, only to resume when the ticks were returned to warmer temperatures.

The models for the Hitchcock and Snowball datasets have good agreement with reported observations. However, the Snowball model has an erroneous rise in pre-ovipositing period at high temperatures as a result of extrapolation. The Hitchcock model also has very good

agreement with the observations and doesn't suffer from the extrapolation problem because it is based on a wider range of underlying data. The two models (both based on *R. microplus*) are similar to one another, even though the Snowball model was based on mean temperatures from field conditions and the Hitchcock model was based on constant laboratory conditions. One can therefore assume that constant laboratory conditions give comparable results to the mean temperature from field conditions, as has been argued for egg incubation periods.

Phalatsi et al. (2010) measured the preovipositing period by placing vials containing engorged *R. decoloratus* into the environment and loosely covering them with sand and grass. The average ambient temperatures during these experiments are available in the Masters thesis of the same main author (M. S. Phalatsi, 2002). The high variability of the datapoints of the Phalatsi model is likely a result of the temperature measurements not taken directly for each observation (as in the Snow model). Regardless, it remains reasonable to conclude that the very different model shape for the field observations of *R. decoloratus* made by Phalatsi (2010) can be ascribed to a species difference. *R. decoloratus* females are clearly less sensitive to cold exposures, suffering less of a delay to start ovipositing.

The current model incorporated the predictions from the Hitchcock and Phalatsi models for the pre-ovipositing periods of *R. microplus* and *R. decoloratus* respectively.

5.3.6. Ovipositing

The fecundity of the female tick is affected by environmental conditions (Oliver Jr., 1989) and host resistance factors (Jonsson et al., 2014; Utech et al., 1978). Of the environmental conditions, it is mainly low temperature that prolongs the ovipositing period and also reduces the number of eggs laid (Corson et al., 2004). Low RH only impacts the egg output when the saturation deficit is above 15 mm Hg (equal to 40% RH at 26 °C) (J. G. Londt, 1977). Even then it only has a minor impact and is typically ignored in models of fecundity (Corson et al., 2004; Estrada-Peña, 2002).

Host resistance factors both reduce the weight of the engorged tick and reduce its efficiency to produce eggs. The latter is measured by the reproductive efficiency index (RPI), which is the number of eggs laid divided by the engorged tick weight (Drummond & Whetstone, 1970). The greatest proportion of the host's resistance is due to an adaptive immune response that requires previous exposure (Tabor et al., 2017). Such host differences are strongly correlated with breed, *Bos indicus* being more resistant compared to *Bos taurus* breeds (Jonsson et al., 2014; Solomon & Kaaya, 1998). Yet, even among individuals of the same breed, there can be large variability (Roberts, 1968) such that it has been suggested that culling the top 20% of the most susceptible animals could reduce the herd prevalence of *R. microplus* by 50% (Utech et al., 1978). This makes comparison of engorged tick weights and their RPI's across different studies challenging.

In the population model of Corson et al. (2004) for *R. microplus*, the eggs produced were modelled as a function of temperature and engorged weight (see Table 18). The weight of the engorged female was set at as a constant 300mg based on the work of Davey et al. (1980) and Ouhelli et al. (1982). The population model of Estrada-Peña (2002) for *R. decoloratus* modelled the eggs produced as a function of temperature only. Although the study of Spickett & Malan (1978) did not record the engorged female weights, it did find that the number of eggs per batch does not differ significantly between *R. microplus* and *R. decoloratus* (around 3000 eggs per batch). The two fecundity models were compared across a range of temperatures (Figure 18). The outcomes of the models show reasonable agreement when the Corson et al. (2004) model accepts a value of 240mg for the female weight. The models also compare well with the point estimate of 3000 eggs by both species at 26°C by Spickett & Malan (1978). The formula of Corson et al. (2004) was used in the current population model for both *R. microplus* and *R. decoloratus*, assuming an engorged female weight of 240mg.

Table 18: The models evaluated to predict female fecundity.

Data source	Underlying data	Equation(s)	Species	Engorged female weight	Number of eggs at 26°C.
(Corson et al., 2004)	(Bennett, 1974; Davey, 1988)	$F = (-159.08 + (16.63 \times T) - (0.3136 \times T^2)) \times m \times 200$	<i>B. annulatus</i> & <i>R. microplus</i>	0.3g	3678
(Estrada-Peña, 2002)	(Robertson, 1981; Solomon & Kaaya, 1998)	$F = (-6211.5 + (647 \times T) - (11.21 \times T^2))$	<i>R. decoloratus</i>	NA	3085

F = is fecundity as eggs laid; T = temperature (°C); m = mass of engorged tick in grams

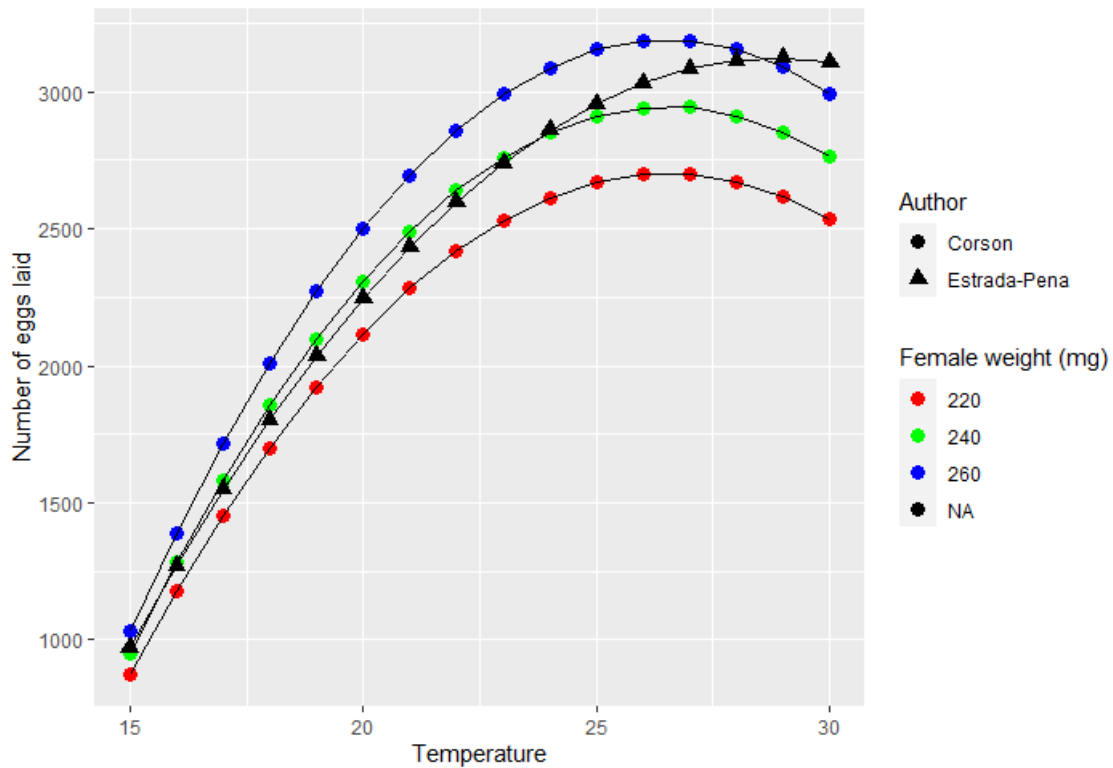


Figure 18: The modelled fecundity of engorged female ticks as eggs laid at different temperatures and engorged female weight.

Few experiments have investigated the rate of ovipositing across different climatic conditions. However, the ovipositing period is mainly determined by temperature (Bennett, 1974; Hitchcock, 1955a; J. G. Londt, 1977). Cold temperatures specifically, delay the development of eggs inside the female and thereby also the ovipositing process. Estrada-Peña (2002) set the cold temperature development threshold for *R. decoloratus* at 13.2°C and combined it with a requirement of 373.8 degree-days to complete ovipositing. This leads to a uniform rate of ovipositing across the entire ovipositing period. This is a simplification when compared to the data of J.G.H. Londt (1977) who provided detailed graphs (without supplying the underlying data) of the changing rate of ovipositing for *R. decoloratus* at different temperatures (Figures 19 and 20). Corson et al. (2004) developed a series of 13 equations to estimate the rate of ovipositing at different temperatures for *R. microplus* (Table 19). The Corson-equations provide a better estimate of the Londt-graphs but the agreement remains

poor. It is tempting to deduce from Figures 19 and 20 that *R. decoloratus* generally has a shorter oviposition period compared to *R. microplus*. This would be an unreliable assumption as there are several reports of short ovipositing periods for *R. microplus*; 8.6 ± 0.85 days at 28°C (Senbill et al., 2018), 8.4 ± 0.37 days at 28°C (Singh et al., 2019) and as short as 5 days during summer (Saha et al., 1999). Without sufficient evidence to suggest different ovipositing periods for *R. decoloratus* and *R. microplus*, we utilised the Corson-equations as the best available estimate of the changing rates of ovipositing at different temperatures (Table 19). Female ticks die after ovipositing is complete (Kiszewski et al., 2001).

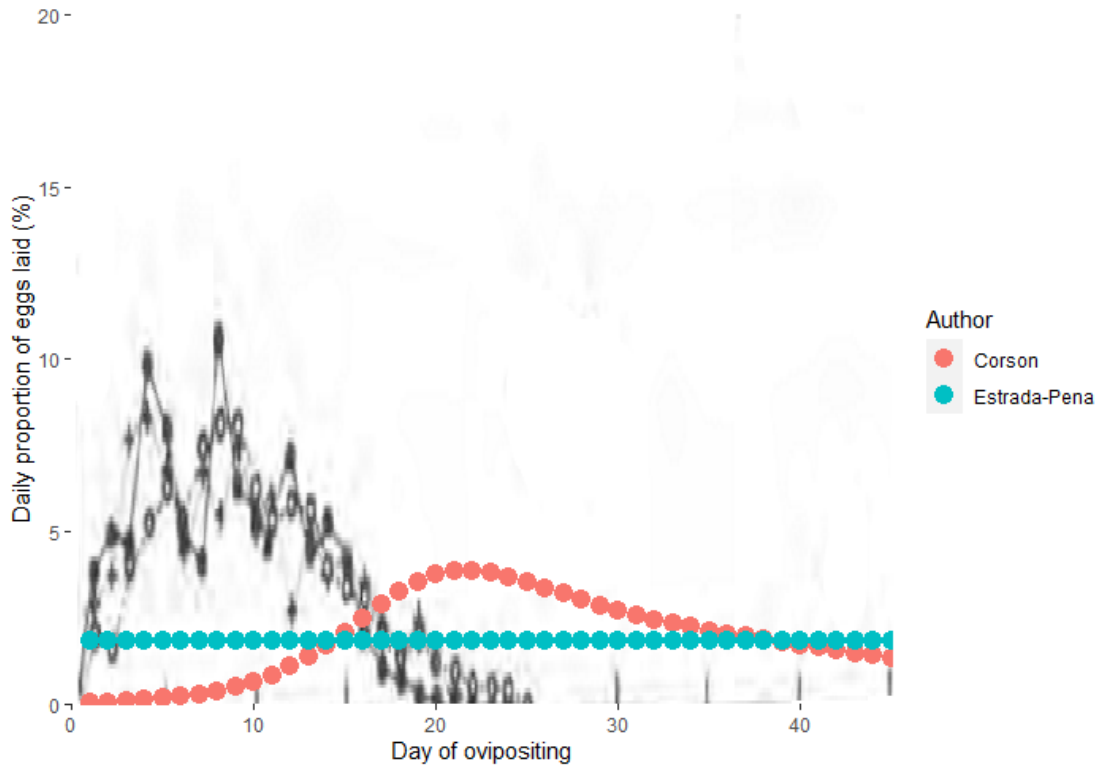


Figure 19: The rate of ovipositing as it changes over time at 20°C. Two models for *R. microplus* are superimposed on the data of Londt (1977) for *R. decoloratus*.

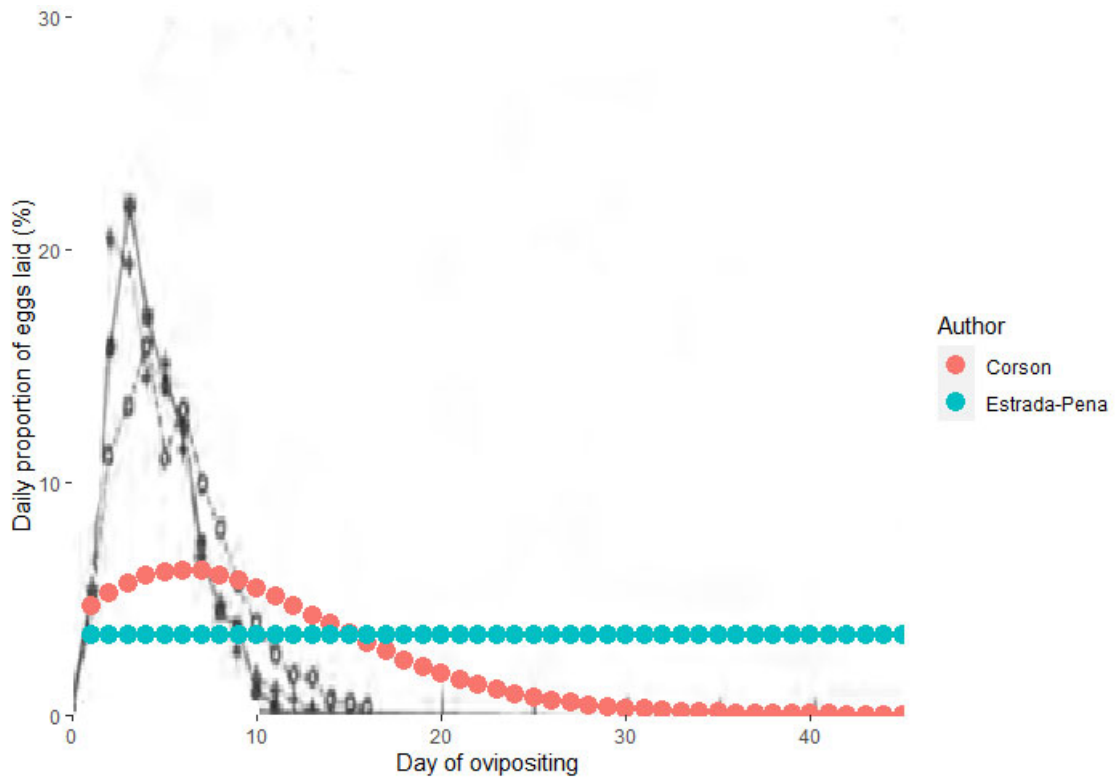


Figure 20: The rate of ovipositing as it changes over time at 26°C. Two models for *R. microplus* are superimposed on the data of Londt (1977) for *R. decoloratus*.

Table 19: The data sources evaluated that inform the rate of ovipositing.

Data source	Species	Underlying references	Model details	
(Estrada-Peña, 2002)	<i>R. decoloratus</i>	(Robertson, 1981; A. Spickett & Heyne, 1990)	Developmental threshold: 13.2°C Degree-days required: 372.8°C.days Uniform rate across the period to reach the required degree-days.	
(Corson et al., 2004)	<i>R. microplus</i>	(Bennett, 1974; Davey, 1986, 1988)	Range covered	Equation y is the hourly proportion of total eggs laid x is the cumulative proportion of total eggs already laid
			<14.17	$y = 0$
			≥ 14.17 to < 16.95	$y = 0.00007 + 0.015x - 0.043x^2 + 0.044x^3 - 0.016x^4$
			≥ 16.95 to < 19.72	$y = 0.00013 + 0.022x - 0.063x^2 + 0.068x^3 - 0.028x^4$

			≥ 19.72 to $<$ 22.50	$y = 0.00053 + 0.034x$ $- 0.102x^2$ $+ 0.115x^3$ $- 0.047x^4$
			≥ 22.50 to $<$ 24.45	$y = 0.00082 + 0.040x$ $- 0.113x^2$ $+ 0.118x^3$ $- 0.046x^4$
			≥ 24.45 to $<$ 26.00	$y = 0.00341 + 0.013x$ $- 0.012x^2$ $+ 0.020x^3$ $+ 0.016x^4$
			≥ 26.00 to $<$ 28.22	$y = 0.00460 + 0.012x$ $- 0.030x^2$ $+ 0.023x^3$ $- 0.010x^4$
			≥ 30.83 to $<$ 33.61	$y = 0.00124 + 0.072x$ $- 0.212x^2$ $+ 0.226x^3$ $- 0.088x^4$
			≥ 33.61 to $<$ 33.61	$y = 0.00117 + 0.073x$ $- 0.196x^2$ $+ 0.187x^3$ $- 0.065x^4$

			≥ 36.39 to 36.39	$y = 0.00248 + 0.065x$ $- 0.148x^2$ $+ 0.107x^3$ $- 0.027x^4$
			≥ 36.39 to 38.34	$y = 0.00234 + 0.064x$ $- 0.184x^2$ $+ 0.187x^3$ $- 0.070x^4$
			≥ 38.34 to 41.95	$y = 0.00042 + 0.069x$ $- 0.165x^2$ $+ 0.141x^3$ $- 0.044x^4$
			≥ 41.95	$y = 0$

5.3.7. Starting numbers of the different life stages

The absolute number of ticks within each compartment was determined by defining the total ticks together with the relative proportions contained in each life-cycle stage. In the field, most of the live ticks are represented in the non-parasitic stages (eggs and questing larvae) such that even under optimum conditions, the survival rate to adulthood is only 1% (Emmanuel et al., 2011). One published model started with 60.15% eggs, 39.81% questing larvae and only 0.04% representing ticks on the host (Beugnet et al., 1998); these proportions were accepted for the current population dynamics model.

The total number of ticks at the start of each iteration was set at 150 000. This number was chosen somewhat arbitrarily, being roughly based on the population size to which a single-species population converged after two-year simulation. The total number of ticks were

multiplied with the proportions of eggs, questing larvae and adult ticks (on the host) resulting in 90 000 eggs, 37 500 questing larvae and 22 500 adult ticks to start each iteration. Of these, the proportion of *R. microplus* was set at 0.3. This number was chosen to represent an established introduction of *R. microplus* into a former *R. decoloratus* population.

Males and females of Ixodid ticks hatch in equal proportions (Oliver Jr., 1989). Males mature slightly faster so that males outnumber females at first. This ratio is quickly restored to 1:1 within a few days (Arthur & Londt, 1973). In field observations, male ticks are often more abundant than females as they remain on the host for longer (Falk-Vairant et al., 1994; Hitchcock, 1955b; Horak et al., 2018). In contrast to these findings, some modellers have adopted high female-to-male ratios (Corson et al., 2004; Mount et al., 1991). This is primarily based on the work of Davey and Cooksey (1988). They reported high and similar sex ratios for *R. microplus* and *R. annulatus* reaching adulthood in the same experiment (1.36:1 and 1.35:1, respectively). In the same experiment, the authors also recorded the female to male ratio of hybrids as 1.2:1. They argued that the XX-XO sex chromosome mechanism of *Rhipicephalus* ticks will predispose male ticks to recessive, lethal mutations on the X chromosome that will be automatically expressed on the XO male. This causes early genetic death of male embryos evidenced by lower-than-normal hatching rates and is to blame for the apparent skewness of the sex ratios in the pure strain ticks. Therefore, we assumed a sex ratio of 1:1 as field strains likely have good genetic diversity.

5.4 Acaricide treatment

No acaricide is expected to kill 100% of the ticks on every animal in a herd. This might be due to a natural low-level acaricide resistance present in a tick population (even before acaricide exposure) or poor reach of the active ingredient everywhere on the entire surface of the treated animals (Dzemo et al., 2022). Usually, acaricidal treatment at the Malelane Research Unit is aimed at multi-host ticks such as *Amblyomma hebraeum* and *Rhipicephalus appendiculatus*. These ticks have known predilection sites that allow targeted spot treatment

(Horak et al., 2018). Applying acaricide would allow more *Rhipicephalus* ticks to be sheltered from the treatment compared to whole-body treatments. The model had a simple variable determining the proportion of ticks killed at each treatment (*acaricide_constant*). The variable could theoretically take any value between 0 and 1. Although laboratory tests conducted on the resistance levels of the field strains at the Malelane Research unit have shown 80% effectivity, 70% effectivity was chosen to reflect the effect of ticks sheltering from the treatment (*acaricide_constant*=0.7).

The treatment frequency was adjusted for the different seasons such that the intensity was highest from December to March (four per month). April was a transition month with three treatment per month. The lowest intensity acaricidal treatment was from May to October (one treatment per month) and November was again a transition month with two treatments per month. This represents 27 treatments per year and was based on recorded acaricide treatments given at the Malelane Research Unit.

5.5 Population model calibration

The first attempts to run the model resulted in a tick population growing exponentially. This prompted to investigate the effect of increasing the frequency of acaricidal treatments. However, this resulted in an imploding population that went extinct. Conversely, when the number of acaricidal treatments were decreased the population exploded again. Balancing implosion and explosion was exceedingly difficult, such that some iterations would implode while others would explode even under the same acaricidal frequency assumption.

It was realised that a density-dependent predatory effect was required to help balance the population. Only at this time of the model development was the predatory effect on tick eggs introduced—this quickly brought stability to the model preventing population implosions and explosions. The value of k for the predatory constant was chosen empirically to maximise model stability. Following the success of the predatory effect to stabilise the model, the

number of times acaricidal treatments are given per annum was returned to the original value of 27.

The results of three different iterations are shown in Figure 21. Each iteration used the same baseline parameter values. It can be seen that an extinction event for *R. decoloratus* occurred in iteration three. This should not be confused with the described implosions and implosions since it is only *R. decoloratus* that went extinct in the third iteration. The *corrAgresponding* high number of *R. microplus* in the same iteration suggests a succesful displacement of *R. decoloratus* by *R. microplus*.

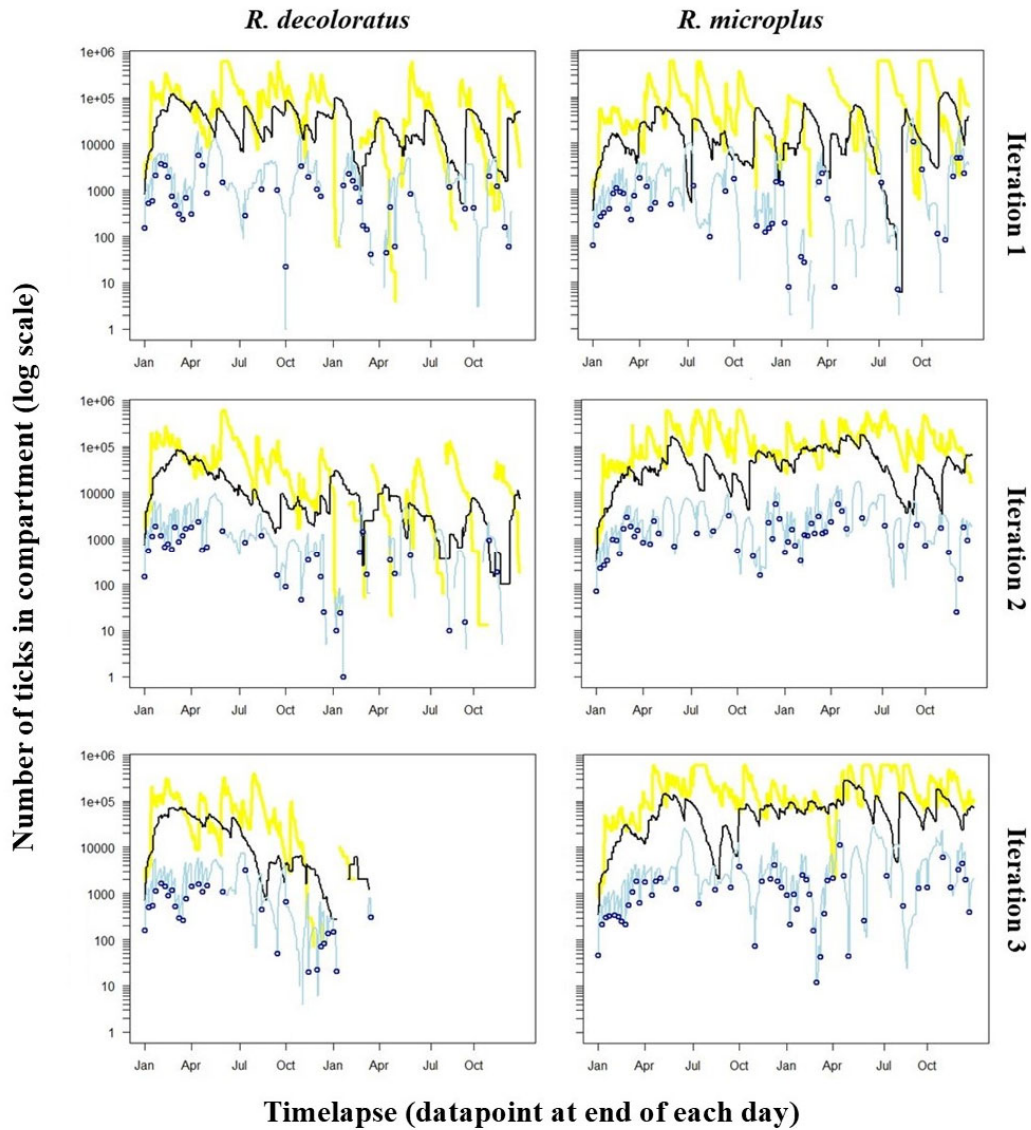


Figure 21: Examples of three iterations of the population model after successful calibration. The yellow line represents the number of eggs, the black line represents the number of questing larvae and the light blue line represents the total of the on-host life-stages. The blue circles are days when acaricides were applied to the animals.

5.6 Population Model validation

The original intention was to validate the model by comparing the response of the modeled and field tick populations to the same acaricidal treatment regimen practiced at the Malelane

Research Unit (MRU). The tick populations should not go extinct following an acaricidal treatment regimen nor should it continue to grow unabated. During the calibration phase of the model, the parameters were adjusted partly in response to the behaviour of the model following acaricidal treatments (notable the predation parameter). Therefore this criteria could no longer be used.

Instead it was decided to examine the modeled tick population's seasonal abundance. Historic records of MRU show marginal increases of *Rhipicephalus* ticks in spring (October); and the highest peak in the population occurring in late April to May after which it suddenly drops when cold spells become more intense in middle May to late May. The ticks at MRU are mainly *R. decoloratus*, recently having had the inadvertent introduction of *R. microplus*.

The population dynamics model was simulated once for ten years (with only *R. decoloratus*) to investigate if there were any seasonal tendencies in the modelled tick population. A daily mean was calculated for each year-day using the ten year data and a moving average was calculated over 30 days to obtain a smoothing effect. Only adult female ticks (in the parasitic phase) were considered. Lastly the total number of adult female ticks was divided by the herd size to obtain an average visible infestation rate per animal. (Figure 22). The modelled seasonal variations compared well with the observed seasonal variations at MRU. The modelled peak in early autumn is a little more extreme and a little earlier compared to the observed early autumn peak at MRU.

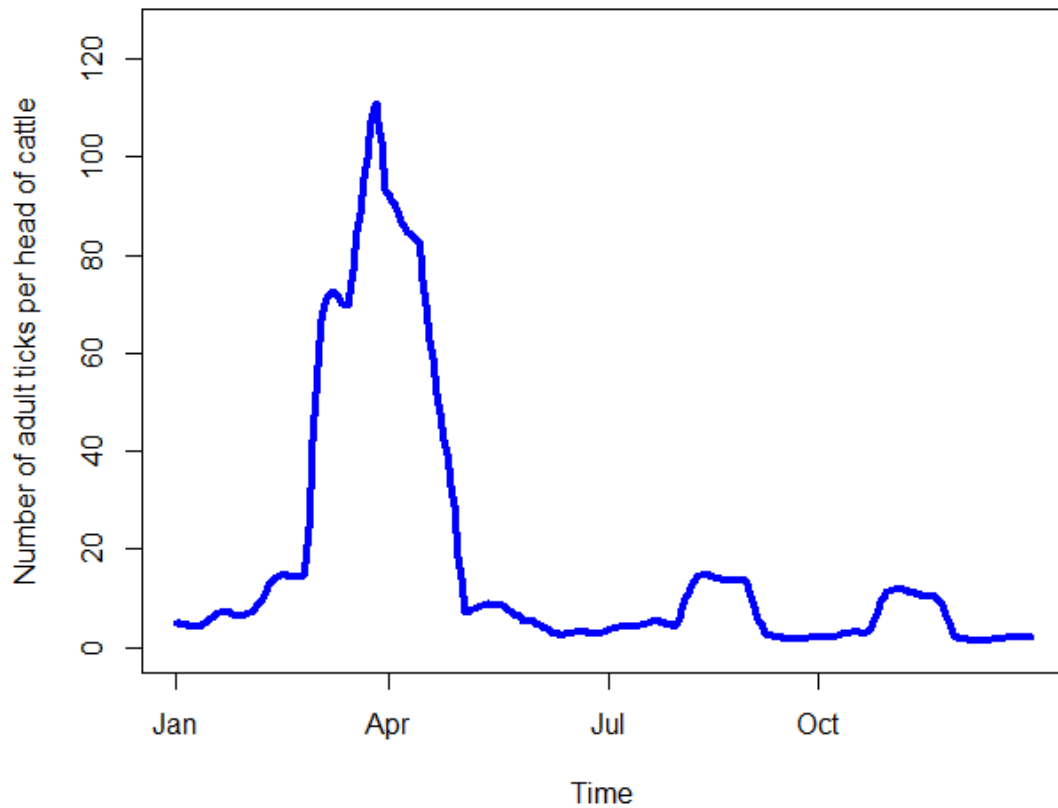


Figure 22: The modelled seasonal variations of the easily visible, adult, female ticks.

5.7 Sensitivity analysis

Sensitivity parameters in the population model assumed different values selected from a list of possible values (Table 20) to evaluate the effect that a change in value would have on the probability of *R. microplus* displacing *R. decoloratus*.

Table 20: The seven sensitivity parameters that were allowed to vary across fixed values to determine their impact on the outcome of the population dynamics model.

Variable name	Description	Value(s)	Source	Notes
<i>dev_threshold_de c_adapt</i>	The development threshold is the temperature above which <i>Rhipicephalus</i> eggs develop. The development threshold for <i>R. decoloratus</i> is slightly lower and is therefore adapted downwards through this variable.	{-1.3; -0.87; -0.43; 0}	(Short et al., 1989)	The development threshold value for <i>R. decoloratus</i> determined by Short et al. is 10.5 and 11.8 for <i>R. microplus</i> (a difference of 1.3). Therefore, the maximum difference of 1.3 and a minimum of 0 was accepted. Two values were chosen in between the extremes at equal intervals.

<i>degree_days_dec_adapt</i>	The degree days is the time-temperature product that is required to complete the egg development.	{0; 21; 42}	(Short et al., 1989)	The value for <i>R. decoloratus</i> determined by Short et al. is 464 (which is 42 days more than the 422 days required for <i>R. microplus</i>). Therefore, the maximum difference between the two species was chosen as 42, the minimum as 0 with one value in between (21).
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<i>cycle_delay_factor</i>	The rate of development of <i>R. decoloratus</i> parasitic stages may be slower compared to <i>R. microplus</i> . The cycle delay factor determines what proportion of the model we developed for the Solomon & Kaaya observations is accepted.	{0; 0.5; 1}	(Solomon & Kaaya, 1998)	A value of 1 would mean a full assumption of the delay for <i>R. decoloratus</i> observed in the Solomon and Kaaya data. A value of zero means that the Solomon & Kaaya data is ignored.
<i>male_survival_decay</i>	A sensitivity parameter that determines if <i>R. decoloratus</i> males remain on the host for shorter or longer periods compared to <i>R. microplus</i> .	{0.5; 1; 2}	(Arthur & Londt, 1973; Legg, 1930; J. G. H. Londt & Arthur, 1975).	A factor of 0.5 would mean that <i>R. decoloratus</i> males remain on the host for only 50% of the time that <i>R. microplus</i> males do.

<i>males_mated</i>	The maximum number of male partners 1 female can have.	{1;2;3}	(Cutullé et al., 2009)	
<i>startDate</i>	The simulations were started on different dates of the year to represent different seasons.	{1-January; 1-April; 1 July; 1 October}		
<i>climate_T</i>	The daily temperature was either adapted upwards or downwards by 1 °C.	{-1; 0; 1}		

5.8 Analyzing the outcome of the population dynamics model

The recorded output from the population dynamics model was the absolute number of ticks for each tick species after two years. The absolute numbers were not considered biologically very meaningful as the study's objective was the displacement of *R. decoloratus* by *R. microplus*, primarily independent of the absolute numbers. Instead, the relative proportion of *R. microplus* compared to the total tick population was calculated.

5.9 Analyzing the effect of the sensitivity parameters on the outcome

The range of values for the proportion of *R. microplus* were presented visually with boxplots. A separate boxplot was produced for each possible value of the sensitivity parameter to enable comparison across the different values of the sensitivity parameter. Besides the graphical representation, the median value for the proportion of *R. microplus* was calculated under four different conditions for the value of the sensitivity parameter. The minimum and maximum, the value of the sensitivity parameter representing no difference between *R. microplus* and *R. decoloratus* (the baseline) and the most likely value of the sensitivity parameter based on our estimation from the literature review. The sensitivity parameter that produced the biggest change in the median proportion for the baseline to the median for the most likely value of the sensitivity parameter was deemed the most influential sensitivity parameter. The median was preferred over the mean to limit the skewness effect produced by excessive zeros or ones.

6.RESULTS

Each unique combination of the seven sensitivity parameters (3888 combinations) had five population model iterations (model run over two years with 730 daily steps). Out of 19,440 iterations, 262 were removed because both tick populations fell to zero. This represents an extinction rate of 1.35%. Extinctions were spread across all combinations in an apparent random pattern. The dataset of 19,178 proportions had a non-normal distribution (Figure 23).

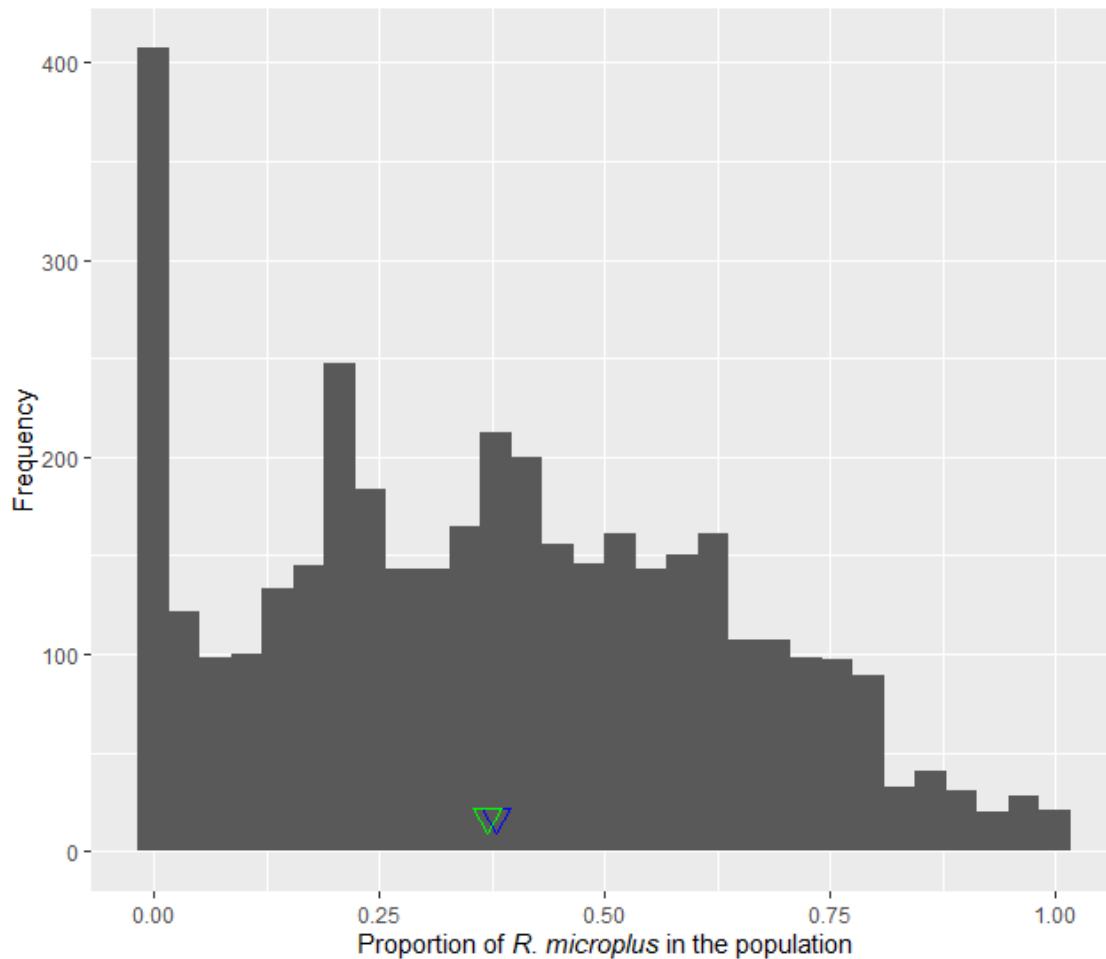


Figure 23: A histogram of the proportion of *R. microplus* in the total tick population after two years of simulation. The mean across all combinations of parameters is indicated with a blue triangle (0.378) and the median with a green triangle (0.373).

The competition between the tick species was measured by comparing the proportion of *R. microplus* at the end of the simulation with the proportion of *R. microplus* at the start of the simulation. All simulations were started with a *R. microplus* proportion of 0.3. It was noticed during model development, that starting the model with very low proportions of *R. microplus* almost invariably led to *R. microplus* extinctions. Conversely starting the model with 50% *R. microplus* or higher almost invariably led to *R. microplus* displacing *R. decoloratus* completely. The starting proportion of 0.3 was chosen to allow for a more balanced competitiveness that

could be better analysed for the factors that affect the outcome. It is however important to note that the starting proportion will have interactions with some of the sensitivity parameters analysed. The model results should therefore be interpreted as valid for only established introductions of *R. microplus* (not recent introductions and not situations where displacement is well underway).

The baseline sensitivity parameter held a value that represented no difference between *R. microplus* and *R. decoloratus*. The most likely sensitivity parameter held the best estimate of the true parameter value. Subtracting the proportion of *R. microplus* obtained at baseline parameter value from the proportion of *R. microplus* at the most likely parameter value, gave a marginal effect. This represented the absolute value by which the proportion of *R. microplus* would change when considering that sensitivity parameter value. (Table 21).

Table 21: The value of the sensitivity parameter (sp) and the corresponding mean and median proportions of *R. microplus* at the end of the simulation. The most likely values of the sensitivity parameters denote the best estimates of the sp. The last column shows the marginal effect when the sp is changed from the baseline to the most likely value.

Sensitivity parameter (sp)	Minimum	Maximum	Baseline sp value	Most likely sp value	Marginal effect (baseline to most likely)
<i>dev_threshold_dec_adapt</i>	sp= -1.3 Mean= 0.286 Median = 0.251	sp= 0 Mean=0.481 Median = 0.502	sp= 0 Mean= 0.481 Median = 0.502	sp= -1.3 Mean= 0.286 Median = 0.251	Mean= - 0.195 Median= -0.251
<i>degree_days_dec_adapt</i>	sp= 0 Mean = 0.306 Median = 0.272	sp= 42 Mean = 0.448 Median = 0.454	sp= 0 Mean = 0.306 Median = 0.272	sp= 42 Mean = 0.448 Median = 0.454	Mean= 0.142 Median= 0.182
<i>cycle_delay_factor</i>	sp= 0 Mean = 0.310 Median = 0.282	sp= 1 Mean = 0.450 Median = 0.441	sp= 0 Mean = 0.310 Median = 0.282	sp= 1 Mean = 0.450 Median = 0.441	Mean= 0.140 Median= 0.159
<i>male_survival_dec</i>	sp= 0.5 Mean = 0.517 Median = 0.531	sp= 2 Mean = 0.261 Median = 0.216	sp= 1 Mean = 0.357 Median = 0.351	sp= 1 Mean = 0.357 Median = 0.351	NA (baseline equals most likely value).
<i>males_mated</i>	sp= 1 Mean = 0.268 Median = 0.215	sp= 3 Mean = 0.473 Median= 0.477	NA (the baseline is currently not known).	sp= 3 Mean = 0.473 Median= 0.477	NA
<i>startDate</i>	sp= 2021-04-01 Mean = 0.279 Median = 0.231	sp= 2021-10-01 Mean = 0.443 Median = 0.443	NA	NA	NA
<i>climate_T</i>	sp= -1 Mean = 0.390 Median = 0.380	sp= 1 Mean = 0.384 Median = 0.376	sp= 0 Mean = 0.360 Median = 0.356	sp= 1 Mean = 0.384 Median = 0.376	Mean=0.024 Median=0.020

6.1 Development threshold for *R. decoloratus*

A reduction of the development threshold adaption from 0°C (the baseline) to -1.3 °C (the most likely value for *R. decoloratus*) reduced the median proportion of *R. microplus* from 0.502 to 0.251 (Figure 24). This corresponds to a change in the development threshold from 11.8 °C (that of *R. microplus*) to 10.5°C (that of *R. decoloratus*). The marginal effect is negative at -0.251.

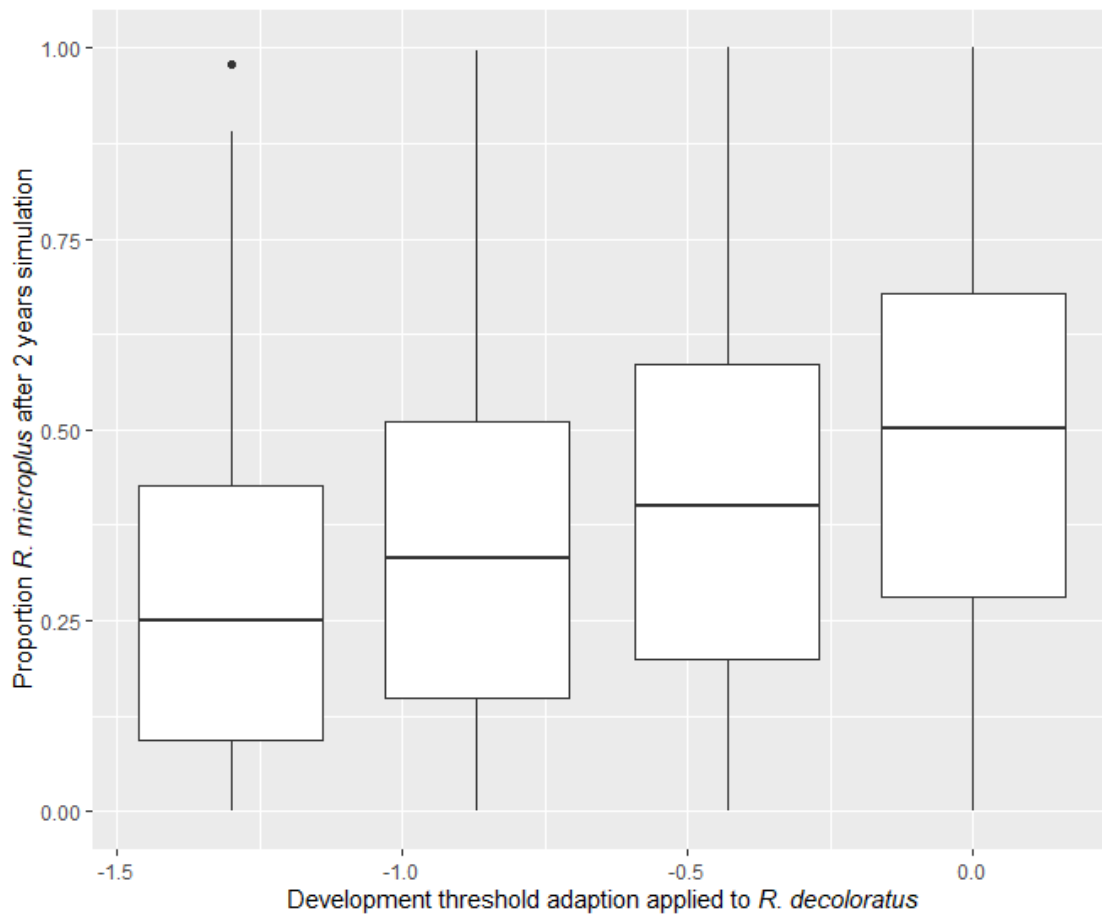


Figure 24: The effect of changes in the development threshold on the predicted proportion of *R. microplus* in the population. The number on the x-axis is the number of degrees in Celsius that the development threshold of *R. decoloratus* is reduced by when compared to *R. microplus*.

6.2 Degree-days required to complete egg development

An increase in the degree-days required to complete the egg development of *R. decoloratus* from 0 to 42 degree-days increased the median proportion of *R. microplus* from 0.272 to 0.454 (Figure 25). The most likely value for the degree-days of *R. decoloratus* is 464 degree-

days, which is 42 days more than the 422 degree-days required for *R. microplus*. The marginal effect is positive at 0.182.

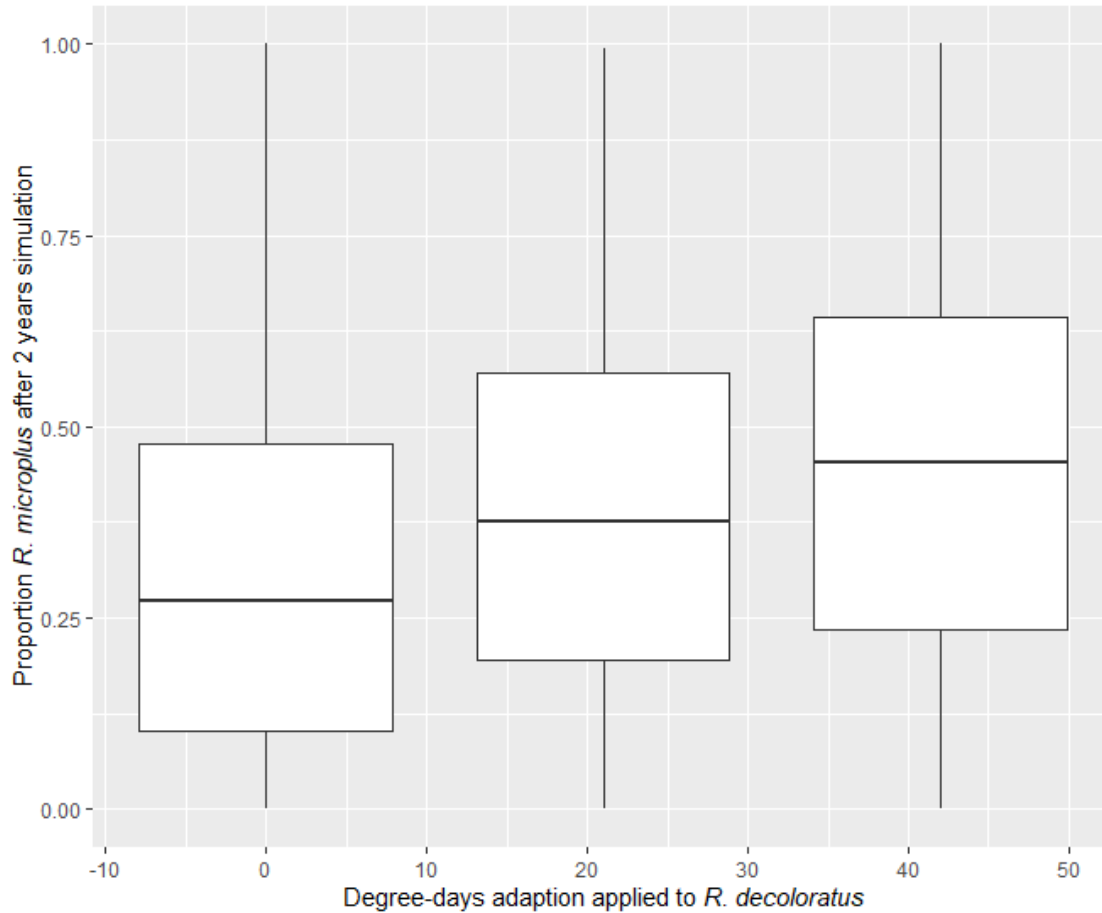


Figure 25: The effect of changes in the degree-days required for egg development on the predicted proportion of *R. microplus* in the population. The number on the x-axis is the number of degree-days added to the degree-days of *R. microplus* to adapt for *R. decoloratus*.

6.3 The delay of the parasitic lifecycle of *R. decoloratus*

An increase in the degree of acceptance of the Solomon and Kaaya (1998) model for a delay in the parasitic lifecycle of *R. decoloratus* from 0 (zero acceptance) to 1 (full acceptance)

increased the median proportion of *R. microplus* from 0.282 to 0.441. (Figure 26). When holding all sensitivity parameters to their most likely values, an upward adjustment in the level of acceptance of the lifecycle delay of *R. decoloratus* resulted in a rise in the proportion of *R. microplus* at simulation-end by 0.159.

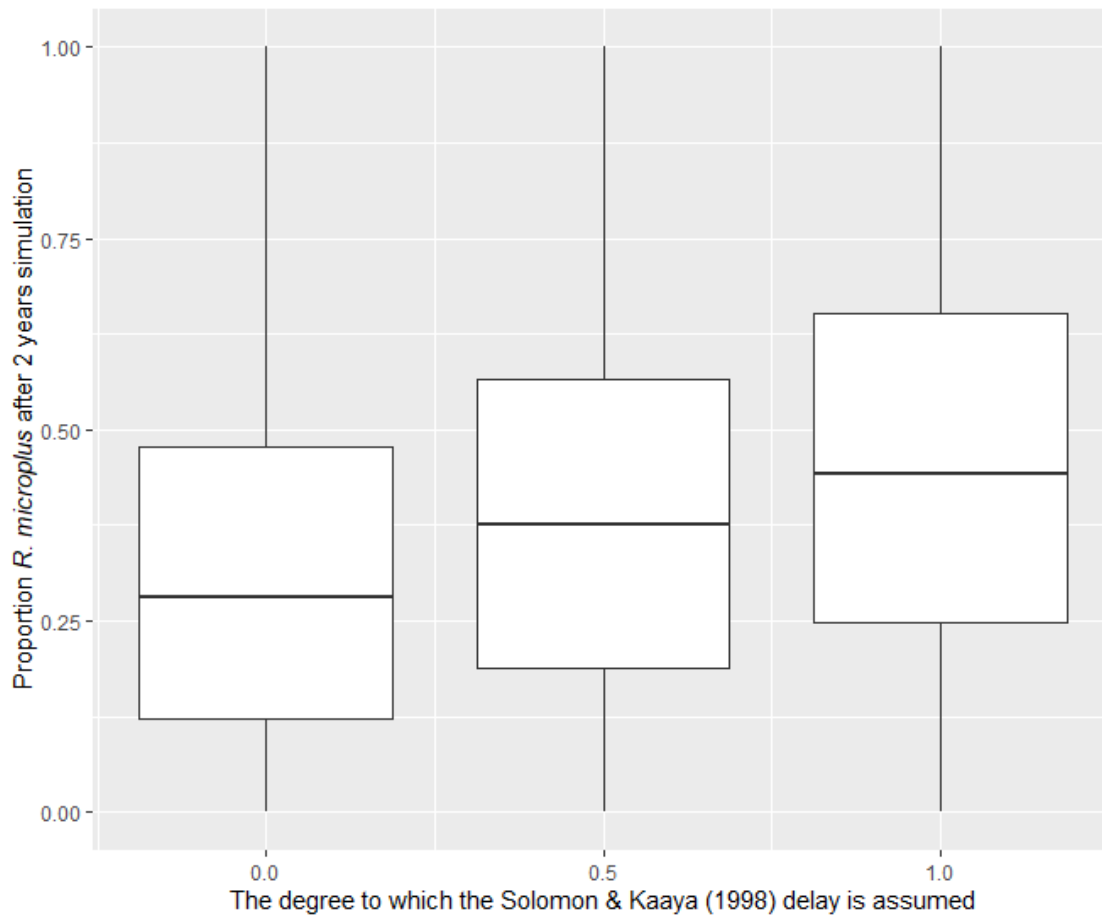


Figure 26: The effect of changes in the level of acceptance of the Solomon and Kaaya (1998) model for a slower parasitic lifecycle of *R. decoloratus*. The number on the x-axis represents the level of acceptance of the model where one equals full acceptance.

6.4 Male survival time on the host

An increase in the survival time of *R. decoloratus* from 50% (0.5) compared to *R. microplus*, to 200% (2) compared to *R. microplus* decreased the median proportion of *R. microplus* at the end of 2 years simulation from 0.531 to 0.216 (Figure 27). This cannot be equated to a marginal effect as it is currently unclear whether different values exist for the survival times of the males of the two species. Yet, should there be a difference, the effect thereof could be substantial. Consideration was also given to a possible interaction of the survival-time

of males on the host with the number of males mated by one female (Figure 28). No interaction was observed.

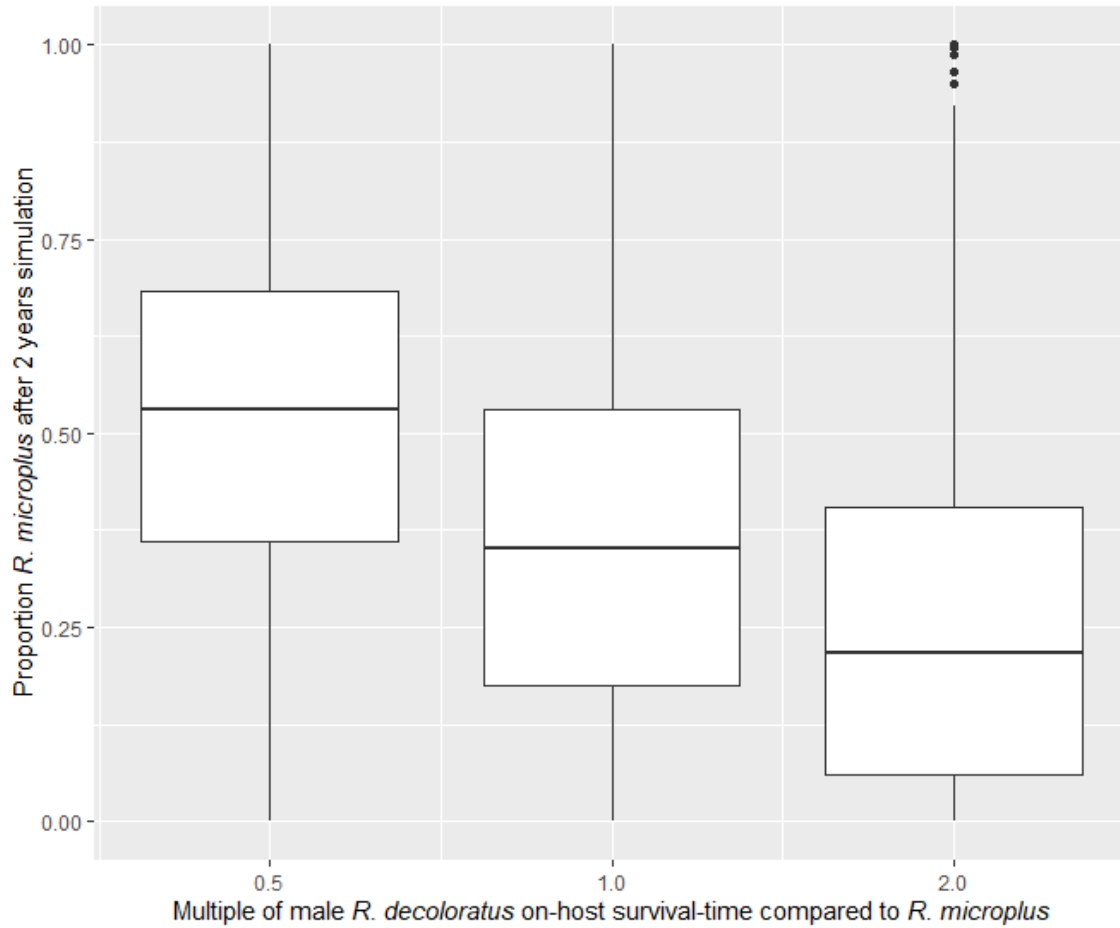


Figure 27: The effect of changes in the on-host survival time of *R. decoloratus* on the proportion of *R. microplus* in the population. The number on the x-axis represents a multiple of the time spent on the host by *R. decoloratus* compared to the accepted time for *R. microplus* (42 days).

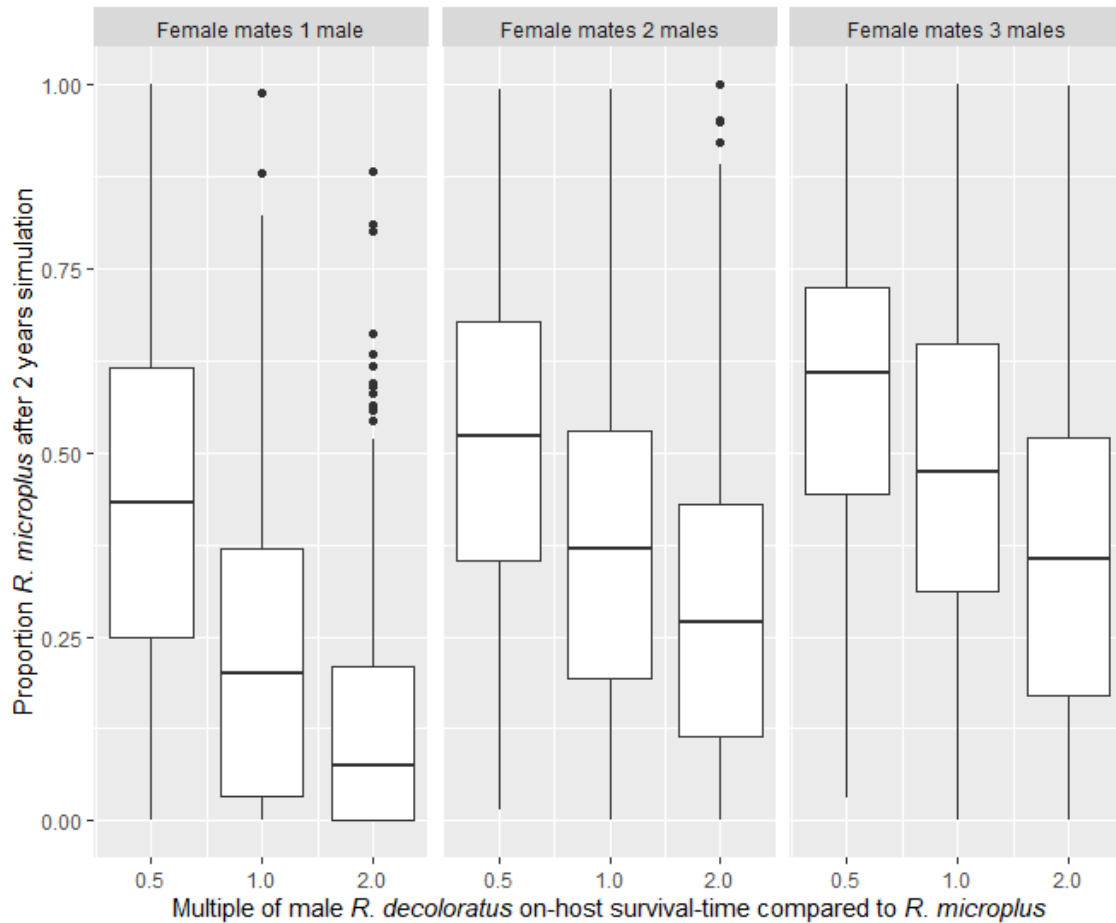


Figure 28: The effect of changes in the on-host survival time of *R. decoloratus* on the proportion of *R. microplus* in the population while controlling for the number of males mated by one female. The number on the x-axis represents a multiple of the time spent on the host by *R. decoloratus* compared to the accepted time for *R. microplus* (42 days).

6.5 The number of males mated by each female

An increase in the number of male partners for female ticks from one to three, increased the median proportion of *R. microplus* at the end of two years simulation from 0.215 to 0.477 (Figure 29). This can not be equated to a marginal effect as it is currently not known if there is a species difference in the number of males mated. However, should a difference exist it would be substantially impact the proportion of *R. microplus*.

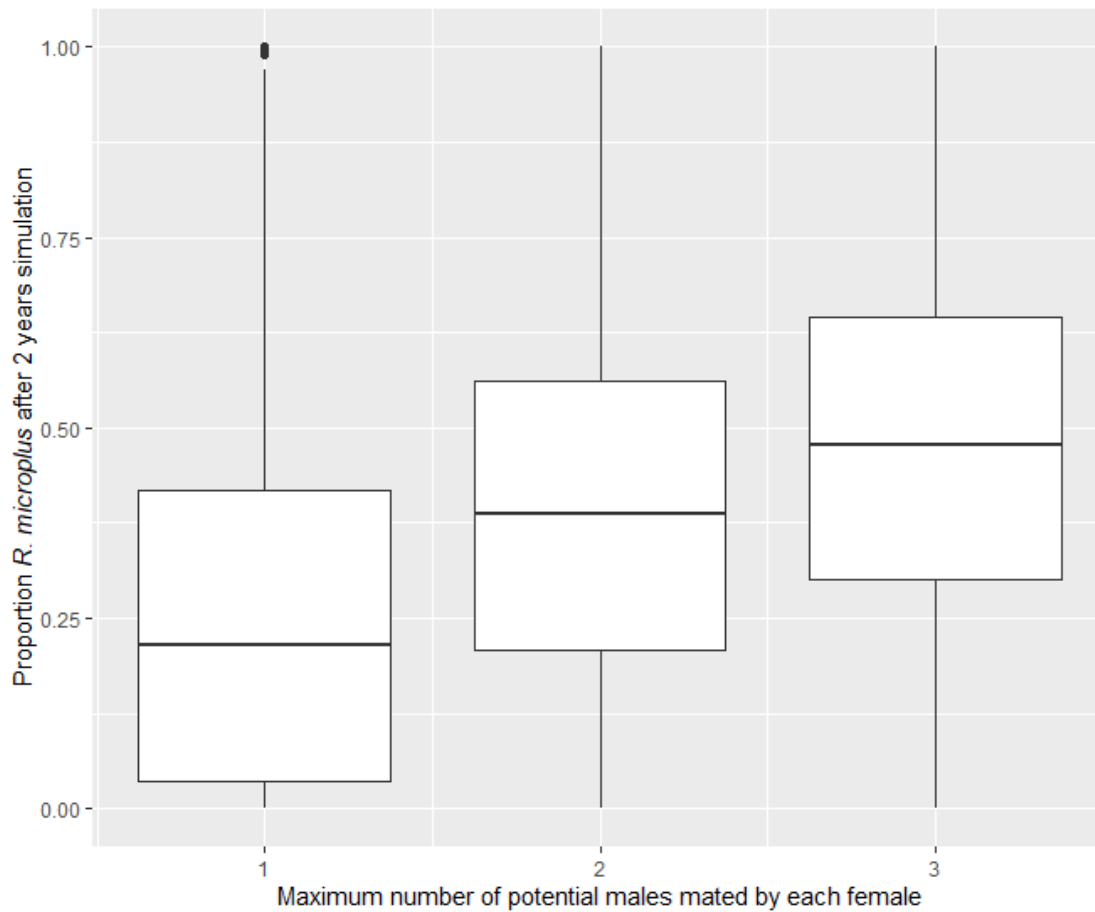


Figure 29: The effect of changes in the maximum potential number of male partners for each female tick on the proportion of *R. microplus* in the population after two years simulation.

6.6 The starting date of the simulation

A starting date in autumn (1-April) is most favourable to *R. decoloratus* whereas a starting date in spring (1-October) is most favourable to *R. microplus* (Figure 30). The respective medians of the proportion of *R. microplus* after two years of simulation using autumn and spring as starting dates were 0.231 and 0.443.

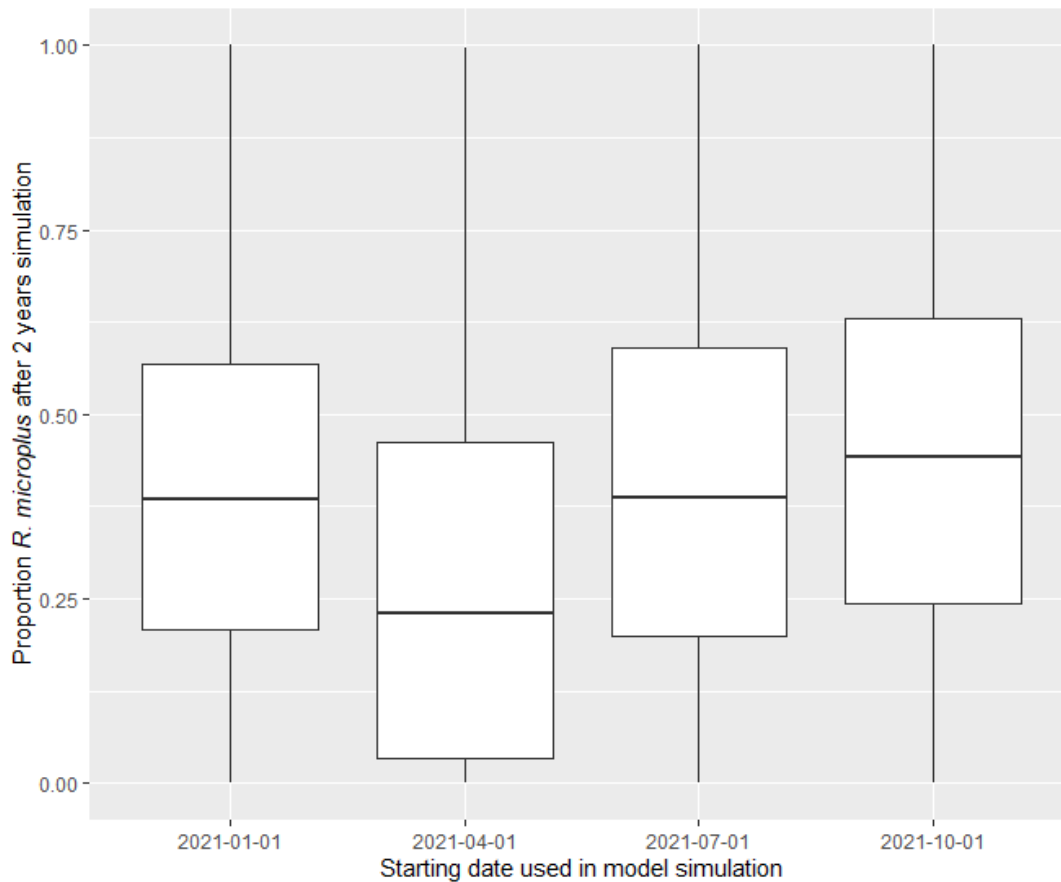


Figure 30: The effect of different starting dates of the simulation on the proportion of *R. microplus* in the population after two years simulation.

6.7 The environmental temperature

A decrease in the mean environmental temperature of 1 °C compared to an increase in the environmental temperature of 1 °C (difference = 2 °C) changed the median proportion from 0.380 to 0.376. A change in the mean environmental temperature of 1 °C had no meaningful effect (Figure 31). A possible interaction of the environmental temperature (*climate_T*) with the temperature dependent cycle delay of *R. decoloratus* (*cycle_delay_factor*) was also investigated but there did not appear to be a noteworthy interaction (Figure 32).

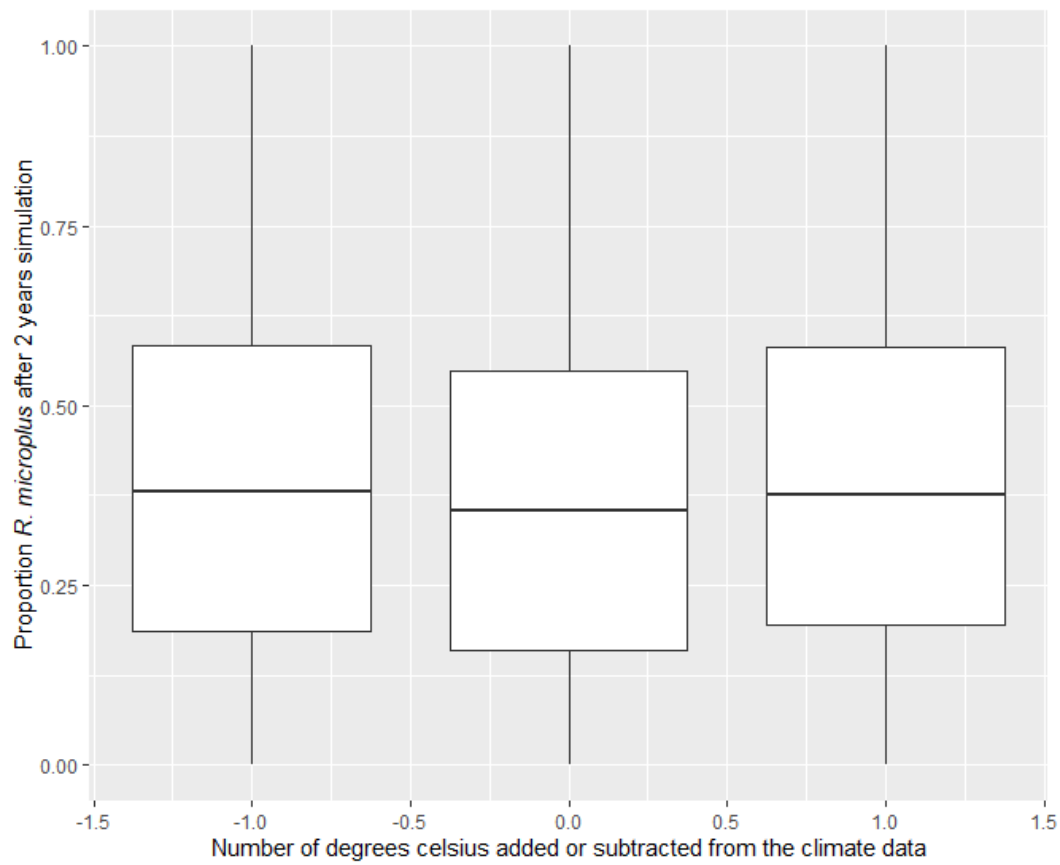


Figure 31: The effect of changes in the mean environmental temperature on the proportion of *R. microplus* in the population after two years simulation.

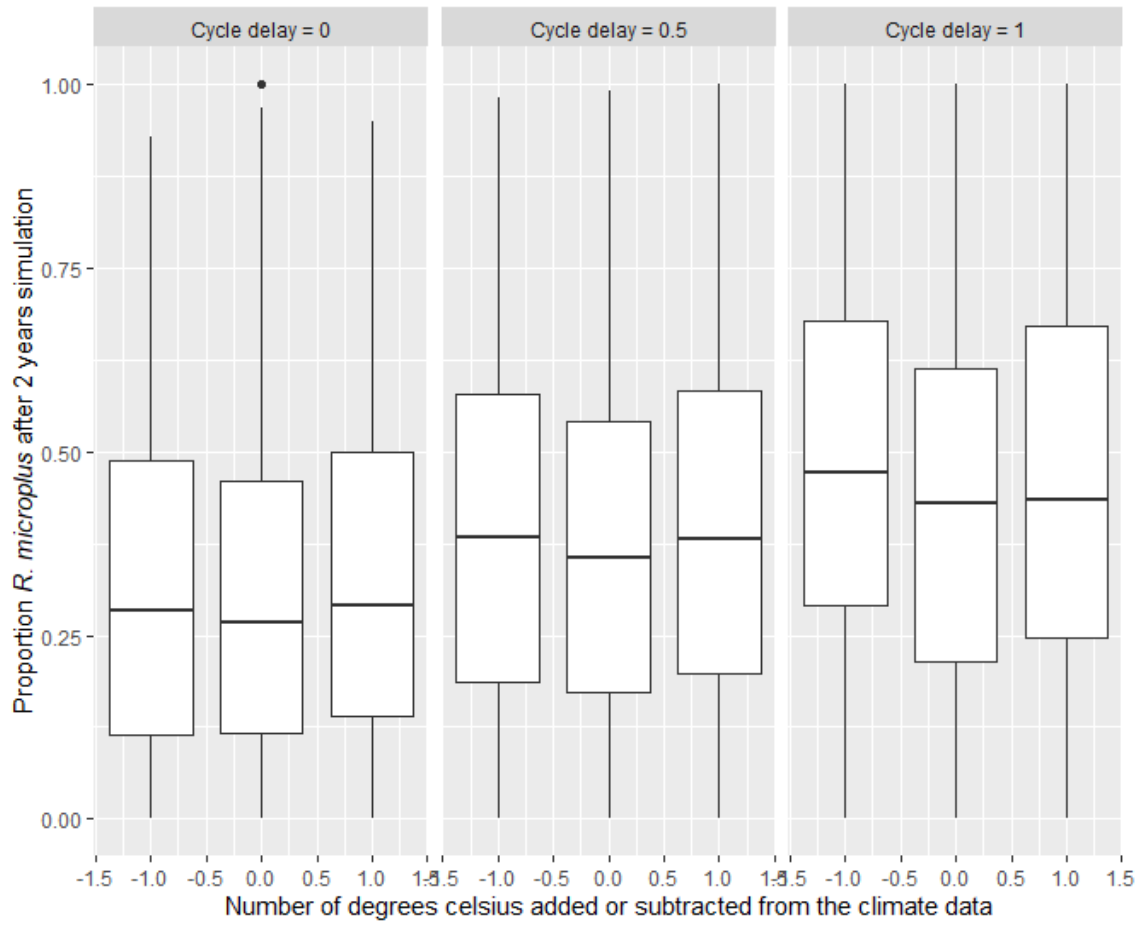


Figure 32: The effect of changes in the mean environmental temperature on the proportion of *R. microplus* in the population after two years simulation whilst controlling for the cycle delay factor. No noteworthy interaction is visible.

7. DISCUSSION

7.1 The relative importance of the sensitivity parameters

The impact of the sensitivity parameters was measured by comparing the model outcome with or without the most likely value of the sensitivity parameter included. Taken as the proportion of *R. microplus* at the end of the simulation, this provided the relative advantage of *R. microplus* over *R. decoloratus* as a result of that sensitivity parameter. It represented a marginal effect between the two values and provided a way of ranking the sensitivity parameters for the size of their impact.

The factors modelled to investigate the relative success of *R. microplus* (in a sub-tropical climate when *R. microplus* represents 30% of the population) can be ranked for their importance as follows:

1. The shorter degree-days required by *R. microplus* to complete egg development (marginal effect on the median is +0.182).
2. The faster parasitic life cycle of *R. microplus* (marginal effect on the median is +0.159)
3. An increase in environmental temperature of 1°C (marginal effect on the median is +0.02)
4. The higher development threshold for eggs of *R. microplus* (marginal effect on the median is -0.251).
5. The time that males survive on the host. The marginal effect cannot be calculated as we could find no evidence of species differences. Should there be any species differences, the impact would be significant since the difference in the means associated with the maximum and minimum values of the sensitivity parameter is +0.315.

6. The number of males mated. The marginal effect cannot be calculated as we could find no evidence of species differences. Should there be any species differences the impact thereof would be significant, since the difference in the means associated with the maximum and minimum values of the sensitivity parameter is +0.262.
7. The time of the introduction of *R. microplus* into a herd. The marginal effect cannot be calculated since any choice for a baseline starting date would be arbitrary. However the maximum difference between different starting dates detected was +0.212.

The shorter degree-days required for *R. microplus* egg development, and a faster parasitic lifecycle are the two most important factors driving *R. decoloratus* replacement. Taken together, the two factors result in a speedier lifecycle, providing *R. microplus* with a substantial advantage. This relative advantage will likely increase in substantially warmer climates as the egg development accelerates at temperatures further away from the development threshold. At colder temperatures, the difference between the developmental threshold and the ambient temperature would not be enough to allow fast *R. microplus* development. In addition, the lower development threshold of *R. decoloratus*, makes it relatively more successful during the Malelane winter. The impact of the season in our model is clear from the effect of the starting date. It can be assumed that regional climate differences are also highly impactful. Changes in the local environmental temperature due to climate change are much more minor in magnitude than seasonal or regional differences. For this reason, the modelled temperature range spanning 2°C that we tested had a little effect even though the temperature is a critical factor.

Of the sensitivity parameters for which a marginal effect could not be calculated, male survival time on the host was the most impactful, followed by the number of males mated by each female. These factors impact the rates at which the different males can mate with females. Since inter-species matings are sterile, it is critically important for the males of a particular species to gain the advantage here. Especially when the proportions of the abundance of the two species are not equal, the species with the higher abundance (and more

successful male matings) will cause higher sterility rates in the females of the species with lower abundance.

The starting date is the only sensitivity parameter that offers potential for manipulation by a farmer. Although introductions of *R. microplus* into a herd are usually accidental, it is precious to know that *R. microplus* is at its weakest during winter. This knowledge can be combined with the importance of high numbers of males to achieve enough fertile matings in its own species. There is a potential opportunity to eliminate already established *R. microplus* from mixed populations by aggressive dipping in autumn, followed by artificial infestations of *R. decoloratus* after the efficacy of the acaricide has waned. This could lead to disproportionately high numbers of *R. decoloratus* males in spring, which would sterilize a high proportion of the *R. microplus* females.

7.2 Development threshold for *R. decoloratus*

The difference in the development thresholds of *R. microplus* and *R. decoloratus* alone appears to substantially favour *R. decoloratus* even in the warm sub-tropical climate of Malelane. The ability of *R. decoloratus* to continue egg development at colder temperatures is likely to also explain the poor performance of *R. microplus* when the model starts in autumn. The magnitude of the effect size of the development threshold is the largest of all sensitivity parameters examined. However, this relative advantage of *R. decoloratus* is not enough to prevent its displacement.

In colder climates, the effect of the development threshold is likely to be enhanced. It probably plays a significant role in sustaining the relatively low abundance of *R. microplus* in the cold Free State province (Horak et al., 2018). The development threshold is a critical factor enabling climate-based models to predict the species' distribution with relative accuracy (Sungirai et al., 2018).

7.3. Degree-days required to complete egg development

The longer degree-days required by *R. decoloratus* eggs to complete development substantially slows the development of *R. decoloratus*, thereby providing an opportunity for *R. microplus* to outcompete it. This appears to be the most important factor enabling *R. microplus* to displace *R. decoloratus*.

7.4 The parasitic lifecycle delay of *R. decoloratus*

When reviewing the work by Solomon & Kaaya (1998) on *R. decoloratus*, it seems probable that the parasitic lifecycle of *R. decoloratus* is delayed during cold and wet weather (compared to the work done by Londt & Arthur (1975) and Arthur & Londt (1973)). Therefore the observed differences in these studies cannot be accepted without the necessary caution. However, our own observations at the Malelane Research Unit confirms that the parasitic development of *R. decoloratus* is substantially slower in winter and during rainy weather. If indeed the observed differences in these studies is a true reflection of reality, the invasion potential of *R. microplus* is greatly enhanced. The delay of the parasitic lifecycle is the second most important factor effecting the displacement of *R. decoloratus* by *R. microplus*.

7.5 Male survival time on the host

Male ticks have high fecundity being able to mate with several females (Thompson et al., 1980). The longer males are able to stay on the host, the more females they can theoretically mate. If one species survives longer than another, this would create an obvious advantage. The model simulation supports this idea but we were unable from available literature to parameterise the two species differently. However, it is likely that a difference exists since *R. decoloratus* males appear to feed more compared to *R. microplus* (Arthur & Londt, 1973; Legg, 1930). Should there be a difference in the time spent on the host by the males, it would substantially affect the ability of *R. microplus* to displace *R. decoloratus*.

7.6 The number of males mated by each female

Whereas the number of males mated by each female does not cause a species to increase its abundance, it is critical to protect the females against the sterility effect after inter-specific matings. The more males the female mates, the higher the chance that at least one will be a conspecific male. This is especially important following early introductions of *R. microplus* when the proportion of *R. microplus* in the population is low, and it is sensitive to stochastic die-out driven by inter-species matings. In our model, the starting proportion of *R. microplus* was chosen to be 0.3. This would have been sufficiently low to make *R. microplus* vulnerable to extinction due to sterile matings. However, when the female was allowed to mate with three males this effect was mitigated long enough to allow *R. microplus* numbers to increase due to other factors.

It is currently unclear how many males can be mated per female and if a difference exists between the two species. Yet, should there be a difference the effect thereof could be substantial.

7.7 The starting date of the simulation

The starting dates chosen for the simulations corresponded to the start of the four quarters of the year. It is clear that *R. microplus* performs poorest when the simulation starts in autumn. The explanation for this would be that *R. microplus* has higher temperature requirements to start egg development (a higher development-threshold); therefore, it would be at a relative disadvantage during winter compared to *R. decoloratus*.

7.8 The environmental temperature

Changes in the temperature can affect ticks in multiple ways. One effect is a faster rate of egg development as maturity is measured in degree-days. This means that higher temperatures

ensure more rapid development for both species. However, during cold spells (below 10°C) an increase in temperature might ensure that only *R. decoloratus* eggs undergo development due to its relatively lower developmental threshold. The higher temperatures rise above 12°C, the relative advantage of *R. decoloratus* is reduced.

Regarding the development of the parasitic stages, *R. decoloratus* is unique because it requires lower relative humidity to complete the parasitic life cycle. If the absolute humidity is kept constant, the relative humidity drops as the temperature increases allowing faster development of *R. decoloratus*. However, in sub-tropical climates with high relative humidity, the development of the parasitic stages of *R. decoloratus* would remain slower.

The effect of slight temperature increases is therefore complicated by several factors and unlikely to produce profound effects. However, significant temperature differences, such as when moving from sub-tropical climates to temperate climates, have a substantial impact on the competition between the two species (Sungirai et al., 2018). The magnitude of the temperature differences across different regions is much larger than the 2°C temperature differences in the parameter space we modelled.

8. LIMITATIONS

The competition between the two species is impacted by the relative abundance of the two species. An established population is much less likely to crash (and go extinct) than a recent introduction. The current study was limited to investigate a 30:70 ratio of *R. microplus* to *R. decoloratus*, representing an introduction of *R. microplus* that has already gained a strong foothold. The relative ranking of the sensitivity parameters investigated in this study may be different at other ratios of the two species.

It has been shown that very high temperatures (above 42°C) result in a reorientation of the wax molecules covering the eggs resulting in very rapid moisture losses (Less & Beament, 1948; Londt, 1977) The critical temperature for *R. decoloratus* has been determined to be

42°C, but no information could be found for *R. microplus* in the literature. This could present a significant factor driving egg desiccation independent of the standard mechanisms of moisture loss when the wax layer is intact. Modelling this difference would require shorter time steps since average daily temperatures would very rarely reach the critical temperature for the wax layer. Still, a few hours of such extreme heat would be relatively common in South Africa. The effect of micro-climate (and, therefore, overgrazing) might prove significant if the disruption of the wax layer is species dependent.

The current population dynamics model only considers cattle as hosts. Both *R. microplus* and *R. decoloratus* can use alternative hosts with varying degrees of success (Horak et al., 2018). The two species differ in their ability to use alternate hosts, *R. decoloratus* being more of a generalist than *R. microplus* (Horak et al., 2018). Even under minimal utilization of alternate hosts, the occurrence thereof is likely to reduce the dramatic impact of acaricide use on the tick population. Although difficult to estimate in a model, including such an effect is expected to stabilise the population further.

R. microplus is a near-obligate parasite of bovid species (Horak et al., 2018; Osterkamp et al., 1999). Conversely (at least in Africa), *R. decoloratus* frequently utilizes an extensive list of alternative hosts (Horak et al., 2018). The implications are that *R. decoloratus* could better protect itself from exposure to acaricides by having significant populations in refugia (Zeman & Lynen, 2010). An improvement on our model would consider the differences in utilising other hosts from the environment. This has the potential to improve the stability of the tick population and reduce the number of occasional extinctions.

9. CONCLUSION

Our model indicates that the primary advantage of *R. microplus* is its relatively faster development rate. In warm sub-tropical climates, the stage of development that provides *R. microplus* with the most significant advantage is the eggs. This effect will likely diminish significantly in colder climates since *R. microplus* is weakest during winter. Second the faster

egg development is the faster parasitic development. These two factors combine to give *R. microplus* a clear advantage. Our model further suggests that male survival time on the host and the number of males mated per female could be important factors. However, the current scientific knowledge does not clearly show a difference between the two species. Our model also indicates that the timing of the initial introduction could be critical with introductions in spring favouring *R. microplus* most.

10. RECOMMENDATIONS

Farmers should be aware that early introductions of *R. microplus* can go extinct if enough *R. decoloratus* males are available to mate with the *R. microplus* females. Unnecessary dipping in winter should be avoided as it would reduce *R. decoloratus* numbers more than *R. microplus* since the former would be more active.

11. FUTURE RESEARCH

Different male tick survival times can substantially impact the invasion potential of *R. microplus*. Future research to detect if such a difference exists would help understand the interplay better. Experimental studies measuring the relative survival times of the two species are needed.

The relative weakness of *R. microplus* during winter might provide opportunities to promote *R. decoloratus*. This conclusion may be tested first with a model that simulates intensive acaricidal treatment in autumn followed by artificial infestations of *R. decoloratus* a few weeks later. The model results would indicate if the number of artificial infestations required are practically feasible in the field. If it is indeed practically possible, field experiments to confirm the effectiveness of the strategy would be required before wide implementation is attempted.

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13. APPENDICES

Appendix 1: R-code

```
#####
#####
###
###
###
###
###      Setting the parameters
###
###
###
###
###      (Eggs)
###
###
###
###
###
#####
```

```
#####
#This script describes the parameterisation from eggs to hatched larvae
#...of the Single-host tick population model.

#define the folder where all required files are kept on the local PC
folder_address <- "c:/Users/user/Desktop/R/Single-host tick model/"

library(ggplot2)
library(dplyr)
library(MASS) #required for StepAIC function
library(DescTools) #required for PseudoR2()

#####
###                               ###
###                               ###
###      Egg incubation period    ###
###                               ###
###                               ###
###                               ###
#####

#####
### The Nava data has no threshold and degree-days defined. ###
### It has to be calculated here.      ###
#####

#####
###      read data          #####
#####

file_address <- paste(folder_address,"parameterisation/eggs/NavaTb11_Tb13_Tb14_combined.csv",sep="")
df_nava<- as.data.frame(read.csv(file_address, header = TRUE))
df_nava
colnames(df_nava)[1] <- "Index" #fix incorrect import of first column name
df_nava<-df_nava[complete.cases(df_nava),] #remove NA's
df_nava
plot(df_nava$incubation_period)

calc_degree_days <- function(thresh,df) {
  #function to calculate the degree-days of the Nava data
  df$T_diff<- df$T-thresh
  df <- df[df$T_diff>0,]
  df$degree_days <- df$incubation_period*df$T_diff
  return(mean(df$degree_days))
}

calc_degree_days(15.5,df_nava)

#####
### Consider the data from the different authors together  ###
###                               ###
#####

#####
###      read summary data          #####
#####
file_address <- paste(folder_address,"parameterisation/eggs/summary_incubation_period.csv",sep="")
df_incubation<- as.data.frame(read.csv(file_address, header = TRUE))
df_incubation
colnames(df_incubation)[1] <- "Source" #fix incorrect import of first column name
df_incubation

#####
###      calculate incubation periods      ###
###      from degree-days                  ###
#####

pred_incubation_period <- function(Indeks,T){
  #calculates the incubation period based on the cumulative development period above the temperature threshold
  return(df_incubation[Indeks,]$maturity/(T-df_incubation[Indeks,]$threshold))
}

T <- seq(13,30) #the temperature range at Malelane for which we want to predict incubation period
#create predictions for each of the 7 sources
Days <- vector() #create an empty variable to store the incubation period in units of days
for(i in 1 : 7){
  #predicts the incubation period for each of the 7 data sources
  Days <- c(Days,pred_incubation_period(i,T))
}

```

```

Days
df_incubation
df_incubation2 <- df_incubation[,c(1,2,5,8)] #select only the variables that will be used for analysis
df_incubation2 <- df_incubation2[rep(seq_len(nrow(df_incubation2)), each = length(T)), ] #create duplicates to...
#...store incubation periods at different temperatures
df_incubation2
df_incubation2$Incubation_period <- Days

df_incubation2$Incubation_period <- replace(df_incubation2$Incubation_period,
                                           which(df_incubation2$Incubation_period < 0), NA)#change negative values to NA

df_incubation2$Temperature <- rep(T,7) #add the temperature column
df_incubation2

#####
###          plot data          ###
#####

ggplot(df_incubation2,aes(x=Temperature,y=Incubation_period,group=dataset))+
  geom_line(aes(colour=Source,linetype=species),size=2)+
  facet_grid(.~method)

ggplot(df_incubation2,aes(x=Temperature,y=Incubation_period,group=dataset))+
  geom_line(aes(colour=species,linetype=Source),size=2)+
  facet_grid(.~method)

#Fig1
ggplot(df_incubation2,aes(x=Temperature,y=Incubation_period,group=dataset))+
  geom_line(aes(colour=species,linetype=method),size=2)+
  labs(x="Temperature in °C",y="Incubation period in days")+
  facet_grid(.~Source)+
  coord_cartesian(xlim=c(20,31),ylim=c(15,50))

#Fig 2
ggplot(df_incubation2,aes(x=Temperature,y=Incubation_period,group=dataset))+
  geom_line(aes(colour=species,linetype=method),size=2)+
  labs(x="Temperature in °C",y="Incubation period in days")+
  facet_grid(.~Source)+
  coord_cartesian(xlim=c(15,20),ylim=c(40,250))

ggplot(df_incubation2,aes(x=Temperature,y=Incubation_period,group=dataset))+
  geom_line(aes(colour=species,linetype=method),size=2)+
  facet_grid(.~Source)+
  coord_cartesian(xlim=c(15,30),ylim=c(0,250))

#####
#####

#####
###          ###
###          ###
###    Egg hatchability success    ###
###          ###
###          ###
###          ###
#####
####general functions
SatDef <- function(T, RH){
  S <- (1-RH/100)*4.9463*exp(0.0621*T)
  return(S) #Saturation deficit is returned in mmHg
}
RelHum <- function(T, SD){
  RH <- (-100*SD)/(4.9463*exp(0.0621*T))+100
  return(pmax(RH,0)) #Saturation deficit is returned in mmHg
}
RelHum(26,1)
#### end of functions
#####
###          Sutherst          ###
#####
#####
###          function          ###
#####
calc_M_heat <- function(T,D,RH){
  #####Calculates mortality as a result of heat stress
  #w represents daily weight loss of the egg as a %
  #T= temperature in C,
  #D= proportion of development completed
  #RH = relative humidity as a percentage
  #S= saturation deficit in mmHg

```

```

S <- (1-RH/100)*4.9463*exp(0.0621*T)

if(T<0){
  W<-0
} else {
  if(D>0.4015) {
    W <- 0.0291*T +
      T*S*(0.0146+0.1158)*(1-D)*exp(0.3318-8.847*D)+
      0.0203*(S^2)*(D-0.4015)^2
  }else{
    W <- 0.0291*T +
      T*S*(0.0146+0.1158)*(1-D)*exp(0.3318-8.847*D)+
      0.0203*(S^2)
  }
}

return(100/(1+(exp(-0.31*(W-30.58)))))
}

calc_M_cold <- function(T,days_exposed=1,D){
  P<-exp(-0.0255*(1-D)*(21-T)*(days_exposed-(1.55*T)+(22.53*T*D)))
  M<-0.01476*days_exposed*(21-T)+2.55*P*(21-T)*(1-D)/(1+P)^2
  return(M)
}

Sutherst_predict <- function(df1) {
  # Arguments: dataframe
  # Return: An updated dataframe with Sutherst predictions on hatching success
  degree_days <- 264 #264 #degree-days required to mature
  threshold <- 15.5
  max_incubation <- 200
  counter <- 1
  #####
  ##### Subset all eggs that still need to grow #####
  while(nrow(df1[df1$Active==TRUE,])>0) & (counter<max_incubation) { #continue if at least one line is still active
    counter <- counter + 1
    rows <- as.integer(rownames(df1[df1$Active==TRUE,]))

    #mature the eggs
    above_threshold <- df1[rows,]$Temp-threshold
    growth <- pmax(above_threshold/degree_days,0) #calculate proportion developed
    df1[rows,]$Maturity <-df1[rows,]$Maturity+growth

    #let some eggs die from cold
    if(nrow(df1[df1$Temp<=15.5,])>0){
      df1[df1$Temp<=15.5,]$Success <-
        df1[df1$Temp<=15.5,]$Success -
        mapply(calc_M_cold,T= df1[df1$Temp<=15.5,]$Temp,D=df1[df1$Temp<=15.5,]$Maturity)}

    #let some eggs die from dessication
    if(nrow(df1[df1$Temp>15.5,])>0){
      df1[df1$Temp>15.5,]$Success <-
        df1[df1$Temp>15.5,]$Success -
        mapply(calc_M_heat,T= df1[df1$Temp>15.5,]$Temp,D=df1[df1$Temp>15.5,]$Maturity,RH=df1[df1$Temp>15.5,]$RH)}

    if(nrow(df1[df1$Success<=0,])>0){df1[df1$Success<=0,]$Active <- FALSE}
    if(nrow(df1[df1$Maturity>=1,])>0){df1[df1$Maturity>=1,]$Active <- FALSE}

  } #close while
  return(df1)
}

#####
### create empty dataframe ready for predictions (Sutherst) #####
#####

T_vector <- seq(16.67,36.67,by=1) #include all of these Temperature values
SD_vector <- seq(0,13, by=0.5) #include all of these SD values
suth <- expand.grid(T_vector,SD_vector) #create combinations
suth$Success <- 100 #add success (default is 100, mortalities subtract from 100)
suth$Maturity <- 0 #add maturity (default is 0, growth will add)
colnames(suth) <- c("Temp","SD","Success","Maturity")
suth$RH <- RelHum(suth$Temp,suth$SD) #calculate RH from SD
suth$Active <- TRUE #the 'active' column keeps track of unhatched eggs that still require simulation

suth<-Sutherst_predict(suth) #predict hatching success
suth$Success <- pmax(suth$Success,0) #make all negative values 0
suth$Hatch <-suth$Success/100

```

```
suth <- suth %>% mutate(Temp_bins = cut(Temp, breaks = 6))

ggplot(suth, aes(Hatch))+
  geom_density(colour="red")

facet_names <- as_labeller(
  c('(16.7,20]' = "T=(16.7,20]",
    '(20,23.3]' = "T=(20,23.3]",
    '(23.3,26.7]' = "T=(23.3,26.7]",
    '(26.7,30]' = "T=(26.7,30]",
    '(30,33.3]' = "T=(30,33.3]",
    '(33.3,36.7]' = "T=(33.3,36.7]"))

#Fig 3
ggplot(data=suth, aes(x=SD,y=Hatch,group=Temp))+
  geom_line(colour="red")+
  labs(x="Saturation deficit in mm Hg",y="Probability of hatching success")+
  facet_wrap(~Temp_bins,labeller=facet_names)

#####

###          Corson          #####

#####
#####
###          function          #####
#####

Corson_predict <- function(df1) {
  # Arguments: dataframe
  # Return: An updated dataframe with Corson predictions on hatching success (based also on Sutherst development rates)
  degree_days <- 264 #degree-days required to mature
  threshold <- 15.5
  max_incubation <- 200
  counter <- 1
  ##### Subset all eggs that still need to grow #####

  while((nrow(df1[df1$Active==TRUE,])>0) & (counter<max_incubation)) { #continue if at least one line is still active
    counter <- counter + 1
    rows <- as.integer(rownames(df1[df1$Active==TRUE,]))
    #mature the eggs
    above_threshold <- df1[rows,]$Temp-threshold
    growth <- pmax(above_threshold/degree_days,0) #calculate proportion developed
    df1[rows,]$Maturity <-df1[rows,]$Maturity+growth
    df1[rows,]$Day <- df1[rows,]$Day + 1

    print(mean(df1$Success))

    if(nrow(df1[df1$Maturity>=1,])>0){df1[df1$Maturity>=1,]$Active <- FALSE}

    #Sys.sleep(0.01)
  } #close while
  x <- (df1$Day*24*df1$SD)
  df1$Success <- (1- (0.169 + 0.000086*x -(2.1*(10^(-9))))*(x^2))*100
  return(df1)
}
SatDef(15.5,RH=99)
SatDef(35,RH=70)
SatDef(15.5,RH=70)

#####
###          create empty dataframe ready for predictions          #####
#####

T_vector <- seq(16.67,36.67,by=1) #include all of these Temperature values
SD_vector <- seq(0.1392,13.0419, by=1) #include all of these SD values
corson <- expand.grid(T_vector,SD_vector) #create combinations
corson$Day <- 0 #add Day counter
corson$Maturity <- 0 #add maturity (default is 0, growth will add)
corson$Success <- 0 #this will show the proportion hatched
colnames(corson) <- c("Temp","SD","Day","Maturity","Success")
corson$RH <- RelHum(corson$Temp,corson$SD) #calculate RH from SD
corson$Active <- TRUE #the 'active' column keeps track of unhatched eggs that still require simulation
corson
corson<-Corson_predict(corson) #predict hatching success

corson$Hatch <- corson$Success/100
```

```
corson$Hatch <- pmin(corson$Hatch,1)
corson$Hatch <- pmax(corson$Hatch,0)

corson$Success <- pmax(corson$Success,0) #make all negative values 0
corson$Success <- pmin(corson$Success,100) #make 1 the maximum value
corson <- corson %>% mutate(Temp_bins = cut(Temp, breaks = 6))

facet_names <- as_labeller(
  c('16.7,20]' = "T=(16.7,20]",
    '(20,23.3]' = "T=(20,23.3]",
    '(23.3,26.7]' = "T=(23.3,26.7]",
    '(26.7,30]' = "T=(26.7,30]",
    '(30,33.3]' = "T=(30,33.3]",
    '(33.3,36.7]' = "T=(33.3,36.7]"))

#Fig 4
ggplot(corson, aes(x=SD,y=Hatch,group=Temp))+
  geom_line(colour="red")+
  labs(x="Saturation deficit in mm Hg",y="Probability of hatching success")+
  facet_wrap(~Temp_bins,labeller=facet_names)

#####
###                               ###
###                               ###
###                               ###
###      Hitchcock data          ###
###                               ###
###                               ###
###                               ###
#####

#####
###      read data               #####
#####

hitch <- as.data.frame(read.csv("C:/Users/kotzej/OneDrive - Merck Sharp & Dohme, Corp/Desktop/R/Single-host tick model/parameterisation/Eggs to
larvae/Hitchcock_Tbl9.csv", header = TRUE))
hitch$Temp <- (hitch$Temp - 32) * 5/9 #fahrenheit to celsius
hitch$SD <- SatDef(hitch$Temp,hitch$RH) #calc saturation deficit
hitch <- hitch[!is.na(hitch$Success),] #remove rows with no data
hitch$Hatch <- hitch$Success/100
summary(hitch)
hitch <- hitch %>% mutate(Temp_bins = cut(Temp,breaks=6)) #create categorical variable for temperature

#####
###      plot data               #####
#####

ggplot(hitch, aes(Hatch))+
  geom_density(colour="red")

#####
###      model Hitchcock data    #####
#####

mdl.hitch <- glm(Hatch ~ Temp*SD*I(Temp^2)*I(SD^2),
  family=binomial, data = hitch)
summary(mdl.hitch)
step.hitch <- mdl.hitch %>% stepAIC(trace = TRUE)
summary(step.hitch)

PseudoR2(step.hitch, which = "McFadden")
PseudoR2(step.hitch, which = "Nagelkerke")
PseudoR2(step.hitch, which = "CoxSnell")

#####
#create new table to enable interpolation by the model predictions
#####
summary(hitch$Temp)
summary(hitch$SD)

T_vector <- seq(min(hitch$Temp),max(hitch$Temp),length.out=15)
SD_vector <- seq(min(hitch$SD),max(hitch$SD),length.out=15)

hitch_pred <- expand.grid(T_vector,SD_vector) #create combinations
hitch_pred$Hatch <- 0 #create the column, the zero is just a place holder for now
colnames(hitch_pred) <- c("Temp","SD","Hatch")
hitch_pred$RH <- RelHum(hitch_pred$Temp,hitch_pred$SD) #calculate RH from SD

hitch_pred$Hatch <- predict(step.hitch,newdata=hitch_pred,type="response")
hitch_pred <- hitch_pred %>% mutate(Temp_bins = cut(Temp,breaks=6)) #create categorical variable for temperature
```

```

facet_names <- as_labeller(
  c('(16.6,20]' = "T=(16.6,20]",
    '(20,23.3]' = "T=(20,23.3]",
    '(23.3,26.7]' = "T=(23.3,26.7]",
    '(26.7,30]' = "T=(26.7,30]",
    '(30,33.3]' = "T=(30,33.3]",
    '(33.3,36.7]' = "T=(33.3,36.7]"))

ggplot(hitch_pred, aes(x=SD,y=Hatch))+
  geom_line(aes(group=Temp),colour="red")+
  geom_point(data=hitch,aes(x=SD,y=Hatch),colour="blue",shape=1,size=2)+
  facet_wrap(~Temp_bins,labeller=facet_names)

#####
###                               ###
###                               ###
###                               ###
###      Londt data                ###
###                               ###
###                               ###
###                               ###
#####
#####
###      read data                 ###
#####
londt <- as.data.frame(read.csv("C:/Users/kotzej/OneDrive - Merck Sharp & Dohme, Corp/Desktop/R/Single-host tick model/parameterisation/Eggs to
larvae/Londt_graphs.csv", header = TRUE))
londt$SD <- SatDef(londt$Temp,londt$RH) #calc saturation deficit

summary(londt)
str(londt)
londt$Hatch <- londt$Success/100
londt

T_vector <- seq(min(londt$Temp),max(londt$Temp),length.out=6) #include all of these Temperature values
SD_vector <- seq(0,13, length.out=6) #include all of these SD values
summary(londt)
T_vector
londt <- londt %>% mutate(Temp_bins = cut(Temp, breaks = 6)) #create categorical variable for temperature
head(londt)
summary(londt)
#####
###      plot data                 ###
#####
ggplot(londt, aes(Hatch))+
  geom_density(colour="red")

#####
###      Model the Londt data      ###
#####
mdl.londt <- glm(Hatch ~ Temp*SD*I(Temp^2)*(SD^2),
  family=binomial, data = londt)
summary(mdl.londt)
step.londt <- mdl.londt %>% stepAIC(trace = TRUE)
summary(step.londt)

PseudoR2(step.londt, which = "McFadden")
PseudoR2(step.londt, which = "Nagelkerke")
PseudoR2(step.londt, which = "CoxSnell")

#####
###      create empty dataframe ready for predictions (Londt)      ###
#####

T_vector <- seq(min(londt$Temp),max(londt$Temp),length.out=15) #include all of these Temperature values
SD_vector <- seq(min(londt$SD),max(londt$SD), length.out=15) #include all of these SD values

londt_pred <- expand.grid(T_vector,SD_vector) #create combinations
londt_pred$Hatch <- 0
colnames(londt_pred) <- c("Temp","SD","Hatch")
londt_pred$RH <- RelHum(londt_pred$Temp,londt_pred$SD) #calculate RH from SD

londt_pred$Hatch <- predict(step.londt,newdata=londt_pred,type="response")
londt_pred <- londt_pred %>% mutate(Temp_bins = cut(Temp, breaks = 6))
summary(londt_pred)

```

```

facet_names <- as_labeller(
  c('(15,18.8]' = "T=(15,18.8]",
    '(18.8,22.7]' = "T=(18.8,22.7]",
    '(22.7,26.5]' = "T=(22.7,26.5]",
    '(26.5,30.3]' = "T=(26.5,30.3]",
    '(30.3,34.2]' = "T=(30.3,34.2]",
    '(34.2,38]' = "T=(34.2,38]"))

ggplot(londt_pred, aes(x=SD,y=Hatch))+
  geom_line(aes(group=Temp),colour="red")+
  geom_point(data=londt,aes(x=SD,y=Hatch),colour="blue",shape=1,size=2)+
  facet_wrap(~Temp_bins,labeller = facet_names)

#####
###                               ###
###                               ###
###                               ###
###      Nava data                 ###
###                               ###
###                               ###
###                               ###
#####
###      read data                 #####
#####

nava <- as.data.frame(read.csv("C:/Users/kotzej/OneDrive - Merck Sharp & Dohme, Corp/Desktop/R/Single-host tick model/parameterisation/Eggs to
larvae/NavaTbl1_Tbl3_Tbl4_combined.csv", header = TRUE))
summary(nava)
nava <- nava[complete.cases(nava[, 'incubation_period']), ]
#nava <- nava[nava$Land=="Forest",]
summary(nava)

nava <- nava[,c(8,10,11)]
colnames(nava) <- c("Hatch", "Temp", "SD")
summary(nava)
nava <- nava %>% mutate(Temp_bins = cut(Temp, breaks = 6)) #create categorical variable for temperature

#####
###      plot data                 #####
#####

ggplot(nava, aes(Hatch))+
  geom_density(colour="red")

#####
###      Model the Nava data       #####
#####
mdl.nava <- glm(Hatch ~ Temp*SD*I(Temp^2)*I(SD^2),
  family=binomial, data = nava)
summary(mdl.nava)
step.nava <- mdl.nava %>% stepAIC(trace = TRUE)
summary(step.nava)

PseudoR2(step.nava, which = "McFadden")
PseudoR2(step.nava, which = "Nagelkerke")
PseudoR2(step.nava, which = "CoxSnell")
#####
###      create empty dataframe ready for predictions (Nava)      #####
#####

T_vector <- seq(min(nava$Temp),max(nava$Temp),length.out=15) #include all of these Temperature values
SD_vector <- seq(min(nava$SD),max(nava$SD), length.out=15) #include all of these SD values

nava_pred <- expand_grid(T_vector,SD_vector) #create combinations
nava_pred$Hatch <- 0
colnames(nava_pred) <- c("Temp","SD","Hatch")
nava_pred$RH <- RelHum(nava_pred$Temp,nava_pred$SD) #calculate RH from SD

nava_pred$Hatch <- predict(step.nava,newdata=nava_pred,type="response")
nava_pred <- nava_pred %>% mutate(Temp_bins = cut(Temp, breaks = 6))
summary(nava_pred)

facet_names <- as_labeller(
  c('(15.8,17.5]' = "T=(15.8,17.5]",
    '(17.5,19.2]' = "T=(19.2,20.9]",
    '(19.2,20.9]' = "T=(19.2,20.9]",

```

```
`(20.9,22.6]' = "T=(20.9,22.6]",
`(22.6,24.3]' = "T=(22.6,24.3]",
`(24.3,26]' = "T=(24.3,26]"))

ggplot(nava_pred, aes(x=SD,y=Hatch))+
  geom_line(aes(group=Temp),colour="red")+
  geom_point(data=nava,aes(x=SD,y=Hatch),colour="blue",shape=1,size=2)+
  facet_wrap(~Temp_bins,labeller = facet_names)

#####

###      Combine different data sources      ###

#####
#####
###      reorder columns      ###
#####
nava$Source <- "Nava"
londt$Source <- "Londt"
hitch$Source <- "Hitchcock"

summary(nava)
summary(londt)
summary(hitch)

nava[,c(1,2,3,5)]
londt[,c(7,3,6,9)]
hitch[,c(5,1,4,7)]

all <- rbind(nava[,c(1,2,3,5)],
             londt[,c(7,3,6,9)],
             hitch[,c(5,1,4,7)])

ggplot(all, aes(Hatch,group=Source))+
  geom_density(aes(fill=Source),size=1,alpha=0.5)+
  scale_fill_manual( values = c("yellow","red","blue"))+
  labs(x="Proportion hatching success",y="Frequency of observation")

ggplot(all, aes(Hatch,group=Source))+
  geom_density(fill="lightgrey",size=1,alpha=0.5)+
  facet_wrap(~Source)+
  labs(x="Proportion hatching success",y="Frequency of observation")

#####
### create empty dataframe ready for predictions from both Hitchcock and Londt      ###
#####

T_vector <- seq(16,35,length.out=6) #use 6 because the graph will be plotted on 6 panels
SD_vector <- seq(0,13, length.out=13) #include all of these SD values
Source_vector <- c("Hitchcock","Londt")
pred <- expand.grid(T_vector,SD_vector,Source_vector) #create combinations

pred$Hatch <- 0
pred
colnames(pred) <- c("Temp", "SD", "Source", "Hatch")

pred[pred$Source=="Hitchcock",]$Hatch <- predict(step.hitch,newdata=pred[pred$Source=="Hitchcock",],type="response")
pred[pred$Source=="Londt",]$Hatch <- predict(step.londt,newdata=pred[pred$Source=="Londt",],type="response")

#pred <- pred %>% mutate(Temp_bins = cut(Temp, breaks = 6))
summary(pred)

facet_names <- as_labeller(
  c('16' = "T=16",
    '19.8' = "T=19.8",
    '23.6' = "T=23.6",
    '27.4' = "T=27.4",
    '31.2' = "T=31.2",
    '35' = "T=35"))
ggplot(pred, aes(x=SD,y=Hatch,group=Source))+
  geom_line(aes(colour=Source),size = 1.5)+
  scale_color_manual(labels =
    c(expression("Hitchcock;~italic(R.microplus)),expression("Londt;~italic(R.decoloratus))), values = c("red", "blue")) +
  facet_wrap(~Temp,labeller=facet_names)

#...end of egg parameterisation
```

```
#
#
#
#
#
#
#
#####
#####
###
###
###
###
###
###
###
###
###
###
###
###
###
###
###
###
#####
#####

library(DescTools) #plotFdist
library(ggplot2)
library(dplyr)
library(MASS) #required for StepAIC function
library(tidyr) #required for gather()
#####
#####      general functions      #####
#####
SatDef <- function(T, RH){
  S <- (1-RH/100)*4.9463*exp(0.0621*T)
  return(S) #Saturation deficit is returned in mmHg
}
RelHum <- function(T, SD){
  RH <- (-100*SD)/(4.9463*exp(0.0621*T))+100
  return(pmax(RH,0)) #Saturation deficit is returned in mmHg
}
#### end of functions

#####
###
###
###      Questing period (larval survival)      ###
###
###
###
###
#####
#####
###
###
###
###
###      specific math functions      ###
###
###
###
#####
#####
#
#      Sutherst & Bourne function for carry-over effect      #
#
#####
P_larvae_survival_from_P_hatch <- function(H){
  #This function calculates the probability for larval survival as per Sutherst & Bourne equation.
  #The function takes egg hatching success as a fraction
  #The function returns larval survival as a fraction.
  H <- H*100
  L<-(29.1+2.296*H-0.031*H^2+0.000148*H^3)/100 #is the proportion larval survival after 20 days
  return(L)
}
P_larvae_survival_from_P_hatch(H=0.4)
#####
#
#
#      Calculate a new log-mean from the arithmetic mean (Wikipedia)      #
```

```
#
#
#####

calc_meanlog_from_mean <- function(mean_arithmetic,SDlog,doPlot=FALSE){
  #This function adjusts the default values for the lognormal distribution of larval survival obtained from Nava.
  #The function calculates a new logmean whilst maintaining the shape of the curve by keeping the SDlog.
  #A new mean (arithmetic) is supplied that adjusts the curve along the x-axis.
  #The formula is obtained from Wikipedia: https://en.wikipedia.org/wiki/Log-normal_distribution
  logmean_new <- (-SDlog^2/2)+log(mean_arithmetic)
  if(doPlot==TRUE) {
    x_new<-rlnorm(n=100000,meanlog=logmean_new,sdlog=SDlog)
    PlotFdist(x_new,xlim=c(0,180),
      args.boxplot=list(col="bisque",pch.mean=19,col.meanci="white",outpch = NA))
  } #if

  return(logmean_new)
}

#####
#
# Calculate mean larval survival (in days) from P(survive) on Day20 #
#
#####
larvae_survival_time_from_P_survival <- function(P_survive,doPlot=FALSE){
  #Input: P(survive). It is the cumulative probability to survive on Day 20.
  # ..P(survive) is stored in the population matrix and calculated by ...
  # ..Egg_development_and_mortality() according to Sutherst & Bourne method.
  #Output: A mean survival time for the larvae aro of the carry-over...
  # ..effect of hatching success.
  #Comments: The function calculates a new mean larval survival time whilst...
  # ..maintaining the shape of the lognormal curve by keeping the SDlog.
  mean<-qlnorm(p=P_survive,meanlog=calc_meanlog_from_mean(mean_arithmetic = 20,SDlog = SDlog_start,doPlot = FALSE))
  if(doPlot==TRUE) {
    logmean <- calc_meanlog_from_mean(mean_arithmetic=mean,SDlog=SDlog_start,doPlot=TRUE)
    x_new<-rlnorm(n=100000,meanlog=logmean,sdlog=SDlog)
    PlotFdist(x_new,xlim=c(0,180),
      args.boxplot=list(col="bisque",pch.mean=19,col.meanci="white",outpch = NA))
  } #if

  return(mean)
}
SDlog_start = 0.66387
larvae_survival_time_from_P_survival(0.8)

#####
#
# Calculate new logmean #
#
#####

stochastic_larval_survival <- function(n=1,mean_arithmetic,SDlog,doPlot=FALSE){
  #Output: stochastic survival time in days
  #The function calculates a new logmean whilst maintaining the shape of the curve by keeping the SDlog.
  #A new mean (arithmetic) is supplied that adjusts the curve along the x-axis.
  #The formula is obtained from Wikipedia: https://en.wikipedia.org/wiki/Log-normal_distribution
  logmean_new <- (-SDlog^2/2)+log(mean_arithmetic)
  if(doPlot==TRUE) {
    x_new<-rlnorm(n=100000,meanlog=logmean_new,sdlog=SDlog)
    PlotFdist(x_new,xlim=c(0,180),
      args.boxplot=list(col="bisque",pch.mean=19,col.meanci="white",outpch = NA))
  } #if
  return(ceiling(rlnorm(n=n,meanlog=logmean_new,sdlog=SDlog)))
}

stochastic_larval_survival(n=1,mean_arithmetic = 36.83,SDlog=SDlog_start,doPlot=TRUE)
weight_larvae_survival_from_eggs <- 1/3

larval_survival <- function(){
  # Arguments: None.
  # Return: An updated population matrix.
  # Purpose: Determines the time eggs will take to hatch and the rate of failure
  ##### Align all new questing larvae #####
  rows <- as.integer(rownames(tickMatrix[tickMatrix$Stage=="Quest" & tickMatrix$DaysIn==0,]))

  if(length(rows)>0){
    mean_egg <- mapply(larvae_survival_time_from_P_survival,P_survive=tickMatrix[rows,]$CarryOver)
    mean_larvae <- predict.glm(mdl.phal,newdata=list(Temperature=T_month,SD=SD_month),type="response")
  }
}
```

```

mean_master <- mean_egg*weight_larvae_survival_from_eggs +
mean_larvae*(1-weight_larvae_survival_from_eggs)

tickMatrix[rows,]$DaysLeft <-mapply(stochastic_larval_survival,mean_arithmetic=mean_master,SDlog=0.66387)
}
return(tickMatrix)
}
tickMatrix
larval_survival()
tickMatrix <- larval_survival()

#####
###                               ###
###                               ###
###                               ###
###      Analysis of data sources      ###
###                               ###
###                               ###
###                               ###
#####

#####
###                               ###
###                               ###
###                               ###
###      Phalatsi data      ###
###                               ###
###                               ###
###                               ###
#####

#####
###      create data      ###
#####
ph_T <- c(10,15,20,25,30)
ph_RH <- c(35,75)
x <- 0
phalatsi <- expand.grid(ph_T,ph_RH,x,x)
colnames(phalatsi) <- c("Temp","RH","SD","Survival")
phalatsi$SD <- SatDef(T=phalatsi$Temp,RH=phalatsi$RH)
phalatsi$Survival<- c(24,14, 13, 12, 11,
54, 34, 23, 20, 12)

phalatsi
phalatsi <- phalatsi %>% mutate(Temp_bins = cut(Temp,breaks=6)) #create categorical variable for temperature
phalatsi
#####
###      plot data      ###
#####
ggplot(phalatsi, aes(Survival))+
geom_density(colour="red")

#####
###      model Phalatsi data      ###
#####
mdl.phal = lm(log(Survival) ~ Temp+SD+Temp*SD, data=phalatsi)

summary(mdl.phal)
step.phal <- mdl.phal %>% stepAIC(trace = TRUE)
summary(step.phal)
phalatsi$Predicted<-exp(predict(mdl.phal,newdata=phalatsi,type="response"))
phalatsi

#####
#create new table to enable interpolation by the model predictions
#####

T_vector <- seq(min(phalatsi$Temp),max(phalatsi$Temp),length.out=15)
SD_vector <- seq(min(phalatsi$SD),max(phalatsi$SD),length.out=15)

phalatsi_pred <- expand.grid(T_vector,SD_vector) #create combinations
phalatsi_pred$Survival <- 0 #create the column, the zero is just a place holder for now
colnames(phalatsi_pred) <- c("Temp","SD","Survival")
phalatsi_pred$RH <- RelHum(phalatsi_pred$Temp,phalatsi_pred$SD) #calculate RH from SD

phalatsi_pred$Survival <-exp(predict(mdl.phal,newdata=phalatsi_pred,type="response"))
phalatsi_pred <- phalatsi_pred %>% mutate(Temp_bins = cut(Temp,breaks=6)) #create categorical variable for temperature

```

```
head(phalatsi_pred)
facet_names <- as_labeller(
  c('(9.98,13.3]' = "T=(9.98,13.3]",
    '(13.3,16.7]' = "T=(13.3,16.7]",
    '(16.7,20]' = "T=(16.7,20]",
    '(20,23.3]' = "T=(20,23.3]",
    '(23.3,26.7]' = "T=(23.3,26.7]",
    '(26.7,30]' = "T=(26.7,30]"))

ggplot(phalatsi, aes(x=SD,y=Survival))+
  geom_point(colour="blue",shape=1,size=2)+
  geom_line(data=phalatsi_pred,aes(x=SD,y=Survival,group=Temp),colour="red")+
  facet_wrap(~Temp_bins,labeller=facet_names)+
  ylab("Mean larval survival (in days)")+
  coord_cartesian(ylim=c(0,75))

phalatsi
saveRDS(step.phal, "mdlphal") #save the model so it can be imported...
#..by the population model for use.

#####

#####

###          ###
###          ###
###          ###
###      Nava data      ###
###          ###
###          ###
###          ###
#####
#####
###      read data      ###
#####

nava <- as.data.frame(read.csv
  ("INSERT APPROPRIATE FOLDER/NavaTbl1_Tbl6_combined.csv",
   header = TRUE))
summary(nava)
nava <- nava[complete.cases(nava[, 'Quest_surv']), ]
summary(nava)

nava <- nava[, c(2,3,5,6)]
colnames(nava) <- c("Quest_surv", "prop_hatch", "Temp", "SD")
summary(nava)
nava <- nava %>% mutate(Temp_bins = cut(Temp, breaks = 6)) #create categorical variable for temperature

#####
###      plot data      ###
#####
ggplot(nava, aes(Quest_surv))+
  geom_density(colour="red")

#####
###      Model the Nava data      ###
#####
#model without proportion of hatching success
mdl.nava = lm(log(Quest_surv) ~ Temp+SD+Temp*SD, data=nava)
summary(mdl.nava)

mdl.nava <- lm(log(Quest_surv) ~ Temp+SD+prop_hatch,
  data = nava)
summary(mdl.nava)

mdl.nava <- lm(log(Quest_surv) ~ Temp*SD*prop_hatch,
  data = nava)
summary(mdl.nava)

mdl.nava <- lm(log(Quest_surv) ~ Temp*SD*prop_hatch*I(prop_hatch^2),
  data = nava)
summary(mdl.nava)

step.nava <- mdl.nava %>% stepAIC(trace = TRUE)
summary(step.nava)
```

```
PseudoR2(step.nava, which = "McFadden")
PseudoR2(step.nava, which = "Nagelkerke")
PseudoR2(step.nava, which = "CoxSnell")
#####
###          create empty dataframe ready for predictions (Nava)          ###
#####
T_vector <- seq(min(nava$Temp),max(nava$Temp),length.out=15) #include all of these Temperature values
SD_vector <- seq(min(nava$SD),max(nava$SD), length.out=15) #include all of these SD values
prop_hatch_vector <- seq(0,1, length.out=11) #include all of these proportion hatch values
nava_pred <- expand.grid(T_vector,SD_vector,prop_hatch_vector) #create combinations
nava_pred$Quest_surv <- 0
nava_pred
colnames(nava_pred) <- c("Temp","SD","prop_hatch","Quest_surv")
nava_pred$RH <- RelHum(nava_pred$Temp,nava_pred$SD) #calculate RH from SD

nava_pred$Quest_surv <- exp(predict(step.nava,newdata=nava_pred,type="response"))
nava_pred <- nava_pred %>% mutate(Temp_bins = cut(Temp, breaks = 6))
nava_pred <- nava_pred %>% mutate(Hatch_bins = cut(prop_hatch, breaks = 6))

summary(nava_pred)

facet_names <- as_labeller(
  c('(15.8,17.5]' = "T=(15.8,17.5]",
    '(17.5,19.2]' = "T=(19.2,20.9]",
    '(19.2,20.9]' = "T=(19.2,20.9]",
    '(20.9,22.6]' = "T=(20.9,22.6]",
    '(22.6,24.3]' = "T=(22.6,24.3]",
    '(24.3,26]' = "T=(24.3,26]"))

ggplot(nava_pred, aes(x=SD,y=Quest_surv,group=prop_hatch))+
  geom_line(aes(group=Temp+Hatch_bins,colour="red"))+
  geom_point(data=nava,aes(x=SD,y=Quest_surv),colour="blue",shape=1,size=2)+
  facet_wrap(~Temp_bins)+
  coord_cartesian(ylim=c(0,200),xlim=c(0,8))

ggplot(nava_pred, aes(x=SD,y=Quest_surv))+
  geom_line(aes(group=Temp+prop_hatch,colour="red"))+
  geom_point(data=nava,aes(x=SD,y=Quest_surv),colour="blue",shape=1,size=2)+
  facet_wrap(~Hatch_bins)+
  coord_cartesian(ylim=c(0,200),xlim=c(0,8))

ggplot(nava_pred, aes(x=SD,y=Quest_surv))+
  geom_smooth(aes(group=prop_hatch+Temp_bins,colour="red"))+
  geom_point(data=nava,aes(x=SD,y=Quest_surv),colour="blue",shape=1,size=2)+
  facet_grid(Hatch_bins~Temp_bins)+
  coord_cartesian(ylim=c(0,200),xlim=c(0,8))

#####
###          ###
###          ###
###          ###
###          Combine data          ###
###          ###
###          ###
###          ###
#####
#####
#Combine Mastropaolo, Nava and Phalatsi predictions for comparison

T_vector <- seq(min(phalatsi$Temp),max(phalatsi$Temp),length.out=15) #include all of these Temperature values
SD_vector <- seq(min(phalatsi$SD),max(phalatsi$SD), length.out=15) #include all of these SD values
prop_hatch_vector <- 0.8
combined <- expand.grid(T_vector,SD_vector,prop_hatch_vector) #create combinations
colnames(combined) <- c("Temp","SD","prop_hatch")

#c$RH <- RelHum(nava_pred$Temp,nava_pred$SD) #calculate RH from SD

combined$Nava <- exp(predict(step.nava,newdata=combined,type="response"))
combined$Phalatsi <- exp(predict(step.phal,newdata=combined,type="response"))
Mastropaolo <- function(T,SD){
  return(38.81-(1.529*T)-(0.429*SD))
}
combined$Mastropaolo <- Mastropaolo(combined$Temp,combined$SD)
combined <- combined %>% mutate(Temp_bins = cut(Temp, breaks = 6))
head(combined)
```

```
combined_long <- gather(combined,Author,Survival,Nava:Mastropaolo)
head(combined_long)

ggplot(combined_long, aes(x=SD,y=Survival))+
  geom_line(aes(group=interaction(Author,Temp),colour=Author,linetype=Author),size=1)+
  scale_color_manual(labels =
    c(expression("Mastropaolo"~italic(R.microplus)),
      expression("Nava;"~italic(R.microplus)),
      expression("Phalatsi;"~italic(R.decoloratus))),
    values = c("red", "red", "blue")) +
  scale_linetype_manual(labels =
    c(expression("Mastropaolo"~italic(R.microplus)),
      expression("Nava;"~italic(R.microplus)),
      expression("Phalatsi;"~italic(R.decoloratus))),
    values = c("dashed", "solid", "solid")) +
  facet_wrap(~Temp_bins,labeller=facet_names)+
  ylab("Mean larval survival (in days)")+
  coord_cartesian(ylim=c(0,75))
```

```
#####
###                                     ###
###                                     ###
###      Questing success (pickup)      ###
###                                     ###
###                                     ###
###                                     ###
#####
```

```
Popham_pickup <- function(a,r,d){
  return(a*(1-exp(-r*d)))
}
d<-seq(0.1,100,by=0.1)
Popham_pickup(1,0.05,d=d)
plot(Popham_pickup(1,0.05,d=d))

dfP <- as.matrix(expand.grid(r_=c(0.01,0.05,0.1),d_=c(1:90)))
dfP <- as.data.frame(dfP)
str(dfP)
dfP$P_ <- Popham_pickup(a=1,r=dfP$r_,d=dfP$d_)
dfP$r_ <- as.factor(dfP$r_)
```

```
ggplot(dfP,aes(x=d_,y=P_))+
  geom_line(aes(linetype=r_),size=2)+
  labs(x="Density as animal per hectare",y="P(Questing success)",linetype="r value")
```

```
#...end of parameterisation of questing larvae
#
#
#
#
#
#
#####
#####
###                                     ###
###                                     ###
###                                     ###
###                                     ###
###      Setting the parameters      ###
###                                     ###
###                                     ###
###                                     ###
###      (Parasitic stage)      ###
###                                     ###
###                                     ###
###                                     ###
###                                     ###
#####
#####
```

```
library(lubridate) #required to extract year day from date (yday())
library(dplyr)
library(mc2d)
```

```

curve(dpert(x,min=3,mode=5,max=10,shape=6), from = 2, to = 11, lty=3)
curve(dpert(x,min=0.1,mode=0.25,max=0.97,shape=12), from = 0, to = 1, lty=3,ylab="Frequency",xlab="P(larvae removed)")
pert<-as.data.frame(rpert(n=100000,min=0.09,mode=0.25,max=0.54,shape=3))
colnames(pert)<-c("Remove")
ggplot(pert,aes(x=Remove))+
  geom_density()

#####
###          #####
###          #####
###      Addis Ababa          #####
###          #####
###          #####
###          #####
#####

maxSD <- SatDef(T=18, RH=52)
minSD <-SatDef(T=15, RH=82)

dfSolKa <- data.frame(c(maxSD,minSD),c(0,6))
colnames(dfSolKa) <- c("SD","Delay")

cycle_delay <- lm(data=dfSolKa,Delay~SD)
-predict.lm(cycle_delay,newdata=list(SD=SD_month),type="response")
SD_month
saveRDS(cycle_delay, "cycle_delay") #save the model so it can be imported...
#..by the population model for use.

cycle_delay<-readRDS(file="cycle_delay")
#####
###          ###
###          ###
###          ###
###      MRU data          ###
###          ###
###          ###
###          ###
#####
#####
###      read data          ###
#####

MRU <- as.data.frame(read.csv("C:/Users/kotzej/OneDrive - Merck Sharp & Dohme, Corp/Desktop/R/Single-host tick
model/parameterisation/Parasitic/MRU.csv", header = TRUE))
summary(MRU)
MRU$Species <-as.factor(MRU$Species)

climate<- as.data.frame(read.csv("C:/Users/kotzej/OneDrive - Merck Sharp & Dohme, Corp/Desktop/R/Single-host tick model/Weather.csv", header = TRUE))
climate<-climate %>% slice(rep(row_number(), 2)) #allows for numbers going over into the new year
climate
#####
###      functions          ###
#####

meanTemp <- function(startDay,how_long){
  #Input: The day of the year that the process starts and over how many...
  #..days into the future the avg temperature needs to be calculated.
  #Output: The mean of the average temperature for those days.
  x<-seq(startDay,startDay+how_long)#get a sequence of days to answer for
  avg<-round(mean(climate[x,]$Avg),1)#calculate average
  return(avg)
}
MRU$Temp <- mapply(meanTemp,startDay=MRU$Year_day,how_long=21)
MRU
plot(MRU$Days~MRU$Temp)
plot(MRU$Days~MRU$Species)
MRU <- MRU[MRU$Use=="Y",]

#####
###      specify model          ###
#####

mdl <- lm(data=MRU,
  Days~Species+Temp+Species*Temp)

summary(mdl)
step.MRU <- mdl %>% stepAIC(trace = TRUE)
summary(step.MRU)
saveRDS(step.MRU, "mdlMRU") #save the model so it can be imported...
#..by the population model for use.

```



```

    ovi_Corson_results[as.numeric(row.names(category)),5] <-pmin(1,track_x[72])
    ovi_Corson_results[as.numeric(row.names(category)),6] <-pmin(1,track_x[96])
    ovi_Corson_results[as.numeric(row.names(category)),7] <-1
  }
  return(ovi_Corson_results)
}
ovi_Corson_results <- Corson_ovi_duration()
ovi_Corson_results

Corson_ovi <- function(T){
  category <- ovi_Corson_results[ovi_Corson_results$T1<=T & ovi_Corson_results$T2>T, ]
  return(category)
}
Corson_ovi(20)

#####
###          ###
###          ###
###      Londt      ###
###          ###
###          ###
#####
img.file <- system.file(file.path(drive,"38.png"),
  package="ggpubr")
pic_38 <- png::readPNG(source=paste(drive,"38.png",sep=""))

points <- 20
ovi_Londt <- as.data.frame(cbind(days=rep(0,points),rate=rep(0,points),T=rep(38,points)))
ovi_Londt[1,(c(1:2))]<-c(0.01,0.1)
ovi_Londt[2,(c(1:2))]<-c(0.1,1)
ovi_Londt[3,(c(1:2))]<-c(0.5,2)
ovi_Londt[4,(c(1:2))]<-c(0.8,5)
ovi_Londt[5,(c(1:2))]<-c(1,9)
ovi_Londt[6,(c(1:2))]<-c(1.5,12)
ovi_Londt[7,(c(1:2))]<-c(2,17)
ovi_Londt[8,(c(1:2))]<-c(2.5,20)
ovi_Londt[9,(c(1:2))]<-c(3,21)
ovi_Londt[10,(c(1:2))]<-c(4,17)
ovi_Londt[11,(c(1:2))]<-c(5,13)
ovi_Londt[12,(c(1:2))]<-c(6,9)
ovi_Londt[13,(c(1:2))]<-c(7,8)
ovi_Londt[14,(c(1:2))]<-c(8,5)
ovi_Londt[15,(c(1:2))]<-c(10,2.5)
ovi_Londt[16,(c(1:2))]<-c(11,1)
ovi_Londt[17,(c(1:2))]<-c(15,0.1)
ovi_Londt[18,(c(1:2))]<-c(25,0.01)
ovi_Londt[19,(c(1:2))]<-c(26,0.01)
ovi_Londt[20,(c(1:2))]<-c(28,0.01)

mdl_Londt <- glm(rate~days+I(days^2)+I(days^3)+I(days^4)+I(days^5),family=Gamma,data=ovi_Londt)

#mdl_Londt <- gam(rate~s(days,bs="cr"),data=ovi_Londt)
#mdl_Londt <- glm(rate~days,family=Gamma,data=ovi_Londt)
#mdl_Londt <- glm(rate~days+I(days^2)+I(days^3),family=Weibull,data=ovi_Londt)
summary(mdl_Londt)

ovi_Londt$model <- predict(mdl_Londt,newdata=ovi_Londt,type="response")
ovi_Londt$model <- predict(glm(mdl_Londt,newdata=ovi_Londt,type="response")

ggplot(ovi_Londt,aes(x=days,y=rate))+
  background_image(pic_38)+
  geom_point(colour="blue",size=4,alpha=0.4)+
  geom_line(aes(y=model),colour="blue")+
  scale_x_continuous(expand=c(0, 0), limits=c(0, 45)) +
  scale_y_continuous(expand=c(0, 0), limits=c(0, 30))

#####
###          ###
###          ###
###          ###
###      Estrada_Pena      ###
###          ###
###          ###
###          ###
#####

eggs_laid_Estrada <- function(T) {
  eggs <- (-6211.5+(647*T)-(11.21*T^2))
  return(eggs)
}

```

```

}
T<-seq(from=1,to=26,by=1)
eggs_laid_Estrada(T)
plot(eggs_laid_Estrada(T))

Estrada_egg_rate <- function(T) {
  threshold <- 13.2
  Cd <- 372.8
  days <- Cd/(T-threshold)
  return(1/days)
}

Estrada_egg_rate(20)
#####
###          ###
###          ###
###          ###
###      Londt      ###
###          ###
###          ###
###          ###
#####
###      read data      ###
#####
ovi_Londt <- as.data.frame(read.csv(paste(drive,"Ovi_Londt.csv",sep=""), header = TRUE))
summary(ovi_Londt)

par(mfrow=c(1,2))
ggplot(data=ovi_Londt,aes(x=egg,y=female))+
  geom_point()+
  geom_smooth(method=lm,se=FALSE)+
  scale_y_continuous(breaks=c(20,40,60,80,100,120,140,160),
    labels = c(20,40,60,80,100,120,140,160))+
  scale_x_continuous(breaks=c(20,40,60,80,100),
    labels = c(20,40,60,80,100))+

  coord_cartesian(ylim=c(0,160))

ovi_Londt$CEI <- ovi_Londt$egg/ovi_Londt$female

ggplot(data=ovi_Londt,aes(x=egg,y=CEI))+
  geom_point()+
  geom_smooth(method=lm,se=FALSE)+
  # scale_y_continuous(breaks=c(20,40,60,80,100,120,140,160),
  #   labels = c(20,40,60,80,100,120,140,160))+
  scale_x_continuous(breaks=c(20,40,60,80,100),
    labels = c(20,40,60,80,100))+

  coord_cartesian(ylim=c(0,1))

#####
###          ###
###          ###
###          ###
###      Corson      ###
###          ###
###          ###
###          ###
#####

eggs_laid_Corson <- function(T,mass) {
  CEI <- (-159.08+(16.63*T)-(0.3136*T^2))
  eggs<-CEI * mass/100*20 #mass is converted from mg to g
  return(eggs)
}
eggs_laid_Corson(26,300)

mass<-seq(from=220,to=260,by=20)

ovi_Corson <- as.data.frame(cbind(mass,eggs_laid_Corson(T=26,mass)))
ovi_Corson$Author <- "Corson"
colnames(ovi_Corson) <- c("female","egg","Author")

ggplot(data=ovi_Corson,aes(y=egg,x=female))+
  geom_point()+
  geom_smooth(method=lm,se=FALSE)+
  # scale_y_continuous(breaks=c(20,40,60,80,100,120,140,160),
  #   labels = c(20,40,60,80,100,120,140,160))+

```

```
# scale_x_continuous(breaks=c(20,40,60,80,100),
#                     labels = c(20,40,60,80,100))+

coord_cartesian(xlim=c(0,300))
ovi_Corson$female
ovi_Corson$SIRE <- ovi_Corson$egg/(ovi_Corson$female/1000)
ovi_Corson$SIRE

#Combine Estrada & Corson
mass<-seq(220,260,by=20)
T<- seq(15,30,by=1)
eggs_laid_Corson(T=15,mass=200)

df <- expand.grid(mass,T)
colnames(df)<-c("Female", "Temperature")

df$Author <- "Corson"
df$eggs <- 0
df
df$eggs <- mapply(eggs_laid_Corson,T= df$T,mass=df$Female)

df2<-as.data.frame(cbind(rep("NA",16),T))
colnames(df2)<-c("Female", "Temperature")
df2
df2$Author <- "Estrada-Pena"
df2$eggs <- 0
df2$eggs <- eggs_laid_Estrada(T= as.numeric(df2$Temperature))

df3<-as.data.frame(cbind(rep("NA",1),T=26))
colnames(df3)<-c("Female", "Temperature")
df3
df3$Author <- "Spickett & Malan"
df3$eggs <- 3000

df<- rbind(df,df2,df3)
df<- rbind(df,df2)
df
df$Female <- as.factor(df$Female)
df$Temperature <- as.numeric(df$Temperature)

head(df)
str(df)
summary(df)

ggplot(df[df$Author!="Estrada_Pena",],aes(x=Temperature,y=eggs,group=Female))+
  geom_line(aes(colour=Female),size=2)+
  geom_point(data=df[df$Author=="Estrada-Pena",],size=2)

ggplot(df,aes(x=Temperature,y=eggs,group=Female))+
  geom_point(aes(colour=Author,shape=Female),size=3)+
  geom_line(aes(group=interaction(Author,Female)))+
  scale_color_manual(values = c("red", "green", "blue", "black"))+
  labs(shape = "Female weight (mg)",
        y="Number of eggs laid")

#use this one when including df3
ggplot(df,aes(x=Temperature,y=eggs,group=Female))+
  geom_point(aes(colour=Female,shape=Author),size=3)+
  geom_segment(aes(x = 28.5, y = 2500, xend = 26, yend = 3000),
               arrow = arrow(length = unit(0.5, "cm")))+
  geom_line(data=df[df$Author!="Spickett & Malan",],aes(group=interaction(Author,Female)))+
  scale_color_manual(values = c("red", "green", "blue", "black"))+
  labs(colour = "Female weight (mg)",
        y="Number of eggs laid")

#use this one when using only df1 and df2
ggplot(df,aes(x=Temperature,y=eggs,group=Female))+
  geom_point(aes(colour=Female,shape=Author),size=3)+
  geom_line(aes(group=interaction(Author,Female)))+
  scale_color_manual(values = c("red", "green", "blue", "black"))+
  labs(colour = "Female weight (mg)",
        y="Number of eggs laid")

#### Combine Londt, Corson & Estrada_Pena
#####

# 20
```

```
#####
#Londt pic
pic_20 <- png::readPNG(source=paste(drive,"20.png",sep=""))

#Corson
hourly_rate<-Corson_ovi_duration(20)
daily_rate<-(10^(24*log10(1+hourly_rate/24)))-1
daily_rate
df_duration <- as.data.frame(cbind(Days=seq(1:45),
                                   rate=daily_rate[1:45],
                                   Author=rep("Corson",45)))

df_duration2 <- as.data.frame(cbind(Days=seq(1:45),
                                   rate=rep(Estrada_egg_rate(20),45),
                                   Author=rep("Estrada-Pena",45)))

df_duration <- rbind(df_duration,df_duration2)
df_duration$Days <- as.numeric(df_duration$Days)
df_duration$Rate <- as.numeric(df_duration$Rate)
head(df_duration)

ggplot(df_duration,aes(x=Days,y=rate*100,group=Author))+
  background_image(pic_20)+
  geom_point(aes(colour=Author),size=4,alpha=1)+
  scale_x_continuous(expand=c(0, 0), limits=c(0, 45)) +
  scale_y_continuous(expand=c(0, 0), limits=c(0, 20))+
  labs(x="Day of ovipositing",y="Daily proportion of eggs laid (%)")
```

```
#####
# 26
#####
#Londt pic
pic_26 <- png::readPNG(source=paste(drive,"26.png",sep=""))

#Corson
hourly_rate<-Corson_ovi_duration(26)
daily_rate<-(10^(24*log10(1+hourly_rate/24)))-1
daily_rate
df_duration <- as.data.frame(cbind(Days=seq(1:45),
                                   rate=daily_rate[1:45],
                                   Author=rep("Corson",45)))

df_duration2 <- as.data.frame(cbind(Days=seq(1:45),
                                   rate=rep(Estrada_egg_rate(26),45),
                                   Author=rep("Estrada-Pena",45)))

df_duration <- rbind(df_duration,df_duration2)
df_duration$Days <- as.numeric(df_duration$Days)
df_duration$Rate <- as.numeric(df_duration$Rate)
head(df_duration)

ggplot(df_duration,aes(x=Days,y=rate*100,group=Author))+
  background_image(pic_26)+
  geom_point(aes(colour=Author),size=4,alpha=1)+
  scale_x_continuous(expand=c(0, 0), limits=c(0, 45)) +
  scale_y_continuous(expand=c(0, 0), limits=c(0, 30))+
  labs(x="Day of ovipositing",y="Daily proportion of eggs laid (%)")
```

```
#####
###          #####
###          #####
###      Pre-Ovipositing      ###
###          #####
###          #####
#####

#####
###          #####
###          #####
###          #####
###      Hitchcock      ###
###          #####
###          #####
```

```
#####
###
#####
#####
### read data #####
#####
drive <- "C:/Users/user/Desktop/R/Single-host tick model/parameterisation/pre_ovipositing/"
preovi_hitch <- as.data.frame(read.csv(paste(drive,"PreOvi_Hitchcock.csv",sep=""), header = TRUE))

summary(preovi_hitch)
preovi_hitch

ggplot(data=preovi_hitch,aes(x=T,y=Period))+
  geom_point()+
  coord_cartesian(xlim=c(0,38),ylim=c(0,50))

#####
### model data #####
#####

#model without proportion of hatching success
mdl = lm(log(Period) ~ T+I(T^2), data=preovi_hitch)
summary(mdl)

preovi_hitch_pred <- data.frame(matrix(ncol = 2, nrow = 38))
colnames(preovi_hitch_pred) <- c("Period","T")
preovi_hitch_pred$T <- c(1:38)

preovi_hitch_pred$Period <- exp(predict(mdl,newdata=preovi_hitch_pred,type="response"))
preovi_hitch_pred

ggplot(data=preovi_hitch,aes(x=T,y=Period))+
  geom_point(colour="blue",shape=1,size=2)+
  geom_line(data=preovi_hitch_pred,aes(y=Period,x=T),colour="red")+
  coord_cartesian(xlim=c(0,38),ylim=c(0,50))+
  labs(y="Preovipositing period",x="Temperature")

saveRDS(mdl, "mdl_pre_ovi_micro") #save the model so it can be imported...
mdl_pre_ovi_micro <- readRDS(file="mdl_pre_ovi_micro")
mdl_pre_ovi_micro

#####
###
###
###
### Phalatsi
###
###
###
#####
#####
### read data #####
#####
drive <- "C:/Users/user/Desktop/R/Single-host tick model/parameterisation/pre_ovipositing/"
preovi_phalat <- as.data.frame(read.csv(paste(drive,"PreOvi_Phalatsi.csv",sep=""), header = TRUE))

summary(preovi_phalat)
preovi_phalat

ggplot(data=preovi_phalat,aes(x=T,y=Period))+
  geom_point()+
  coord_cartesian(xlim=c(0,38),ylim=c(0,50))

#####
### model data #####
#####

#model without proportion of hatching success
mdl_ph = lm(log(Period) ~ T+I(T^2), data=preovi_phalat)
summary(mdl_ph)

preovi_phalat_pred <- data.frame(matrix(ncol = 2, nrow = 38))
colnames(preovi_phalat_pred) <- c("Period","T")
preovi_phalat_pred$T <- c(1:38)

preovi_phalat_pred$Period <- exp(predict(mdl_ph,newdata=preovi_phalat_pred,type="response"))
preovi_phalat_pred

ggplot(data=preovi_phalat,aes(x=T,y=Period))+
  geom_point(colour="blue",shape=1,size=2)+
  geom_line(data=preovi_phalat_pred,aes(y=Period,x=T),colour="red")+
```

```
coord_cartesian(xlim=c(0,38),ylim=c(0,50))+
labs(y="Preovipositing period",x="Temperature")

saveRDS mdl_ph, "mdl_pre_ovi_deco") #save the model so it can be imported...
mdl_pre_ovi_deco <- readRDS(file="mdl_pre_ovi_deco")
mdl_pre_ovi_deco

#####
###                               ###
###                               ###
###                               ###
###      Snowball                ###
###                               ###
###                               ###
###                               ###
#####
#####
###      read data                #####
#####
drive <- "C:/Users/user/Desktop/R/Single-host tick model/parameterisation/pre_ovipositing/"
preovi_snow <- as.data.frame(read.csv(paste(drive,"PreOvi_Snow.csv",sep=""), header = TRUE))

summary(preovi_snow)
preovi_snow

ggplot(data=preovi_snow,aes(x=T,y=Period))+
  geom_point()+
  coord_cartesian(xlim=c(0,38),ylim=c(0,50))

#####
###      model data                #####
#####

#model without proportion of hatching success
mdl_snow = lm(log(Period) ~ T+I(T^2), data=preovi_snow)
summary(mdl_snow)

preovi_snow_pred <- data.frame(matrix(ncol = 2, nrow = 38))
colnames(preovi_snow_pred) <- c("Period","T")
preovi_snow_pred$T <- c(1:38)

preovi_snow_pred$Period <- exp(predict(mdl_snow,newdata=preovi_snow_pred,type="response"))
preovi_snow_pred

ggplot(data=preovi_snow,aes(x=T,y=Period))+
  geom_point(colour="blue",shape=1,size=2)+
  geom_line(data=preovi_snow_pred,aes(y=Period,x=T),colour="red")+
  coord_cartesian(xlim=c(0,38),ylim=c(0,50))+
  labs(y="Preovipositing period",x="Temperature")

#####
###      combine data                #####
#####
head(preovi_phalat_pred)
preovi_phalat_pred$Author <- "Phalatsi"
head(preovi_hitch_pred)
preovi_hitch_pred$Author <- "Hitchcock"
head(preovi_snow_pred)
preovi_snow_pred$Author <- "Snowball"

preovi_pred <- rbind(preovi_hitch_pred,preovi_phalat_pred,preovi_snow_pred)

head(preovi_phalat)
head(preovi_hitch)
head(preovi_snow)
preovi <- rbind(preovi_hitch,preovi_phalat,preovi_snow)
italic('s')

paste(italic('this text is italic'))

authors <- c("R. microplus; Hitchcock; Laboratory.", "R. decoloratus; Phalatsi; Field.", "R. microplus; Snowball; Field.")
names(authors) <- c("Hitchcock", "Phalatsi", "Snowball")

ggplot(data=preovi,aes(x=T,y=Period))+
  geom_point(colour="blue",shape=1,size=2)+
  geom_line(data=preovi_pred,aes(y=Period,x=T),colour="red")+
  coord_cartesian(xlim=c(5,30),ylim=c(0,40))+
  labs(y="Preovipositing period",x="Temperature")+
  facet_wrap(~factor(Author,levels=c("Hitchcock","Snowball","Phalatsi")),
    ncol=1,labeler = labeller(Author = authors))
```

```
preovi_hitch$Period
preovi_snow$Period
```

```
#####
###                               ###
###                               ###
###                               ###
###      Sutherst predation      ###
###                               ###
###                               ###
###                               ###
#####
#####
###      read data      #####
#####
drive <- "C:/Users/user/Desktop/R/Single-host tick model/parameterisation/pre_ovipositing/"
predation <- as.data.frame(read.csv(paste(drive,"SutherstPredationData.csv",sep=""), header = TRUE))

summary(predation)
str(predation)
predation$y <- predation$y/100+0.0001
plot(predation)

fit.gamma <- fitdist(predation$y, distr = "gamma", method = "mle")
fit.weibull <- fitdist(predation$y, distr = "weibull", method = "mle")
fit.lognormal <- fitdist(predation$y, distr = "lnorm", method = "mle")
fit.log <- fitdist(predation$y, distr = "logis", method = "mle")
fit.beta <- fitdist(predation$y,distr="beta",method="mle")
denscomp(list(fit.beta), legendtext = c("beta distribution"),
  main = "", xlab = "P(predated)",ylim=c(0,2.5),xlim=c(0,1), xlegend = "topright")

summary(fit.beta)

#...end of parameterisation of fecundity and mating stages
#
#
#
#
#
#
#

#...end of all parameterisations
#
#
#
#
#
#
#
#####
#####
###                               ###
###                               ###
###                               ###
###                               ###
###      Functions required to run model      ###
###                               ###
###                               ###
###                               ###
###      (includes setting of constants)      ###
###                               ###
###                               ###
###                               ###
###                               ###
#####
#####
```

```
library(beepr)
library(reshape) #required for untable command in EpanLarvae
library(dplyr) #data rearrangement
library(ggplot2)
```

[illegible]

[illegible]

```

predation <- 0.001
#####
### functions to effect parameters in population model ###
#####

EggDevelopment_and_mortality <- function() {
  # Arguments: None.
  # Return: An updated population matrix.
  # Purpose: Determines the time eggs will take to hatch and the rate of failure

  ##### Align all fresh eggs to enable counting hatch rate #####
  rows <- as.integer(rownames(tickMatrix[tickMatrix$Stage=="Egg" & tickMatrix$DaysIn==0,]))
  tickMatrix[rows,]$Success <- tickMatrix[rows,]$Enter

  ##### Hatch all eggs that are mature #####
  rows <- as.integer(rownames(tickMatrix[tickMatrix$Stage=="Egg" & tickMatrix$DaysIn>=max_incubation_period,]))
  if(length(rows)>0){
    tickMatrix[rows,]$Maturity <- 1 #mature all live eggs that have reached the maximum age
  }

  rows <- as.integer(rownames(tickMatrix[tickMatrix$Stage=="Egg" & tickMatrix$Maturity>=1,]))
  if(length(rows)>0){
    H <- (tickMatrix[rows,]$Success/tickMatrix[rows,]$Enter)*100 #hatch success as percentage
    L <- 29.1 + 2.2296*H - 0.031*H^2 + 0.000148*H^3 #larval survival on day 20, Sutherst & Bourne 2006
    tickMatrix[rows,]$Stage<-"Quest"
    tickMatrix[rows,]$DaysLeft<-999
    tickMatrix[rows,]$Enter<-tickMatrix[rows,]$Success
    tickMatrix[rows,]$Success<-0
    tickMatrix[rows,]$DaysIn <- 0
    tickMatrix[rows,]$Maturity <- 0
    tickMatrix[rows,]$Fail<-0
    tickMatrix[rows,]$CarryOver<-L/100
  } #close if

  #####
  #mature the eggs and kill off some eggs as a result of environmental stress, Sutherst & Bourne
  #####
  # _____ #
  # microplus #
  # _____ #

  ##### Subset all eggs that still need to grow #####
  rows <- as.integer(rownames(tickMatrix[tickMatrix$Stage=="Egg" & tickMatrix$Maturity<1 &
    tickMatrix$Species=="microplus",]))

  if(length(rows)>0){
    #####
    #mature the eggs
    #####
    tickMatrix[rows,]$DaysIn <- tickMatrix[rows,]$DaysIn+1

    ### work out rate of growth using Hitchcock method
    T_todays <- runif(n=length(rows),min=T_today-microclimate_range/2,max=T_today+microclimate_range/2)
    above_threshold <- T_todays-dev_threshold_mic
    above_threshold[above_threshold<0] <- 0

    growth <- above_threshold/degree_days_mic #calculate proportion developed attained

    tickMatrix[rows,]$Maturity <- tickMatrix[rows,]$Maturity + growth #add new growth

    #####
    #kill eggs, function of stress
    #####
    #death from heat
    mort_perc <- mapply(calc_M_heat,T= runif(length(rows),min=T_today-microclimate_range/2,max=T_today+microclimate_range/2),
      D=tickMatrix[rows,]$Maturity,RH=RH_today)

    #death from cold
    if(T_today<=15.5){mort_perc<-
      mapply(calc_M_cold,
        T= runif(length(rows),min=T_today-microclimate_range/2,max=T_today+microclimate_range/2),
        D=tickMatrix[rows,]$Maturity)}

    mort_perc <- oob_squish(mort_perc, range = c(0, 100)) #censor values outside of range that may have occurred stochastically

    tickMatrix[rows,]$Success <- round(tickMatrix[rows,]$Success*(1-mort_perc/100))
    rownames(tickMatrix) <- NULL #ensure fresh ordering to prevent confusion with "rows"
  } #close if

  # _____ #
  # decoloratus #

```

[illegible]

```
#####

#####
### functions to determine parameters ###
#####
Popham_pickup <- function(a=1,r=0.05,d){
  #Required: The stocking density.
  #Output: The proportion of ticks successfully finding a host.
  #Ref: formula to determine questing success by Popham and Garri
  return(a*(1-exp(-r*d)))
}

calc_meanlog_from_mean <- function(mean_arithmetic,SDlog,doPlot=FALSE){
  #This function adjusts the default values for the lognormal distribution of larval survival obtained from Nava.
  #The function calculates a new logmean whilst maintaining the shape of the curve by keeping the SDlog.
  #A new mean (arithmetic) is supplied that adjusts the curve along the x-axis.
  #The formula is obtained from Wikipedia: https://en.wikipedia.org/wiki/Log-normal_distribution
  logmean_new <- (-SDlog^2/2)+log(mean_arithmetic)
  if (doPlot==TRUE) {
    x_new<-rlnorm(n=100000,meanlog=logmean_new,sdlog=SDlog)
    PlotFdist(x_new,xlim=c(0,180),
      args.boxplot=list(col="bisque",pch.mean=19,col.meanci="white",outpch = NA))
  } #if

  return(logmean_new)
}

larvae_survival_time_from_P_survival <- function(P_survive,doPlot=FALSE){
  #Input: P(survive). It is the cumulative probability to survive on Day 20.
  # ..P(survive) is stored in the population matrix and calculated by ...
  # ..Egg development and mortality() according to Sutherst & Bourne method.
  #Output: A mean survival time for the larvae aro of the carry-over...
  # ..effect of hatching success.
  #Comments: The function calculates a new mean larval survival time whilst...
  # ..maintaining the shape of the lognormal curve by keeping the SDlog.
  mean<-qlnorm(p=P_survive,meanlog=calc_meanlog_from_mean(mean_arithmetic = 20,SDlog = SDlog_start,doPlot = FALSE))
  if (doPlot==TRUE) {
    logmean <- calc_meanlog_from_mean(mean_arithmetic=mean,SDlog=SDlog_start,doPlot=TRUE)
    x_new<-rlnorm(n=100000,meanlog=logmean,sdlog=SDlog)
    PlotFdist(x_new,xlim=c(0,180),
      args.boxplot=list(col="bisque",pch.mean=19,col.meanci="white",outpch = NA))
  } #if

  return(mean)
}

stochastic_larval_survival <- function(n=1,mean_arithmetic,SDlog,doPlot=FALSE){
  #Input: The arithmetic mean and the SDlog of larval survival times.
  #Output: stochastic survival times in days following a lognormal distribution
  #The function calculates a new logmean whilst maintaining the shape of.
  # ..the curve by keeping the SDlog.
  #A new mean (arithmetic) is supplied that adjusts the curve along the x-axis.
  #The formula is obtained from Wikipedia:
  #https://en.wikipedia.org/wiki/Log-normal_distribution
  logmean_new <- (-SDlog^2/2)+log(mean_arithmetic)
  if (doPlot==TRUE) {
    x_new<-rlnorm(n=100000,meanlog=logmean_new,sdlog=SDlog)
    PlotFdist(x_new,xlim=c(0,180),
      args.boxplot=list(col="bisque",pch.mean=19,col.meanci="white",outpch = NA))
  } #if
  return(ceiling(rlnorm(n=n,meanlog=logmean_new,sdlog=SDlog)))
}

##### Quest constants #####
#####
mdl.phal<-readRDS(file="mdlphal")
SDlog_start = 0.66387
weight_larvae_survival_from_eggs <- 0.67
r_Popham <- 0.025
#####
### functions to effect parameters in population model ###
#####

Quest_survival <- function(){
  # Arguments: None.
  # Return: An updated population matrix.
  # Purpose: Determines the time eggs will take to hatch and the rate of failure
  ##### Align all new questing larvae #####
}
```

```

rows <- as.integer(rownames(tickMatrix[tickMatrix$Stage=="Quest" & tickMatrix$DaysIn==0,]))

if(length(rows)>0){
  mean_egg <- mapply(larvae_survival_time_from_P_survival,P_survive=tickMatrix[rows,]$CarryOver)
  mean_larvae <- predict.glm(mdl.phal,newdata=list(Temp=T_month,SD=SD_month),type="response")
  mean_master <- mean_egg*weight_larvae_survival_from_eggs +
    mean_larvae*(1-weight_larvae_survival_from_eggs)

  tickMatrix[rows,]$DaysLeft <-mapply(stochastic_larval_survival,mean_arithmetic=mean_master,SDlog=0.66387)

}
return(tickMatrix)
}

QuestFunction <- function() {
  # Arguments: None.
  # Return: An updated population matrix.
  # Purpose: Moves questing larvae to larvae on cattle

  ##### Subset all rows where questing larvae should die of age #####

  rows <- as.integer(rownames(tickMatrix[tickMatrix$Stage=="Quest"&
    tickMatrix$DaysLeft==0,]))
  if(length(rows)>0){

    ##### Old larvae die #####
    tickMatrix<-tickMatrix[-rows,]
  }#close if

  ##### Loop through each camp with cattle #####
  stocked_camps<-unique(stockingMatrix$Camp)

  for (c in 1:length(stocked_camps)){

    #The rate of larvae being succesful (questing to larvae per unit time for a given number of larvae)
    #is proportional to the cattle in that camp (stockingrate),
    #indirectly proportional to the size of the camp and
    #indirectly proportional to the larvae in that camp.
    #A formula is therefore  $r=k*\text{stockingrate}/(\text{questing\_larvae}*ha)$  (where k is a constant of some value)

    stockingrate<-sum(stockingMatrix[stockingMatrix$Camp==stocked_camps[c,]$LSU)
    ha <- 3 #this can be customized per camp in later developments
    questing_larvae<-sum(tickMatrix[tickMatrix$Stage=="Quest"&
      tickMatrix$DaysLeft>0&
      tickMatrix$Location==stocked_camps[c,]$Enter)

    p_success<-Popham_pickup(1,r_Popham,stockingrate/ha)
    #subset rows
    rows <- as.integer(rownames(tickMatrix[tickMatrix$Stage=="Quest"&
      tickMatrix$DaysLeft>0&
      tickMatrix$Location==stocked_camps[c,]]))

    if(length(rows)>0){

      #move successful questers to larvae (on animal)
      newrows<-tickMatrix[rows,]
      newrows$Stage<-"Larvae"
      newrows$DaysLeft<-999
      newrows$DaysIn <- 0
      newrows$Enter<-ceiling(tickMatrix[rows,]$Enter*p_success)

      #select one of the animals in that camp as a host for the larvae
      newrows$Location<-sample(stockingMatrix[stockingMatrix$Camp==stocked_camps[c,]$Sid,nrow(newrows),replace=TRUE)
      #remove succesful questors from questing population
      tickMatrix[rows,]$Enter<-tickMatrix[rows,]$Enter-round((tickMatrix[rows,]$Enter*p_success),digits = 0)
      #add new rows to df
      tickMatrix<-rbind(tickMatrix,newrows)
      tickMatrix <- na.omit(tickMatrix)

    }#close if
  }#for c camps

  ##### Mature all questing larvae by one day #####
  tickMatrix[tickMatrix$Stage=="Quest",]$DaysIn <- tickMatrix[tickMatrix$Stage=="Quest",]$DaysIn +1

  return(tickMatrix)
}

```

```
#####  
#####  
#####  
##### larvae to nymphs to adults #####  
#####  
#####  
#####  
  
#####  
#####  
##### Parasitic phase constants #####  
#####  
cycle_length_micro <- 21  
cycle_length_dec <- 22  
cycle_delay<-readRDS(file="cycle_delay")  
cycle_prop_larvae <- 0.27  
cycle_prop_nymphs <- 0.41  
cycle_prop_adults <- 0.32  
groomed_mode <- 0.25  
groomed_min <- 0.09  
groomed_max <- 0.54  
male_survival_min <- 0  
male_survival_max <- 70  
male_survival_mode <- 42  
female_detachment_unmated <- 1  
  
SetParasiticTime <- function() {  
# Arguments: None.  
# Return: An updated population matrix.  
# Purpose: Determines the time for the parasitic cycle to be completed..  
  
##### Subset all rows of new larvae #####  
rows <- as.integer(rownames(tickMatrix[tickMatrix$Stage=="Larvae"&  
tickMatrix$DaysLeft==999,]))  
if(length(rows)>0){  
  
##### Set failure rate #####  
tickMatrix[rows,]$Fail <- floor(mapply(rpert,n=length(rows),  
min=groomed_min,  
mode=groomed_mode,  
max=groomed_max,  
shape=3))  
tickMatrix[rows,$Success<-tickMatrix[rows,]Enter-tickMatrix[rows,]$Fail  
  
tickMatrix[rows,]Enter<-0  
  
##### microplus ##  
#####+#####  
rows <- as.integer(rownames(tickMatrix[tickMatrix$Stage=="Larvae"&  
tickMatrix$DaysLeft==999 &  
tickMatrix$Species=="microplus",])))  
if (length(rows) > 0){  
tickMatrix[rows,$DaysLeft <-  
round(mnorm(length(rows),cycle_length_micro,1,digits=0)  
tickMatrix[rows,]$CarryOver <- tickMatrix[rows,]$DaysLeft  
}  
  
##### decoloratus #  
#####  
rows <- as.integer(rownames(tickMatrix[tickMatrix$Stage=="Larvae"&  
tickMatrix$DaysLeft==999 &  
tickMatrix$Species=="decoloratus",])))  
if (length(rows) > 0){  
tickMatrix[rows,$DaysLeft <-  
round(mnorm(length(rows),  
cycle_length_dec+  
pmax(predict(cycle_delay,newdata=data.frame(SD=c(SD_today),type="response"))),0)[1]*  
cycle_delay_factor,  
#the 2 lines above adds the predicted delay for decoloratus due to slow drying
```

```

1),digits=0)
tickMatrix[rows,]$CarryOver <- tickMatrix[rows,]$DaysLeft
}
} #close if

return(tickMatrix)
} #close function

Parasitic_die <- function() {
# Arguments: None.
# Return: An updated population matrix.
# Purpose: Removes larvae that didn't succeed

##### Remove all rows where zero larvae succeed #####
rows <- as.integer(rownames(tickMatrix[tickMatrix$Stage=="Larvae"&
tickMatrix$Success<1,]))

if(length(rows)>0){
tickMatrix <- tickMatrix[-rows,]
row.names(tickMatrix) <- NULL
}
return(tickMatrix)
}

Parasitic_mature <- function() {
# Arguments: None.
# Return: An updated population matrix.
# Purpose: Matures larvae and nymphs

##### Subset all larvae and nymphs #####
rows <- as.integer(rownames(tickMatrix[tickMatrix$Stage=="Larvae"|tickMatrix$Stage=="Nymphae",]))
if (length(rows) > 0){

tickMatrix[rows,]$DaysIn <-tickMatrix[rows,]$DaysIn+1
tickMatrix[rows,]$Maturity <-tickMatrix[rows,]$DaysIn/tickMatrix[rows,]$CarryOver
}
return(tickMatrix)
}

Parasitic_molt_larvae <- function() {
# Arguments: None.
# Return: An updated population matrix.
# Purpose: Lets all larvae molt

##### Subset all larvae that should become nymphs #####
rows <- as.integer(rownames(tickMatrix[tickMatrix$Maturity>=cycle_prop_larvae &
tickMatrix$Maturity<(cycle_prop_nymphs+cycle_prop_larvae) &
tickMatrix$Stage=="Larvae",]))

if (length(rows) > 0){
tickMatrix[rows,]$Stage <-"Nymphae"
}
return(tickMatrix)
}

Parasitic_molt_nymphs <- function() {
# Arguments: None.
# Return: An updated population matrix.
# Purpose: Lets all nymphs molt

##### Subset all Nymphs that should become adults #####
rows <- as.integer(rownames(tickMatrix[tickMatrix$Maturity>=(1-cycle_prop_adults) & tickMatrix$Stage=="Nymphae",]))
if (length(rows) > 0){

tickMatrix[rows,]$Stage <-"Adult"
tickMatrix[rows,]$DaysLeft<-999
tickMatrix[rows,]$Enter <- tickMatrix[rows,]$Success
tickMatrix[rows,]$Success <- 0

row.names(tickMatrix) <- NULL
}
return(tickMatrix)
}

Parasitic_micro_males <- function() {
# Arguments: None.
# Return: An updated population matrix.
# Purpose: Sets survival times for males

rows <- as.integer(rownames(tickMatrix[tickMatrix$Stage=="Adult"&
tickMatrix$DaysLeft==999 &

```

```

        tickMatrix$Sex=="male"&
        tickMatrix$Species=="microplus",)))
#calc survival time for males
if (length(rows) > 0){
  tickMatrix[rows,]$DaysLeft <- ceiling(mapply(rpert,length(rows),
        min=male_survival_min - cycle_length_micro,
        mode=male_survival_mode - cycle_length_micro,
        max=male_survival_max - cycle_length_micro,
        shape=3))

  tickMatrix[rows,]$DaysIn <- 0
  tickMatrix[rows,]$CarryOver <- 0
  tickMatrix[rows,]$Maturity <- 0

}
return(tickMatrix)
}

Parasitic_micro_females <- function() {
# Arguments: None.
# Return:  An updated population matrix.
# Purpose:  Sets survival times for females

rows <- as.integer(rownames(tickMatrix[tickMatrix$Stage=="Adult"&
        tickMatrix$DaysLeft==999 &
        tickMatrix$Sex=="female"&
        tickMatrix$Species=="microplus",])))

if (length(rows) > 0){
  tickMatrix[rows,]$DaysLeft <- tickMatrix[rows,]$CarryOver - tickMatrix[rows,]$DaysIn + female_detachment_unmated
  tickMatrix[rows,]$CarryOver <- 0
  tickMatrix[rows,]$Maturity <- 0
  tickMatrix[rows,]$Success <- 0
  tickMatrix[rows,]$Fail <- 0
}

return(tickMatrix)
}

Parasitic_dec_males <- function() {
# Arguments: None.
# Return:  An updated population matrix.
# Purpose:  Sets survival times for males

rows <- as.integer(rownames(tickMatrix[tickMatrix$Stage=="Adult"&
        tickMatrix$DaysLeft==999 &
        tickMatrix$Sex=="male"&
        tickMatrix$Species=="decoloratus",])))

#calc survival time for males
if (length(rows) > 0){
  tickMatrix[rows,]$DaysLeft <- ceiling(male_survival_dec*(mapply(rpert,length(rows),
        min=male_survival_min - cycle_length_dec,
        mode=male_survival_mode - cycle_length_dec,
        max=male_survival_max - cycle_length_dec,
        shape=3)))

  tickMatrix[rows,]$DaysIn <- 0
  tickMatrix[rows,]$CarryOver <- 0
  tickMatrix[rows,]$Maturity <- 0

}
return(tickMatrix)
}

Parasitic_dec_females <- function() {
# Arguments: None.
# Return:  An updated population matrix.
# Purpose:  Sets survival times for females

rows <- as.integer(rownames(tickMatrix[tickMatrix$Stage=="Adult"&
        tickMatrix$DaysLeft==999 &
        tickMatrix$Sex=="female"&
        tickMatrix$Species=="decoloratus",])))

if (length(rows) > 0){
  tickMatrix[rows,]$DaysLeft <- tickMatrix[rows,]$CarryOver - tickMatrix[rows,]$DaysIn + female_detachment_unmated
  tickMatrix[rows,]$CarryOver <- 0
  tickMatrix[rows,]$Maturity <- 0
  tickMatrix[rows,]$Success <- 0
  tickMatrix[rows,]$Fail <- 0
}
}

```

```

return(tickMatrix)
}

#####
#####
#####
#####
##### adults & mating #####
#####
#####
#####
#####
#####
#####
#####
#####
#####
#####
mating_time <- 3 #males are engaged with females for this long
male_maturation <- 3 #number of days males take to become fertile after maturing to adults
females_mated <- 11 #the maximum number of females 1 male can mate
#males_mated is specified as a sensitivity parameter


MatingFunction1 <- function() {
# Arguments: None.
# Return: An updated population matrix.
# Purpose: Lets adult ticks mature. Simulates time lapse of mating ticks (being occupied).

##### Subset adults for aging #####
rows <- as.integer(rownames(tickMatrix[tickMatrix$Stage=="Adult",]))
if (length(rows) > 0){
tickMatrix[rows,$DaysIn <- tickMatrix[rows,$DaysIn + 1
}#close if

#### Change Adult males to Sexually Mature adult males after male_maturation days
rows <- as.integer(rownames(tickMatrix[tickMatrix$Stage=="Adult" &
tickMatrix$Sex=="male" & tickMatrix$DaysIn>=male_maturation,]))
if(length(rows)>0){
tickMatrix[rows,$Stage<-"SexuallyMature"
}#close if

##### Subset already mating males #####
rows <- as.integer(rownames(tickMatrix[tickMatrix$Stage=="SexuallyMature" & tickMatrix$CarryOver>0,]))
if (length(rows) > 0){
tickMatrix[rows,$CarryOver <- tickMatrix[rows,$CarryOver + 1
}#close if

##### Subset already mating females #####
rows <- as.integer(rownames(tickMatrix[tickMatrix$Stage=="Adult" & tickMatrix$CarryOver>0,]))
if (length(rows) > 0){
tickMatrix[rows,$CarryOver <- tickMatrix[rows,$CarryOver + 1
}#close if

##### release mating males for new mating #####
rows <- as.integer(rownames(tickMatrix[tickMatrix$Stage=="SexuallyMature" & tickMatrix$CarryOver>mating_time,]))
if (length(rows) > 0){
tickMatrix[rows,$CarryOver <- 0
}#close if

##### release mating females for new mating #####
rows <- as.integer(rownames(tickMatrix[tickMatrix$Stage=="Adult" & tickMatrix$Sex=="female"
& tickMatrix$CarryOver>mating_time,]))
if (length(rows) > 0){
tickMatrix[rows,$CarryOver <- 0
}#close if

#rownames(tickMatrix) <- 1:nrow(tickMatrix)

return(tickMatrix)
}

MatingFunction2 <- function() {
# Arguments: None.
# Return: An updated population matrix.
# Purpose: Combines males and females for mating

##### Loop through females #####
females <- as.integer(rownames(
tickMatrix[tickMatrix$Stage=="Adult" &
tickMatrix$Sex=="female" &
tickMatrix$Maturity<females_mated &
tickMatrix$CarryOver<1 &
```

[illegible]

[illegible]

```

ovi_Corson <- as.data.frame(read.csv(paste(drive,"Ovi_Corson.csv",sep=""), header = TRUE))
ovi_Corson_results <- ovi_Corson
colnames(ovi_Corson_results) <- c("T1","T2",1:5)
ovi_Corson_results[,c(3:7)]<- 0

Corson_ovi_duration <- function(){
  temperatures<- c(15,17,20,23,25,27,29,31,34,37,39,40,42)
  for (te in temperatures){

    category <- ovi_Corson[ovi_Corson$T1<=te & ovi_Corson$T2>te, ]
    x <- 0 #cumulative proportion of eggs laid
    track_x <- 0
    counter <- 1
    rate <- 0

    while(counter<97){
      rate[counter] <- (category[3]+category[4]*x + category[5]*x^2 + category[6]*x^3 + category[7]*x^4)*10
      x <- as.numeric(x) + as.numeric(rate[counter])

      track_x[counter]<- x
      counter<- counter+1
    }
    ovi_Corson_results[as.numeric(row.names(category)),3] <-pmin(1,track_x[24])
    ovi_Corson_results[as.numeric(row.names(category)),4] <-pmin(1,track_x[48])
    ovi_Corson_results[as.numeric(row.names(category)),5] <-pmin(1,track_x[72])
    ovi_Corson_results[as.numeric(row.names(category)),6] <-pmin(1,track_x[96])
    ovi_Corson_results[as.numeric(row.names(category)),7] <-1
  }
  return(ovi_Corson_results)
}
ovi_Corson_results <- Corson_ovi_duration()

Corson_ovi <- function(T){
  #Returns the line of results from ovi_corson_results corresponding to today's temperature
  category <- ovi_Corson_results[ovi_Corson_results$T1<=T & ovi_Corson_results$T2>T, ]
  return(category)
}

set_clutch_size <- function(){
  # Arguments: None.
  # Return: An updated population matrix.
  # Purpose: determine the number of eggs to be laid
  ##### Subset new females for ovipositing #####
  rows <- as.integer(rownames(tickMatrix[tickMatrix$Stage=="Ovipositing" &
    tickMatrix$DaysLeft==999,]))

  if (length(rows) > 0){
    tickMatrix[rows,]$DaysIn <-0
    tickMatrix[rows,]$DaysLeft <- 6
    tickMatrix[rows,]$Maturity <- 0
    tickMatrix[rows,]$CarryOver <-ceiling((-159.08+(16.63 * T_today)-(0.3136*T_today^2))*
      female_weight*200) #this is the number of eggs to be laid
  }
  return(tickMatrix)
}

Ovipositing <- function(){
  # Arguments: None.
  # Return: An updated population matrix.
  # Purpose: Lets ticks lay eggs
  # All ticks will lay the eggs within 6 days. "Maturity" will keep track of the proportion of total clutch that has been laid.
  # "CarryOver" is the total clutch size that will be laid

  newEggs <- tickMatrix[0,]
  ##### Subset females for ovipositing #####
  rows <- as.integer(rownames(tickMatrix[tickMatrix$Stage=="Ovipositing" &
    tickMatrix$CarryOver>1 &
    tickMatrix$DaysLeft>0,]))

  if (length(rows) > 0){
    tickMatrix[rows,]$DaysIn <-tickMatrix[rows,]$DaysIn+1
    for (female in rows){
      laying_day<-tickMatrix[female,]$DaysIn

      if (laying_day<6){
        lay_prop <- Corson_ovi(T_today)[2+laying_day]
        lay_prop_yesterday<- Corson_ovi(T_today)[2+laying_day-1]
        ifelse(lay_prop_yesterday>1,lay_prop_yesterday<-0,lay_prop_yesterday)
        newRow <- tickMatrix[female,]
        newRow$Stage <- "Egg"
      }
    }
  }
}

```

```
newRow$Enter <- ceiling((lay_prop * tickMatrix[female,]$CarryOver)-(lay_prop_yesterday*tickMatrix[female,]$CarryOver))
newRow$Success <- 0
newRow$Fail <- 0
newRow$DaysLeft<-999
newRow$DaysIn<-0
newRow$Maturity<- 0
newRow$CarryOver<-0.8
newEggs[nrow(newEggs)+1,]<-newRow
}
}
}

##### Subset spent females #####
to_remove <- as.integer(rownames(tickMatrix[tickMatrix$Stage=="Ovipositing" &
tickMatrix$DaysLeft<1,]))

if (length(to_remove) > 0){
tickMatrix <- tickMatrix[-to_remove,]
row.names(tickMatrix)<-1:nrow(tickMatrix)
}

row.names(newEggs) <- NULL#(1+nrow(tickMatrix)):(nrow(tickMatrix)+nrow(newEggs))
tickMatrix <- rbind(tickMatrix,newEggs)
tickMatrix$Enter <- as.numeric(as.character(tickMatrix$Enter))
return(tickMatrix)
}

#####
#####
#####
#####
##### Genetics, acaricide resistance #####
#####
#####
#####
#####
#####
#####
#####
#####
##### Genetic constants #####
Gene_Levels<- seq(1,3)
Gene_Prob_m<-c(0.8,0.15,0.05) #the probability to select that gene in the starting population
Gene_Prob_d<-c(0.9,0.1,0) #as above but for decoloratus

#There are 5 different gene combinations. 1,1 is the most naive and 3,3 is the most resistant
Gene_resistance_max <- 0.9 #the homozygotic resistant tick will be this resistant
Gene_resistance_min <- 0.01 #the homozygotic susceptible tick will be this resistant

temp_x<- c(1:5) #the sum of the gene numbers can only take on values from 2 to 6 (5 different values)
Gene_Effect<-Gene_resistance_min*temp_x^(log(Gene_resistance_max/Gene_resistance_min)/log(5)) #the different potential effects of resistance genes.
Assuming exponential increase.
separate_MatingSterility <- TRUE

##### Acaricide Rx #####
RxDates <- as.Date(c("01/01/2021","08/01/2021","15/01/2021","22/01/2021",
"01/02/2021","08/02/2021","15/02/2021","22/02/2021",
"01/03/2021","08/03/2021","15/03/2021","22/03/2021",
"01/04/2021","15/04/2021","22/04/2021",
"01/05/2021",
"01/06/2021",
"15/07/2021",
"15/08/2021",
"15/09/2021",
"01/10/2021",
"01/11/2021","15/11/2021",
"01/12/2021","08/12/2021","15/12/2021","22/12/2021",
"01/01/2022","08/01/2022","15/01/2022","22/01/2022",
"01/02/2022","08/02/2022","15/02/2022","22/02/2022",
"01/03/2022","08/03/2022","15/03/2022","22/03/2022",
"01/04/2022","15/04/2022","22/04/2022",
"01/05/2022",
"01/06/2022",
"15/07/2022",
"15/08/2022",
"15/09/2022",
"01/10/2022".
```

```
"01/11/2022","15/11/2022",
"01/12/2022","08/12/2022","15/12/2022","22/12/2022",
"01/01/2023","08/01/2023","15/01/2023","22/01/2023",
"01/02/2023","08/02/2023","15/02/2023","22/02/2023",
"01/03/2023","08/03/2023","15/03/2023","22/03/2023",
"01/04/2023","15/04/2023","22/04/2023",
"01/05/2023",
"01/06/2023",
"15/07/2023",
"15/08/2023",
"15/09/2023",
"01/10/2023",
"01/11/2023","15/11/2023",
"01/12/2023","08/12/2023","15/12/2023","22/12/2023")
,"%d/%m/%Y")
```

```
acaricide_constant <- 0.7 #sets the efficacy of each treatment (this is more related to the penetration into
#...the on-host population than to the resistance factor of the acaricide. But it is really combination of both.)
```

[illegible]

```

include_Matrix<-tickMatrix[tickMatrix$Stage=="Quest",]
include_Matrix <- data.frame(include_Matrix %>%
  group_by(Stage,Species,Sex,Location,Gene1,Gene2,Gene1_Male,Gene2_Male,DaysIn,CarryOver,Maturity) %>%
  summarise(Enter = sum(Enter),
    Success = sum(Success),
    Fail = sum(Fail),
    DaysLeft=ceiling(mean(DaysLeft))
  ))
include_Matrix$DaysLeft<-round(include_Matrix$DaysLeft,digits=0)
#include_Matrix$Gene1_Male<-0
#include_Matrix$Gene2_Male<-0
tickMatrix<-rbind(exclude_Matrix,include_Matrix)

rownames(tickMatrix) <- NULL #renumber the rows starting from 1

return(tickMatrix)
}

RemoveDead <- function(){
#remove all rows that have zero ticks alive
rows <- as.integer(rownames(tickMatrix[tickMatrix$Enter==0 & tickMatrix$Success==0,]))
if(length(rows)>0){
  tickMatrix <- tickMatrix[-rows,]
}
return(tickMatrix)
}

RemoveDead2 <- function(){
#remove all rows that have zero ticks alive
rows <- as.integer(rownames(tickMatrix[tickMatrix$DaysLeft<0,]))
if(length(rows)>0){
  tickMatrix <- tickMatrix[-rows,]
}
return(tickMatrix)
}

OrderLines <- function(){
# Arguments: None.
# Return: The population matrix
# Purpose: Sum the number of ticks for each unique combination of Stage, Species etc.
tickMatrix <- na.omit(tickMatrix)
tickMatrix <-data.frame(tickMatrix[order(tickMatrix$Stage),])
rownames(tickMatrix) <- NULL
return(tickMatrix)
}

Expand_Adults <- function() {
# Arguments: None.
# Return: The population matrix
# Purpose: Expand all adults to ensure modelling of individual ticks
rows <- as.integer(rownames(tickMatrix[tickMatrix$Stage=="Adult" & tickMatrix$DaysLeft==999,]))
if (length(rows)>0){

  adultMatrix <-tickMatrix[rows,]
  tickMatrix <- tickMatrix[-rows,]
  row.names(tickMatrix) <- NULL

  adultMatrix <- untable(adultMatrix,num=pmax(adultMatrix$Enter,1))
  adultMatrix$Enter <- 1

  adultMatrix$Sex <- sample(Sex_Levels,nrow(adultMatrix),replace=TRUE,prob=Sex_Prob)

  row.names(adultMatrix) <- NULL

  tickMatrix <- rbind(tickMatrix,adultMatrix)
  row.names(tickMatrix) <- NULL
}
return(tickMatrix)
}

#####
FixStockingSchedule <- function() {
# Arguments: None.
# Return: The population matrix of cattle in camps
# Purpose: Construct the initial stocking rates of cattle in camps.

stockingSchedule<-array(rep(c(cattle_id,
  rep(1,length(cattle_id)),
  rep(camps[1],length(cattle_id))),timespan),
  dim=c(length(cattle_id), 3,timespan))

```

```

colnames(stockingSchedule) <- c("id", "LSU", "Camp")

y<-NULL
for(i in 1:length(camps)){
  x<-rep(camps[i],graze_cycle*length(cattle_id))
  y<-c(y,x)
}
if (timespan*length(cattle_id)/length(y)>1){y<-rep(y,ceiling(timespan*length(cattle_id)/length(y)))}
y<-y[1:(timespan*length(cattle_id))]

stockingSchedule[,3,]<-y
return(stockingSchedule)
}

stockCamp <- function() {
  stockingMatrix<-data.frame(stockingSchedule[,t])
  stockingMatrix$Id <- as.numeric(as.character(stockingMatrix$Id))
  stockingMatrix$LSU <- as.numeric(as.character(stockingMatrix$LSU))
  stockingMatrix[c(41:60),]$Camp<-rep(camps[ifelse(match(stockingMatrix[1,]$Camp,camps)+10>18,
    match(stockingMatrix[1,]$Camp,camps)+10-18,
    match(stockingMatrix[1,]$Camp,camps)+10)],20)

  return(stockingMatrix)
}

InitialPopulation <- function() {
  # Arguments: None.
  # Return: The population matrix
  # Purpose: Construct the initial population matrix for the ticks.
  initialPopSize <- tick_Population
  nr_groups<-tick_groups #the number of rows

  tickMatrix <- data.frame(matrix(0, nrow=nr_groups, ncol=length(traitList)))
  colnames(tickMatrix) <- traitList

  ##### Stage #####

  tickMatrix$Stage <- factor(tickMatrix$Stage, levels = Stage_Levels)
  tickMatrix[, 'Stage'] <- sample(Stage_Levels, nr_groups, replace=TRUE, prob = Stage_Prob)
  tickMatrix$Stage <- factor(tickMatrix$Stage, levels = Stage_Levels)

  ##### Numbers #####
  tickMatrix$Enter<- rep(round(initialPopSize/nr_groups),nr_groups)
  tickMatrix$Success<- 0
  tickMatrix$Fail<-0
  tickMatrix$CarryOver <- 0.1

  if (nrow(tickMatrix[tickMatrix$Stage=="Egg"|tickMatrix$Stage=="Quest",])>0){
    tickMatrix[tickMatrix$Stage=="Egg"|tickMatrix$Stage=="Quest",]$CarryOver<-0.8}
  if (nrow(tickMatrix[tickMatrix$Stage=="Adult"|tickMatrix$Stage=="SexuallyMature",])>0){
    tickMatrix[tickMatrix$Stage=="Adult"|tickMatrix$Stage=="SexuallyMature",]$CarryOver<-0}

  ##### Species #####
  tickMatrix$Species <- factor(tickMatrix$Species, levels = Species_Levels)
  tickMatrix$Species <- sample(c(rep(Species_Levels[1],nr_groups*Species_Prob[1]),rep(Species_Levels[2],nr_groups*Species_Prob[2])),
    nr_groups,replace=FALSE)

  ##### Sex #####
  tickMatrix$Sex <- factor(tickMatrix$Sex, levels = Sex_Levels)
  tickMatrix$Sex <- sample(Sex_Levels, nr_groups,replace=TRUE,prob=Sex_Prob)

  Stage_Levels
  ##### Location #####
  ticks_in_camps<- tickMatrix[tickMatrix$Stage=="Egg"|
    tickMatrix$Stage=="Quest"|
    tickMatrix$Stage=="PreOvi"|
    tickMatrix$Stage=="Ovipositing",]
  Location_Levels<- camps
  ticks_in_camps$Location <- sample(Location_Levels, size=nrow(ticks_in_camps),replace=TRUE)

  ticks_on_cattle<- tickMatrix[tickMatrix$Stage=="Larvae"|
    tickMatrix$Stage=="Nymphae"|
    tickMatrix$Stage=="Adult"|
    tickMatrix$Stage=="SexuallyMature",]
  Location_Levels<- cattle_id
  ticks_on_cattle$Location <- sample(Location_Levels, nrow(ticks_on_cattle),replace=TRUE)

  tickMatrix<-rbind(ticks_in_camps,ticks_on_cattle)

  ##### DaysLeft #####

```



```
#####
#####

Save_results2 <- function(){
  tempResults2[t,'Day']<-t
  tempResults2[t,'dec']<- sum(tickMatrix[tickMatrix$Stage=="Adult"&tickMatrix$Species=="decoloratus",]$Enter)
  tempResults2[t,'micro']<- sum(tickMatrix[tickMatrix$Stage=="Adult"&tickMatrix$Species=="microplus",]$Enter)
}

Save_results <- function(){
  #save results of the day that has passed
  tempResults[t,'Species'] <- "microplus"
  tempResults[t,'Egg']<-sum(tickMatrix[tickMatrix$Stage=="Egg"&tickMatrix$Species=="microplus",]$Success)+
    sum(tickMatrix[tickMatrix$Stage=="Egg"&tickMatrix$Species=="microplus",]$Fail)
  tempResults[t,'Quest']<-sum(tickMatrix[tickMatrix$Stage=="Quest"&tickMatrix$Species=="microplus",]$Enter)
  tempResults[t,'Larvae']<-sum(tickMatrix[tickMatrix$Stage=="Larvae"&tickMatrix$Species=="microplus",]$Enter)+
    sum(tickMatrix[tickMatrix$Stage=="Larvae"&tickMatrix$Species=="microplus",]$Success)+
    sum(tickMatrix[tickMatrix$Stage=="Larvae"&tickMatrix$Species=="microplus",]$Fail)
  tempResults[t,'Nymphae']<-sum(tickMatrix[tickMatrix$Stage=="Nymphae"&tickMatrix$Species=="microplus",]$Fail)+
    sum(tickMatrix[tickMatrix$Stage=="Nymphae"&tickMatrix$Species=="microplus",]$Success)
  tempResults[t,'Adult']<-sum(tickMatrix[tickMatrix$Stage=="Adult"&tickMatrix$Species=="microplus",]$Enter)
  tempResults[t,'SexuallyMature']<-sum(tickMatrix[tickMatrix$Stage=="SexuallyMature"&tickMatrix$Species=="microplus",]$Enter)
  tempResults[t,'Ovipositing']<-sum(tickMatrix[tickMatrix$Stage=="Ovipositing"&tickMatrix$Species=="microplus",]$Enter)

  tempResults_dec[t,'Species'] <- "decoloratus"
  tempResults_dec[t,'Egg']<-sum(tickMatrix[tickMatrix$Stage=="Egg"&tickMatrix$Species=="decoloratus",]$Success)+
    sum(tickMatrix[tickMatrix$Stage=="Egg"&tickMatrix$Species=="decoloratus",]$Fail)
  tempResults_dec[t,'Quest']<-sum(tickMatrix[tickMatrix$Stage=="Quest"&tickMatrix$Species=="decoloratus",]$Enter)
  tempResults_dec[t,'Larvae']<-sum(tickMatrix[tickMatrix$Stage=="Larvae"&tickMatrix$Species=="decoloratus",]$Enter)+
    sum(tickMatrix[tickMatrix$Stage=="Larvae"&tickMatrix$Species=="decoloratus",]$Success)+
    sum(tickMatrix[tickMatrix$Stage=="Larvae"&tickMatrix$Species=="decoloratus",]$Fail)
  tempResults_dec[t,'Nymphae']<-sum(tickMatrix[tickMatrix$Stage=="Nymphae"&tickMatrix$Species=="decoloratus",]$Fail)+
    sum(tickMatrix[tickMatrix$Stage=="Nymphae"&tickMatrix$Species=="decoloratus",]$Success)
  tempResults_dec[t,'Adult']<-sum(tickMatrix[tickMatrix$Stage=="Adult"&tickMatrix$Species=="decoloratus",]$Enter)
  tempResults_dec[t,'SexuallyMature']<-sum(tickMatrix[tickMatrix$Stage=="SexuallyMature"&tickMatrix$Species=="decoloratus",]$Enter)
  tempResults_dec[t,'Ovipositing']<-sum(tickMatrix[tickMatrix$Stage=="Ovipositing"&tickMatrix$Species=="decoloratus",]$Enter)
}

#####
#####
#
# Population demographics and parameters
#
#####
#####
camps<-c("A1","A2","A3","A4","A5","B1","B2","B3","B4","B5","C1","C2","C3","C4","C5","E1","E2","E3")

graze_cycle <- 8 #time spent in each camp

cattle_id<- seq(1,60)
cattle_LSU <- rep(1,length(cattle_id))
tick_Population<-150000
tick_groups<-9000 #the number of distinct tick groupings
Stage_Levels<-c("Egg","Quest","Larvae","Nymphae",
  "Adult","SexuallyMature","PreOvi","Ovipositing")
Stage_Prob <- c(1,0,0,0,
  0,0,0,0)

Stage_Prob<-c(0.6,0.25,0,0,
  0.15,0,0,0)
traitList <- c('Stage','Species','Sex','Location','Gene1','Gene2','Gene1_Male','Gene2_Male',
  'Enter','Success','Fail','DaysLeft',
  'DaysIn','Maturity','CarryOver')
Species_Levels<- c("decoloratus","microplus")
Species_Prob<-c(0.7,0.3)
release_over <- 60
release_every <- 2

Sex_Levels<- c("male","female")
ratio_f_to_m <- 1:1 # 1.36:1 female:male Davey & Cooksey 1988
Sex_Prob<-c(1-ratio_f_to_m/(ratio_f_to_m+1),ratio_f_to_m/(ratio_f_to_m+1))
#####
#...end of functions
#

#####
#####
```

```
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#####
#####
#####
### system settings   ###
#####
options(dplyr.summarise.inform=F) #silence runtime feedback from summarise function

#####
#
# Run model:
#
#####
#####
### Run once before all iterations ###
#####

timespan <- 365*5
years<-ceiling(timespan/365)

ImportClimateData()
climate<-climate %>% slice(rep(row_number(), years)) #repeats the climate data to have enough years to cover the timespan

combinations <- 1:nrow(sensitivity_Combos) #the list of combinations of parameters for sensitivity analysis

keep_tally_of<-c(Stage_Levels,c("Species"))
#####
### iteration settings ###
#####

iterations <- 5
resultsMatrix <- array(data=0, dim=c(timespan,length(keep_tally_of)+1,iterations,length(combinations)))
colnames(resultsMatrix) <- c(keep_tally_of,"Rx")
resultsMatrix_dec <- resultsMatrix
RESULTS <- data.frame(Day=NA,microplus=NA,decoloratus=NA,iteration=NA,combination=NA)[0,]
saveDay <- c(365,730)

for(combo_counter in combinations){
  SensitivityAdjustment(combo_counter) #adjusts the values of the parameters involved in the sensitivity analysis

for(i in 1:iterations) {
  tempResults <- array(data=0, dim=c(timespan,length(keep_tally_of)+1))
  colnames(tempResults) <- c(keep_tally_of,"Rx")
  tempResults_dec <- tempResults
  #####
  tempResults2 <- as.data.frame(array(data=NA, dim=c(timespan,3)))
  colnames(tempResults2) <- c("Day","dec","micro")
  #####
  dateDay <-startDate

  SeasonalAdjustment()
  T_today<-T_today+climate_T
  RH_today<-RH_today

  print(paste('Running iteration', i, 'of parameter combination set', combo_counter))
  flush.console()
  t<-1
  stockingSchedule<-FixStockingSchedule()
  stockingMatrix<-stockCamp()
  tickMatrix <- InitialPopulation()
  tickMatrix <- InitialPopulation2()
  tickMatrix <- InitialPopulation3()
  tickMatrix <- Expand_Adults()

  startMatrix <-tickMatrix
```

```

tickMatrix <- startMatrix[0,]

startMatrix_rows <- as.integer(row.names(startMatrix))
release_seq <- c(0,seq(from=release_every, to=release_over, by=release_every))
release_nr <- floor(nrow(startMatrix)/length(release_seq))
tickMatrix <- release_more()
tickMatrix <- SumLines()
tickMatrix <- OrderLines()

for(t in 1:timespan) { # Loop through time

  if (t %in% release_seq){
    tickMatrix <- release_more()
    tickMatrix <- SumLines()
    tickMatrix <- OrderLines()
  }

  print(paste('Day', t))

  tickMatrix <- EggDevelopment_and_mortality()
  tickMatrix <- OrderLines()
  tickMatrix <- EggPredation()
  tickMatrix <- OrderLines()

  tickMatrix <- Quest_survival()
  tickMatrix <- QuestFunction()
  tickMatrix <- OrderLines()

  tickMatrix <- SetParasiticTime()
  tickMatrix <- OrderLines()
  tickMatrix <- Parasitic_die()
  tickMatrix <- Parasitic_mature()
  tickMatrix <- Parasitic_molt_larvae()
  tickMatrix <- Parasitic_molt_nymphs()
  tickMatrix <- Expand_Adults()

  if (nrow(tickMatrix[tickMatrix$Stage=="Adult",])>0){tickMatrix[tickMatrix$Stage=="Adult",]$Sex<-"male"}
  tickMatrix <- Parasitic_micro_males()
  tickMatrix <- Parasitic_micro_females()
  tickMatrix <- Parasitic_dec_males()
  tickMatrix <- Parasitic_dec_females()

  tickMatrix <- OrderLines()
  tickMatrix <- MatingFunction1()
  tickMatrix <- MatingFunction2()
  tickMatrix <- drop_engorged()

  tickMatrix <- OrderLines()
  tickMatrix <- Preovipositing_survival()
  tickMatrix <- Preovipositing()

  tickMatrix <- OrderLines()
  tickMatrix <- set_clutch_size()
  tickMatrix <- Ovipositing()

  if(dateDay %in% RxDates){
    tickMatrix <- Rx_with_acaricide()
    tempResults[t,'Rx'] <- "TRUE"
    tempResults_dec[t,'Rx'] <- "TRUE"
  } else {
    tempResults[t,'Rx'] <- "FALSE"
    tempResults_dec[t,'Rx'] <- "FALSE"
  }

  tickMatrix <- OrderLines()
  tickMatrix <- SumLines()
  tickMatrix <- RemoveDead()
  tickMatrix <- RemoveDead2()

  #move time forward
  tickMatrix$DaysLeft <- tickMatrix$DaysLeft-1
  dateDay <- dateDay +1
  SeasonalAdjustment()

  stockingMatrix <- stockCamp() #move cattle for the next day
  tickMatrix <- tickMatrix[tickMatrix$DaysLeft>1,] #remove dead ticks from tickMatrix

  Save_results()

```

```
Save_results2()
} # close "for", t timespan

RESULTS[nrow(RESULTS)+1,]<-c(saveDay[1],
                             sum(as.integer(tempResults[saveDay[1],c(1:8)])),
                             sum(as.integer(tempResults_dec[saveDay[1],c(1:8)])),
                             i,
                             combo_counter)
RESULTS[nrow(RESULTS)+1,]<-c(saveDay[2],
                             sum(as.integer(tempResults[saveDay[2],c(1:8)])),
                             sum(as.integer(tempResults_dec[saveDay[2],c(1:8)])),
                             i,
                             combo_counter)
write.csv(RESULTS,paste("Results",combo_counter,".csv"))
} # close "for", i iteration

} # close "for", combo_counter
beep(4)
```