Master's thesis

NTNU
Norwegian University of Science and Technology
Faculty of Natural Sciences
Department of Biology

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Modelling activity of terrestrial insects in differet temperature and water availability scenarios

Master's thesis in Natural Science with Teacher Education
Supervisor: Irja Ida Ratikainen
Co-supervisor: Cameron K. Ghalambor
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Abstract

Climate change is predicted to alter the external environment of living organisms. For terrestrial ectotherms, the combined impacts of warmer temperatures and altered precipitation regimes are likely to represent a fundamental challenge. A large body of research has focused on the effect of temperature. Less is known about the effects of altered precipitation patterns and the combined effect of these two abiotic stressors on terrestrial organisms' performance. Temperature and water availability can influence insects' internal energy and water budget, and thermo- and hydro regulation can be mediated through behavioural decisions of activity and habitat choice. Thermal performance curves (TPC), which describe the temperature-dependent performance of a trait, have often been the conceptual framework used to predict performance from a physiological tolerance perspective. However, this framework has not been extended to include effects of precipitation and humidity.

In this thesis, I develop a theoretical model where a combination of stochastic dynamic programming and simulations is used to investigate the state-dependent activity choices of a generic individual female insect over the breeding season. This method allows the investigation of insect's behavioural strategies and the realized patterns of activity, survival and reproduction under different temperature and water availability scenarios.

My results predict that external environmental conditions of temperature and water availability interact with internal water and energy states in shaping the optimal behavioural strategies. Low water availability is negatively impacting fitness, and warm and dry conditions are predicted to be especially severe for the organisms from a hydrational and energetic perspective. Individuals optimized for and simulated through this scenario display a more semelparous life history strategy, reproducing earlier and in lower states. Behavioural strategy is influencing fitness, as physiological tolerance in the model is the same for all individuals in all environments, indicating a role of behavioural strategy when predicting consequences of climate change. The value of an adapted behavioural strategy is predicted to be most valuable in harsh dry conditions. My work is a starting point, including the role of behaviour and a joint hydrational and thermal perspective in the theoretical framework for predicting performance. To be able to predict whole-organism performance in altered climates, further work should focus on integrating more traits and stressors.

Sammendrag

Klimaendringer er forventet å endre de ytre omgivelsene til levende organismer. For terrestriske ektoterme dyr vil den kombinerte effekten av høyere temperaturer og endrede nedbørsmøster kunne utgjøre en fundamental utfordring. En stor mengde forskning har studert effekten av temperatur. Vi har mindre kunnskap om effekten av endrede nedbørsmønstre og den kombinerte innvirkningen av de to aboitiske faktorene på terrestriske organismers prestasjon. Temperatur og vanntilgang kan påvirke insekters indre energi- og vannbalanse og termo- og hydroregulering kan foregå gjennom adferdsmessige beslutninger om aktivitet og valg av habitat. Termiske prestasjonskurver, som beskriver den temperaturavhengige ytelsesevnen til en egenskap, har ofte vært det teoretiske rammeverket man har brukt for å predikere organismers prestasjon ut fra fysiologisk toleranse. Dette rammeverket har imidlertid ikke blitt utvidet til å inkludere effekten av nedbør og fuktighet.

I denne masteroppgaven utvikler jeg en teoretisk modell. En kombinasjon av stokastisk dynamisk programmering og simularinger gjør det mulig å undersøke valg av aktivitet for et huninnsekt gjennom den reproduktive sesongen, der valgene baseres på insektets indre tilstand og ytre forhold i dets omgivelser. Metoden gjør det mulig å undersøke insektets adferds strategier og de realiserte møstrene for aktivitet, overlevelse og reproduksjon under scenarioer med ulik temperatur og vanntilgang.

Mine resultater predikerer at de ytre miljøfaktorene temperatur og vanntilgang sammen med intern vann- og energitilstand former de optimale adferdsmessige strategiene. Liten vanntilgang har negativ påvirkning på fitness og varme og tørre forhold er predikert å være spesielt alvorlige for individene gjennom påvirkningen på indre vann og energitilstand. Individer som er optimalisert for og simulert gjennom dette senarioet viste en mer semelparøs livsstrategi, med tidligere reproduksjon for lavere indre tilstander. Fysiologisk toleranse er i modellen lik for alle individer i alle miljø, så når ulike strategier gir ulik fitness, indikerer dette at adferdsstrategi spiller en rolle når vi skal forutsi konsekvensene av klimaendringer. Verdien av å ha en tilpasset strategi er predikert å være mest verdifull under krevende tørre forhold. Min oppgave er en start på arbeidet med å inkludere verdien av adferd og et kombinert hydrologisk og termisk perspektiv i det teoretiske rammeverket for å predikere organismers prestasjon. Videre forskning bør fokusere på å integrere flere egenskaper og miljøfaktorer for å gjøre det mulig å predikere organismers ytelse i endrede klimatiske forhold.

Preface

This master thesis is written at the Institute of Biology at NTNU as the final part of my science teacher education. Many aspects of the work and process have been relevant to my future career in teaching natural science, biology and mathematics.

During this project I have been given the opportunity to combine my interdisciplinary background in math and biology. Taking advantage of knowledge, competencies and ways of thinking from different disciplines is an important skill to meet the new curriculum's aims with a high focus on interdisciplinary teaching. Developing a theoretical model has also given me insight into the use of theoretical models, and working with my supervisors has taught me more about how theoretical science and empirical studies interact to inspire each other. Using models is part of the high school curriculum of both practical math and biology. When teaching mathematics, it is common to inspire the use of more representations of a problem. This master serves as a good example of moving back and forth between the real-world biology of the problem, mathematical equations to describe it and representation of the problem as code.

One aim of this thesis was to improve the programming skills I gained from an introductory course in computer science and Phyton programming. Through this work, I have become more trained in the logic and creative skill of coding, learning to work with larger coding structures as well as valuable programs and platforms for text compiling, storing and sharing. As programming is a part of the new curriculum, improving my skills and exploring the creative world of coding is helpful to be able to incorporate it into my teaching and supervising of my students.

The new curriculum in science and math has increased focus on inquiry-based teaching. My aim as a teacher is to guide students in their learning process to develop a growth mindset where they are led not by the fear of failing but by the possibility of developing and acquiring new knowledge and skills. This thesis and my supervisors have challenged me to aim at this growth mindset and to be more inspired by curiosity and the desire to gain insight and learn new skills rather than the fear of a new problem, being out of control and the chance of failing. This is a valuable experience that makes me more competent at planning and guiding students in the process of problem-solving and inquiry-based learning.

Several people deserve to be thanked for their contribution, help and support in the process. First, thanks to my supervisors, Irja Ida Ratikainen and Cameron K. Ghalambor, for sharing your knowledge, ideas, proofreading and guiding me through the process. Your contagious enthusiasm, kindness and curiosity have not only helped me with this thesis but inspired me to become a better teacher. A special thanks to Irja for giving me the courage to learn a new method and a new programming language. Thanks for both the academic advice and coding guidance. And to Cameron, for your never-ending enthusiasm and willingness to share your broad knowledge. Thanks to both of you for inviting me into your professional community and letting me do a small piece of work in your field of science. I always enjoyed our meetings.

A thanks also to Christianne, André and Mari for being my stochastic dynamic modelling fellowship this semester. Thanks for the inspiration and tips in learning and becoming more familiar with this new method and way of thinking. A special thanks to Christianne for your willingness to share advice on Julia language and script structuring.

I have to thank my fellow students, friends and family for always giving me invaluable moral support and enjoyable breaks in between the work sessions to load the batteries.

Last, a huge thanks to my boyfriend, Andreas, for patiently listening to my thoughts and willingness to discuss my thesis over the dinner table. I am touched by your unreserved love and overwhelmingly grateful for your support during this demanding semester.

Line Skåland Gilberg

Line Skåland Gilberg
Trondheim, June 20, 2022

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Acronyms

CWL	cuticular water loss.
RRV	residual reproductive value.
RWL	respirational water loss.
SDP	stochastic dynamic programming.
TPCs	thermal performance curves.

Introduction

In this chapter, the theoretical background and context of this thesis is presented, followed by the research aim.

1.1 Background

Climate change is altering the external environment of living organisms and thereby possibly negatively impacting the previously successful life-history strategies that evolved under historic climates (Parmesan, 2006). A population's ability to persist in the face of climate change depends on how abiotic stress affects an individual's physiological performance, survival and reproduction (Kingsolver et al., 2011; Musolin, 2007). Thus, the ability to predict the consequences of climate change requires an integrated approach that looks at how multiple components of the organism's phenotype interact with the environment. For example, understanding how changes in temperature and precipitation will influence an organism's physiological conditions requires knowing how traits like energy and water balance are impacted. This information can then be used to investigate how performance changes depending on physiological states and thereby allows predicting fitness consequences (Buckley et al., 2018; Sinclair et al., 2016). However, measuring the relationship between climate, physiological- and behavioural responses, and fitness is extremely difficult in natural populations because of numerous complicating factors. For example, the opportunity to respond through behavioural plasticity, acclimatization, range shifts, biotic interactions and adaptation can complicate predictions when considering the population consequences of altered abiotic conditions (Ghalambor et al., 2007; Gienapp et al., 2008; Huey et al., 2012; Renner and Zohner, 2018; Seebacher et al., 2015; Urban et al., 2016). Thus, a complementary approach to empirical studies of natural populations is to model the relationships between environmental change, physiological and behavioural responses and fitness.

Ectotherms constitute the majority of the world's terrestrial biodiversity, and climate change has the potential to disproportionally impact this group (Boggs, 2016; Halsch et al., 2021; Kingsolver et al., 2011). The reason ectotherms are especially vulnerable to changing temperatures is because the environmental temperature determines their body temperature and, thereby, physiological functions, which are essential for survival, reproduction, and ultimately their fitness (Huey and Stevenson, 1979; Huey and Kingsolver, 1989; Sinclair et al., 2016). Thus, ectotherms responses to climate change are often investigated as the temperature-dependent performance, through the concept of thermal performance curves (TPCs) (Angilletta Jr et al., 2002; Deutsch et al., 2008; Kellermann et al., 2019; Sinclair et al., 2016). Performance curves can be generated for any temperature-dependent trait (e.g. growth, locomotor ability, reproductive output) and are typically depicted as being asymmetric by rising slowly with increasing temperature to an optimum, followed by a more rapid decrease (Huey and Stevenson, 1979; Huey and Kingsolver, 1989; Sinclair et al., 2016). To be able to get a better picture of overall organismal response to temperature, there is a need to integrate TPCs for several traits as well as investigate and take into account the effect of multiple environmental stressors in shaping TPCs (Huey and Stevenson, 1979; Sinclair et al., 2016).

Much of the research undertaken in the context of ectotherms and climate change has focused almost exclusively on the effect of altered temperatures on ectotherm performance (Huey et al., 2012; Sinclair et al., 2016). However, climate change also alters precipitation, atmospheric humidity and water availability (IPCC, 2021). We know relatively little about the fitness consequences of altered water conditions compared with altered temperature. However, some studies have shed light on the interplay between temperature and precipitation in shaping performance curves of ectotherms (Bonebrake and Mastrandrea, 2010; Clusella-Trullas et al., 2011). Changes in precipitation patterns and water availability are potentially important aspects of climate change because hydration state and desiccation stress are also known to impact ectothermic performance (Anderson and Andrade, 2017). Reduced precipitation and increased temperatures could be particularly challenging for terrestrial insects. Terrestrial insects face a challenge in keeping a balanced hydration state because they experience a relatively high water loss with increasing temperature and are vulnerable to water stress due to their small body size and high surface-to-volume ratio (Edney, 1977; Kühsel et al., 2017). Thus, predicting how terrestrial ectotherms will respond to climate change requires not only looking at the effect of temperature but the combined effect of this stressor with water availability. Comparative physiologists have been studying these stressors jointly, but the evolutionary and ecological implications have so far mostly studied temperature and hydration stressors independently. Changes in water availability might either buffer or accentuate the ecological effect of climate warming depending on how it changes the hydration state of the organism and the effect of hydration state on performance (Chown et al., 2004b, 2011; Le Galliard et al., 2021; Rozen-Rechels et al., 2019). Predicting the combined effects of warming and water availability requires attention being focused not only on the changes in mean but also on the increased variability and the frequency of more extreme events of precipitation, drought and heat (Boggs, 2016; Clusella-Trullas et al., 2011; Ummenhofer and Meehl, 2017; Vasseur et al., 2014).

Given that temperature and water availability are significant factors influencing the fitness and geographical distribution of insects (Addo-Bediako et al., 2001; Chown et al., 2004b; Deutsch et al., 2008), the concept of thermo-hydro regulation is proposed to describe the physiological and behavioural processes that maintain thermal and water balance at the same time; - emphasizing the possible interaction between these two phenotypic traits. Thermo- and hydro regulation and tolerance are both mediated through behavioural decisions of activity patterns and habitat choice (Chown et al., 2011; Rozen-Rechels et al., 2019). Such regulatory behaviour can be costly and make use of resources that could have contributed to fitness in other ways. The costs can be loss of internal resources (e.g. energy, lipids), predation risk or missed opportunities to either forage or breed (Huey and Slatkin, 1976). Temperature and water regulation also influence the water and energy budget of the individual organism (Kearney et al., 2009, 2013). This is assumed to impact whole organism performance through locomotion, growth and reproduction and ultimately on population dynamics and species distributions and ranges (Rozen-Rechels et al., 2019). For example, research on amphibians has shown that the water state of the organism can affect performance and thermoregulatory behaviour (Anderson and Andrade, 2017). Also, there is accumulating evidence of dehydration constraining behavioural thermoregulation of dry-skinned ectotherms (Le Galliard et al., 2021; Rozen-Rechels et al., 2020), although Padilla Perez et al. (2021) point out that the energy intake may be more critical than the hydration state in determining activity and behavioural thermoregulation. By developing a mechanistic model for a lizard, Kearney et al. (2013) highlights the potential of thermo- and hydro regulation processes to interact in shaping ecological responses through the energy and water balance of the organism.

1.2 Research aim

This master's thesis contributes to the larger puzzle of exploring how terrestrial insects meet the double challenge of altered temperature and water conditions. This project will look into behavioural strategies as a complement to the more physiologically focused research. The overall aim is to theoretically explore individual terrestrial insects' choice of activity in light of the combined environmental conditions of temperature and water availability. The thesis will explore the choice of activity, survival and reproduction under different temperature and water availability scenarios and investigate the state-dependent behavioural strategies for different environments and how well the strategies perform in new environments.

My aim with this thesis is to shed some light on the more ecological aspects of the double challenge of behavioural thermo- and hydro regulation through general behaviour such as reproducing, hiding and feeding. This aim will be achieved by associating these activities with different costs in terms of energy and water gain and loss. These costs are not only influenced by the decisions but also by the external environmental conditions of temperature and water availability. In this thesis, I will explore how the internal states interact with the external conditions in shaping strategies and how different strategies performs in terms of survival and reproduction under different climatic conditions. More than investigating a hypothesis, the aim of this thesis is to be a starting point, exploring concepts and generating new hypotheses and predictions.

This is an ambitious first attempt at a model of this kind, looking at both energy and water state and the double effect of temperature and water availability through the lens of fitness optimization. This is a step into a new theoretical territory. Therefore it is desirable to keep the model quite general and flexible to allow change of parameters, relationships and remove and add complexity.

Method

The method used in this thesis, stochastic dynamic programming (SDP), has the advantage of making it possible to connect the internal states of the organism with the stochastic environment it lives in and predict the fitness effects of different state-dependent behavioural decisions. This approach is, therefore, suitable to connect physiology with more ecologically relevant whole organism performance of survival and reproduction. These models have the additional advantage of making it possible to theoretically explore how natural selection has shaped the life history trade-offs between phenotypic traits that have emerged from the combined internal and external constraints and predict the optimal strategy (Clark and Mangel, 2000; Houston and McNamara, 1999; Mangel, 2015).

In this chapter, it will be explained how the biological problem is explored through the development of a theoretical model, using a combination of SDP and simulations. The components and the parameters of the model will be explained and described, together with the logic of the backwards optimization to calculate optimal strategy and the following Monte Carlo forward simulation.

2.1 Model development and description

This state-dependent stochastic dynamic model (Clark and Mangel, 2000; Houston and McNamara, 1999) takes the perspective of an individual female insect over the breeding season, each time step (t) being one day. Assuming the breeding season consists of a maximum of 60 days and lasts until the terminal time (T), and that it is in this time interval from winter-emergence to death that reproduction must take place. In each time step, the individual makes the decision to choose between three different main activities; "Hiding", "feeding", or "searching for a mate" to try to reproduce.

In the model, hiding is considered a low cost alternative due to lower activity level and the possibility of hiding in a more favourable micro climate. The benefits of hiding are, therefore, low water loss and energy consumption, but at the cost of lost opportunity to feed or reproduce. When it comes to feeding and searching for a mate, these are considered to have higher water and energy cost of being active and more exposed. Searching for a mate is assumed to require some more resources than feeding. Feeding has the possible benefit, depending on weather, of also gaining energy and water to increase internal states. Searching for a mate has the probabilistic benefit of reproduction. Succeeding in reproduction has an additional cost of the investment of water and energy into offspring. The costs of each choice in terms of water and energy depend on the current external environment that the insect experiences.

The model considers two intrinsic state variables. These are the energetic condition ($X(t)$) and hydration state ($Y(t)$) of the insect. These states are affected by the cost and benefits of the decisions taken by the individual at each time step. The costs and benefits of each decision are also influenced by the environmental states temperature (z) and water availability (w). In the model, water availability should be seen as a quite general environmental condition combining aspects of both humidity and water availability.

The two external states, temperature and water availability, are divided into 5 discrete steps from low to high, assuming only positive temperatures. There is a probabilistic distribution Z for the different temperatures to occur each time step, and similar, there is a probability distribution W for water availabilities. These combined give the probability for different weather scenarios. In the model, the individual has information about the current environmental condition and optimizes for its environment that is characterized by a certain and known probability distribution for different weathers (i.e. combinations of temperature and water availability).

In this model, reproductive success over the season is the sum of the pay-off from every reproduction. An individual who searches succeeds in finding a mate and gets to reproduce with probability p. The pay-off from a single reproductive event is the number of offspring/reproductive units produced from the energy and water available for reproduction after searching. The reproductive output $R(x^{**}, y^{**})$ is given from resources available for investment after searching, depending on the energy cost (k_1) and water cost (k_2) of one reproductive unit and what is the limiting state. The ** notation marks that it is not the internal states at the beginning of the time step but states after searching.

The state transition for energy from $X(t)$ to $X(t+1)$ can be described as:

$$X(t+1) = \begin{cases} x - A_1(z) & \text{if Hide} \\ x - A_2(z) + C(z) & \text{if Feed} \\ x - A_3(z) & \text{If Search mate and don`t find} \\ x - A_3(z) - pR(x^{**}, y^{**})k_1 & \text{If Search mate and find,} \end{cases} \tag{2.1}$$

where $Y(t) = y$ and $A_i(z)$ is temperature dependent energy loss function for the

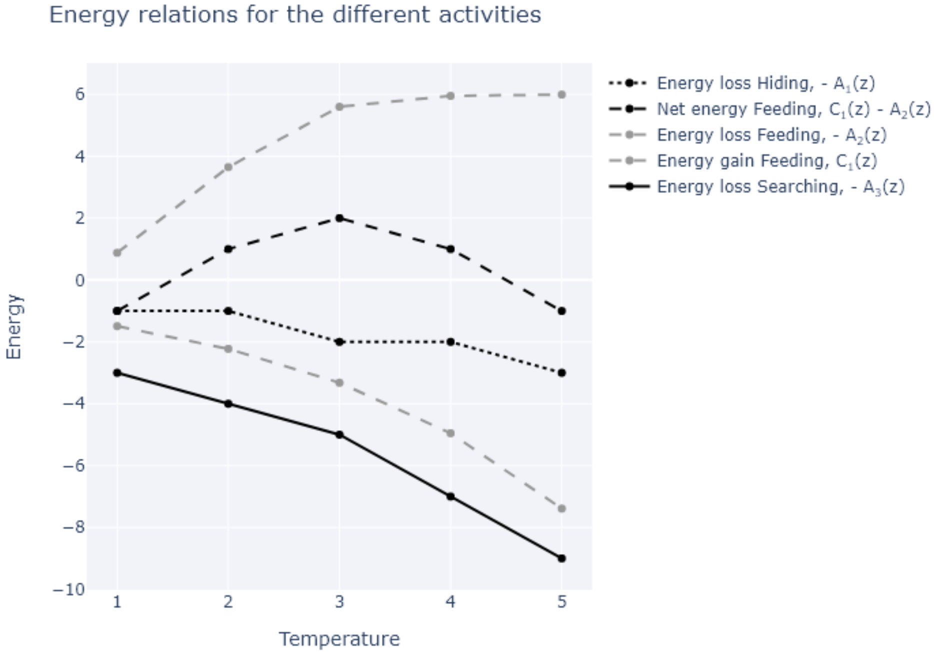


Figure 2.1: Energy transition for the different activities. $A_i(z)$ and $C_i(z)$ for is calculated by using values from continuous functions that are rounded and takes discrete values. Mark that for net energy the two are firs combined, then rounded and the gray lines thereby display the non-rounded values.

different activities, $i = 1, 2, 3$, where $1 =$ is "hide", 2 is "feed" and 3 is "searching for mate". $C(z)$ is the energy gain function and k_1 is the energy cost of each offspring or reproductive unit. $A_i(z)$ and $C(z)$ is displayed in Figure 2.1.

The energetic cost is assumed to have an exponential increase with temperature because of the relation between temperature and metabolic rate (Gillooly et al., 2001; Huey and Kingsolver, 2011). Metabolic rate and, therefore, energy use can not only be assumed from the resting metabolic rate but is also dependent on activity level (Halsey et al., 2015). In this model, hiding is a low energy expenditure activity, while feeding and trying to reproduce are high energy expenditure activities. In the model, a is a scaling factor for the increase with temperature, and hiding has been given a lower scaling value compared to the two other activity choices. Energy gain is dependent on foraging efficiency, which is a temperature-dependent trait in ectotherms, as temperature affects the speed of body processes and mobility (Avery et al., 1982; Angilletta Jr, 2009; Huey and Stevenson, 1979). This is modelled through a logistic function. The state transition for energy is displayed in Figure 2.1.

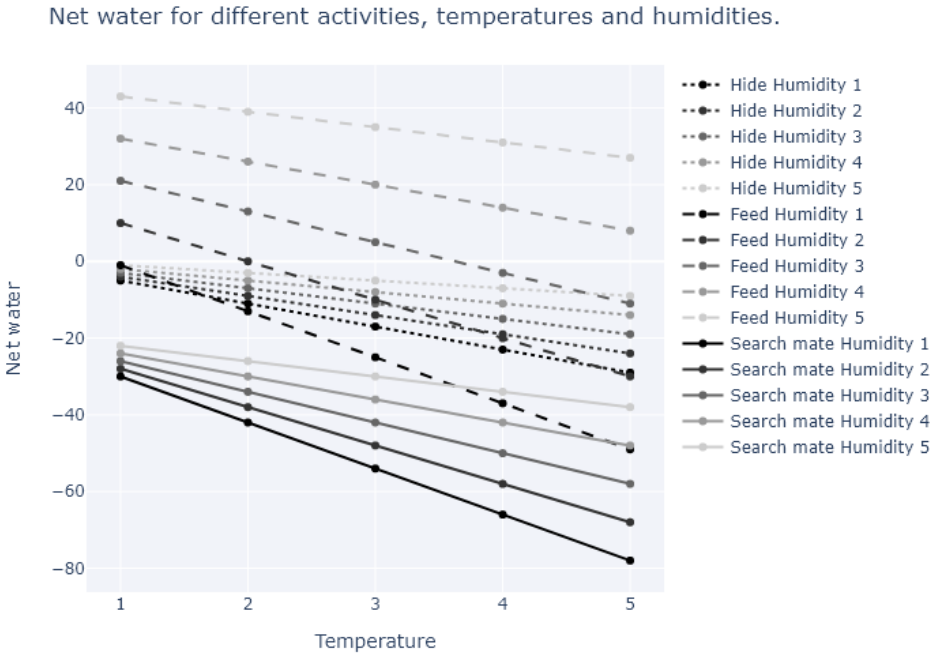


Figure 2.2: Net water from doing different activities in different temperatures and humidities. Humidity is in this model a quite general term combination of humidity and water availability in the environment.

The state transition for water from $Y(t)$ to $Y(t+1)$ is given by:

$$Y(t+1) = \begin{cases} y - B_1(z,w) & \text{if Hide} \\ y - B_2(z,w) + C(w) & \text{if Feed} \\ y - B_3(z,w) & \text{If Search mate and don't find} \\ y - B_3(z,w) - pR(x^{**}, y^{**})k_2 & \text{If Search mate and find,} \end{cases} \tag{2.2}$$

where $Y(t) = x$ and $B_i(z,w)$ is water loss function depending on temperature z and humidity w, different for the the different activities, $i = 1,2,3$. The water cost should increase with temperature due to increased cuticular water loss (CWL) and also respirational water loss (RWL) with temperature (Chown et al., 2011; Terblanche et al., 2010). In the model, a linear increase is assumed. Water loss does also increase with decreasing humidity (Chown et al., 2011; Terblanche et al., 2010). The water cost is, therefore, dependent on both temperature and water availability. In the model assuming an interaction effect between the two. A higher activity level is assumed to have higher water loss due to higher RWL.

In the model, it is assumed water is gained from feeding. The variable $E(w)$ is the water gain depending on water availability (w). Water gain increases with water availability and is modelled with a linear increase. The net water is visualized in Figure 2.2. The parameter p is the probability of finding a mate, and $R(x^{**}, y^{**})$ is the number of offspring/reproductive units made from resources left after searching times, the water cost of each, k_2. Notice that the decision to search for a mate can have two different state outcomes, depending on whether the individual finds a mate or not. If deciding to search for a mate, there is a certain high water and energy cost of being in high activity. If finding a mate, there is an additional cost of the reproductive investment, but also an additional fitness benefit.

If the insect reaches either the critical energy (x_{crit}) or water level (y_{crit}), being the lowest state level, it dies from starvation or dehydration, respectively. In the model, there is also a mortality risk (m) for every time step that captures a constant chance of dying from predation or parasitism.

The parameters and variables of the model is displayed in table 2.1, and only discrete steps of state transitions are used in the model. Mark that energy and water are modelled with respectively 20 and 200 discrete steps. This does only reflect a difference in resolution. A more in-depth description of the expressions and parameters that the functions for energy and water gain and loss consist of can be found in Appendix A.

Table 2.1: Definition of model parameters and variables with symbol, description and values.

Parameters/ variables	**Description and values**
$X(t)$	Energetic condition/energy reserves of female insect at the beginning of time step t.
x_{max}	Maximum level of energy reserves. x_{max} set to 20.
x_{crit}	Citical level of energy reserves. Insect dies if $x < x_{crit}$ x_{crit} set to 1.
$Y(t)$	Hydrational condition/water reserves of female insect at the beginning of time step t. One time step being one day.
y_{max}	Maximum level of water reserves. y_{max} set to 200.
y_{crit}	Critical level of water reserves. Insect dies if $y < y_{crit}$. y_{crit} set to 1.
$Z(z)$	Discrete probability distribution Z for environmental temperatures $z = 1, 2, 3, 4, 5$.
$W(w)$	Discrete probability distribution W for habitat water availabilities/humidities $w = 1, 2, 3, 4, 5$.
$A_i(z)$	Energy loss as a function of temperature z, differs between activities i.
$B_i(z, w)$	Water loss as a function of temperature z and humidity w, differs between activities i.
$C(z)$	Energy gain from feeding as a function of temperature z.
$E(w)$	Water gain from feeding as a function of water availability w.
$R(x^{**}, y^{**})$	Reproductive output if finding a mate. Depending on the limiting state after searching. ** notation to mark that it is not the state at the start of time step, but after searching
k_1	Energy cost of one offspring/one reproductive unit. Set to 2.
k_2	Water cost of one offspring/one reproductive unit. Set to 10.
m	Mortality risk. Probability of dying from predation/parasitism each time step. Set to 0.01.
p	Probability of finding a mate if decision $i = 3$, "Search for mate". Set to 0.9.
T	Length of season. Days from winter emergence to max of lifespan, set to 60.

2.2 Optimization

Some major assumptions of evolutionary and behavioural ecology form the basis of using optimality models (Mangel, 2015). An underlying assumption of this model is that the individual female insect behaves optimally to maximize her reproductive success over the breeding season. This optimal strategy is assumed to have evolved through natural selection as a way to maximize fitness by behaving optimally within the constraints of internal states and the external environment.

Optimal behavioural strategies are determined using the method of SDP (Clark and Mangel, 2000; Houston and McNamara, 1999). The process of backwards iteration produces three different matrices for fitness values of the different decisions: "Hide", "feed", or "search for a mate". $V_i(x, y, z, w, t)$ is the fitness value of choosing activity i for the given combination of states and time. V_i is obtained by evaluating every possible outcome of time step t and the corresponding probability for that outcome, assuming optimal choices will be made at later time steps.

To simplify the writing of all possible combinations of probabilities and state outcomes the following is specified:

$$\text{Combinations } (C) = \begin{cases} weather_p \text{ takes the value of the weather probabilities} \\ \text{(25 combinations)} \\ mate_p \text{ takes the value of } p \text{ or } (1-p) \end{cases}$$

The expected fitness for the different activities is then

$$\begin{aligned} V_{1C} &= (1-m) \cdot weather_p \cdot F(x^*, y^*, z^*, w^*, t+1) \\ V_{2C} &= V_1 \\ V_{3C} &= mate_p \cdot D(x^{**}, y^{**}, t) \\ &\quad + (1-m) \cdot mate_p \cdot weather_p \cdot F(x^*, y^*, z^*, w^*, t+1), \end{aligned} \tag{2.3}$$

where

$$V_i = \sum_c V_{iC}$$

is the sum of all possible combinations. The ** notation again marks that this water and energy state is the states after searching. The * notation marks the state at time step t+1, dependent on the experienced weather and activity performed in the current time step. For V_3, x^*, and y^* take either the state after searching and reproducing or only searching, depending on finding a mate or not, respectively. The matrices for the three different activities are compared to decide which activity maximizes fitness for each combination of state and time. The optimal behavioural decision is choosing the activity that maximizes fitness for this combination of intrinsic and external states and time. The optimal behavioural strategy of the insect is then the combination of these calculated optimal choices. This result from the backwards iteration is called the decision rule or the optimal strategy.

The fitness value of the optimal decision is kept in the fitness matrix $F(x, y, z, w, t)$. This matrix then contains the expected reproductive success between t and T given that the individual behaves optimally.

$$F(x, y, z, w, t) = max\left(V_1(x, y, z, w, t), V_2(x, y, z, w, t), V_3(x, y, z, w, t)\right) \tag{2.4}$$

The fitness value is calculated iteratively, which means that the fitness value is first calculated for the optimal decisions for each state at time step T. These values are then used to calculate the fitness of the optimal decision at time step $T - 1$. The process continues like this backwards until the start of the season.

The fitness value in the model is approximated by reproductive value consisting of two components, current reproductive output, $D(x^{**}, y^{**})$ and the residual reproductive value (RRV), being the expected future reproductive output, $F(x^*, y^*, z^*, w^*, t + 1)$. Life-history theory predicts a trade-off between the two. Allocating resources to current reproduction to increase fitness may imply both post- and pre-breeding cost. Post breeding cost in terms of reduced future fitness can occur because of the resource cost of reproduction and its downstream effect on the parent survival and fecundity (Williams, 1966).

In the model, if the female reproduces, the expected fitness consists of both current reproduction and the expected future fitness she can gain from behaving optimally trough out the rest of the season. In accordance with the terminal investment hypothesis, the optimal decision in the last time step will be to reproduce since there are no future reproductive opportunities (Williams, 1966). However, at earlier time steps, the expected fitness gained from reproducing in the future is also taken into consideration.

If the female instead either doesn't find a mate or chooses to hide or feed, there is no reproduction occurring. The fitness component then consists only of the expected future reproduction. The future fitness depends on the probability of surviving until the next time step, $(m - 1)$, and the expected fitness from doing so depending on states.

2.3 Simulations

For easier interpretation of the results and realized patterns of behaviour, survival and reproduction forward simulations of 1000 individuals are performed. Individuals that follow the behavioural strategy obtained from the backwards iteration are used in a forward simulation to gain insight into weather, water and energy condition, activity choices, reproductive events, survival and fitness. The Monte Carlo simulation method (Clark and Mangel, 2000) is suitable because of the probabilistic nature of some of the parameters in the model, namely the mating probability, mortality and the weather distributions.

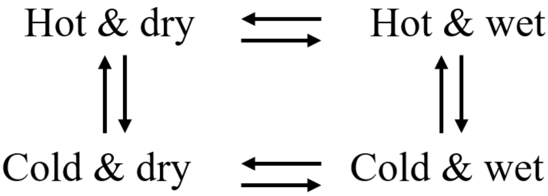


Figure 2.3: Visual presentation of experiments. Arrows indicating the eight transplant experiments that was performed.

Starting energy and hydration state of the animals are drawn from normal distributions truncated to fit the state limits (for energy: $\mu_x = 10$ and $\sigma^2 = 3.33$ and for water: $\mu_y = 100$ and $\sigma^2 = 33.3$). For each time step throughout the breeding season, the expected activity choice is determined from the decision matrix. Each time step, the probabilistic events of dying from predation/parasitism can either occur or not, with the probability specified in the parameter value. Whether the individual finds a mate or not is drawn in the same probabilistic manner if the individual has chosen to search for a mate. Temperature and water availability are also drawn from the given probability distributions.

2.4 Scenarios

The model can be used to explore the effect of altered model parameters, and the focus of this thesis is altered weather distributions. The output from the backwards iteration is an optimal strategy for each combination of states and time, often called the decision rule matrix and the fitness matrix. To be able to investigate optimal strategies under different environmental conditions, the backwards process was performed for 5 different scenarios. These scenarios have different probability distributions for temperature and water availability; the other model parameters were kept the same. The first scenario is an intermediate scenario, acting as a baseline, and the rest are distributions skewed towards the more extreme temperatures and humidities (Table 2.2).

First, individuals are simulated through scenarios they are optimized for. This is performed by using the decision rule for one scenario and performing a forward simulation where the probability distributions of temperature and water availability are equal to the ones used in the backwards iteration. The weather distribution is, in these cases, similar to the environment the individuals are optimized for.

Second, the strategies are tested in novel environments. This is done by using the decision rule for one scenario and running forward simulations where the probability distributions of weather are altered compared to what it was in the backwards

Table 2.2: Description of scenarios investigated. Z(z) is the probability distribution for temperature z=1,2,3,4,5. W(w) is the probability distribution for humidity w=1,2,3,4,5.

Scenario label	**Probability distribution**	**Description**
Baseline	$Z(z) = [0.05, 0.25, 0.40, 0.25, 0.05]$ $W(w) = [0.05, 0.25, 0.40, 0.25, 0.05]$	Highest probabilities for the middle temperature and water availability scenarios
Warm and dry	$Z(z) = [0.05, 0.05, 0.25, 0.40, 0.25]$ $W(w) = [0.25, 0.40, 0.25, 0.05, 0.05]$	Distribution skewed towards higher temperatures and lower water availabilities
Warm and wet	$Z(z) = [0.05, 0.05, 0.25, 0.40, 0.25]$ $W(w) = [0.05, 0.05, 0.25, 0.40, 0.25]$	Distribution skewed towards higher temperatures and higher water availabilities
Cold and dry	$Z(z) = [0.25, 0.40, 0.25, 0.05, 0.05]$ $W(w) = [0.25, 0.40, 0.25, 0.05, 0.05]$	Distribution skewed towards lower temperatures and lower water availabilities
Cold and wet	$Z(z) = [0.25, 0.40, 0.25, 0.05, 0.05]$ $W(w) = [0.05, 0.05, 0.25, 0.40, 0.25]$	Distribution skewed towards lower temperatures and higher water availabilities

simulation. Using this method, eight transplant experiments are performed. For comparison, transplants experiments are chosen to be so that only one environmental parameter is altered at the time, either temperature or water availability, as shown in Figure 2.3.

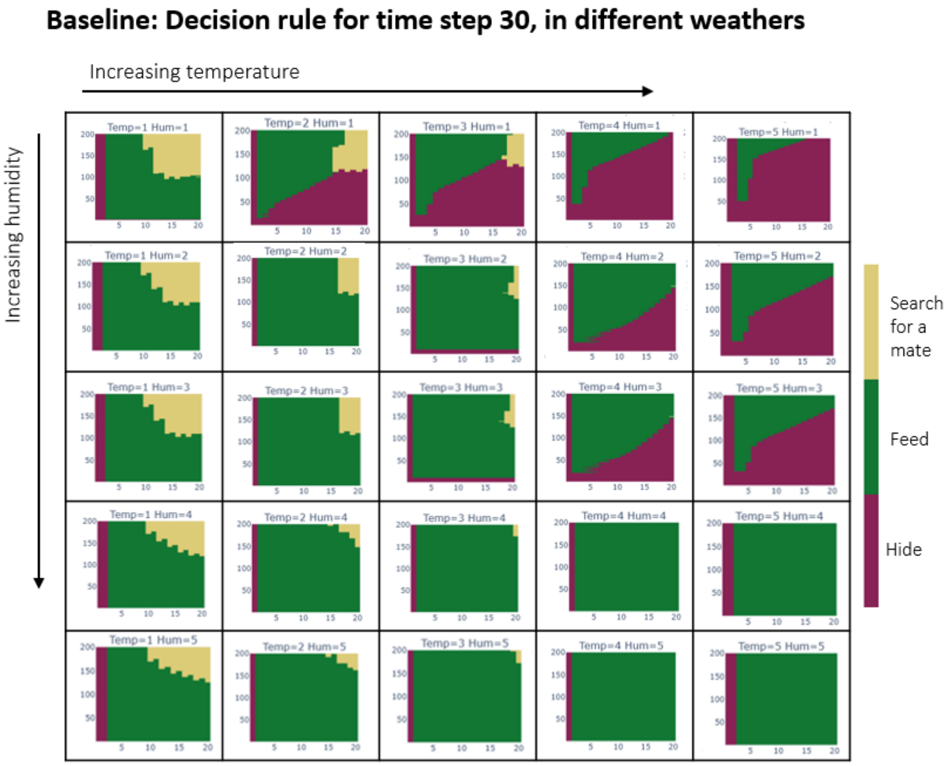
The entire model was created with Julia programming language version 1.6.5 (Bezanson et al., 2017) with additional packages IterTools (Jones et al., 2017), StatsBase (Lin et al., 2013), Distributions (Lin et al., 2022), DataFrames (Kamiński et al., 2022) and JLD2 (Isensee et al., 2015). PlotlyJS (Lyon, 2015) was used for visualizing results. The model code is available on my GitHub repository `https://github.com/Linegil/Model`.

Results

This chapter presents a selection of results from the backwards iteration and the simulations for the different scenarios. First, results for environmental scenarios optimized for are presented. Second, the transplant experiments.

3.1 Baseline scenario

The most important result from the backwards iteration is the decision rule. In the baseline scenario, the optimal decision depends on time, the internal states of water and energy, as well as the external environment, the temperature and humidity/water availability that the individual encounters. Some example slices of the multidimensional decision rule matrix that illustrates this can be found in Figure 3.1. The most visible effect of time is that more combinations of internal states lead to the choice of searching for a mate towards the end of the season (example in Figure 3.2). Other than that, the effect of time on the optimal decision is less strong than the effect of internal states and external weather. Still, for some combinations of weather, there are additional changes with time regarding which combinations of internal energy and water state should hide, feed or search. This effect differs between different weathers (example in Figure 3.2 and Appendix B Figure B.1 and Figure B.2).



Weather probabilities

0.0025	0.0125	0.02	0.0125	0.0025
0.0125	0.0625	0.1	0.0625	0.0125
0.02	0.1	0.16	0.1	0.02
0.0125	0.0625	0.1	0.0625	0.0125
0.0025	0.0125	0.02	0.0125	0.0025

Figure 3.1: Decision rule for baseline scenario showing the optimal choice of activity given state and weather for time step 30. For each subplot energy is on the x-axis and water on the y-axis. Mark that the weather combinations occur with different probabilities given in the table.

3.1.1 Simulation in baseline environment

In this scenario, individuals use some time steps to build up their water and energy states before deciding to search for a mate and trying to reproduce (Figure 3.3). Relatively few individuals fails to reproduce, and most individuals reproduce more than once (Figure 3.4). Through most of the season, the mortality is mainly due to predation/parasitism (Figure 3.5). For the last three time steps, the mortality is highly increasing due to a higher number of individuals dying from starvation and desiccation because of terminal investment in reproduction. The amount of

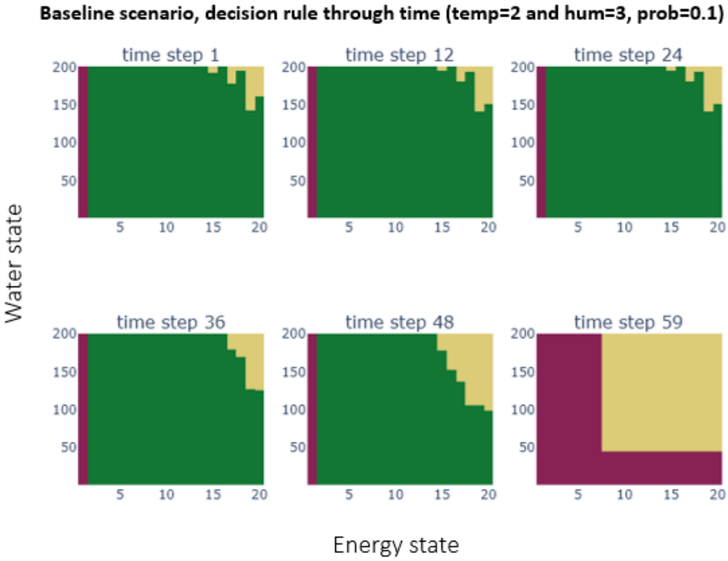


Figure 3.2: Decision rule for baseline scenario showing the optimal choice of activity given for 6 time steps. This weather combination occurs with a lower probability than the intermediate weather, but is among the most commonly occurring weathers in the baseline scenario.

individuals hiding is relatively low, and the proportion is quite similar throughout the season except for the last time steps where there is an increase in individuals hiding. In the last time step, individuals either choose to hide or search for a mate. From the decision rule (for example, see Figure 3.2), we can see that individuals who cannot get any offspring choose to hide and the individuals that have states that allow reproductive output choose to search for a mate. How high in states the individuals need to be to search for a mate therefore also depends on the weather encountered in this time step (for example compare Figure 3.2, and Appendix B Figure B.1 and Figure B.2).

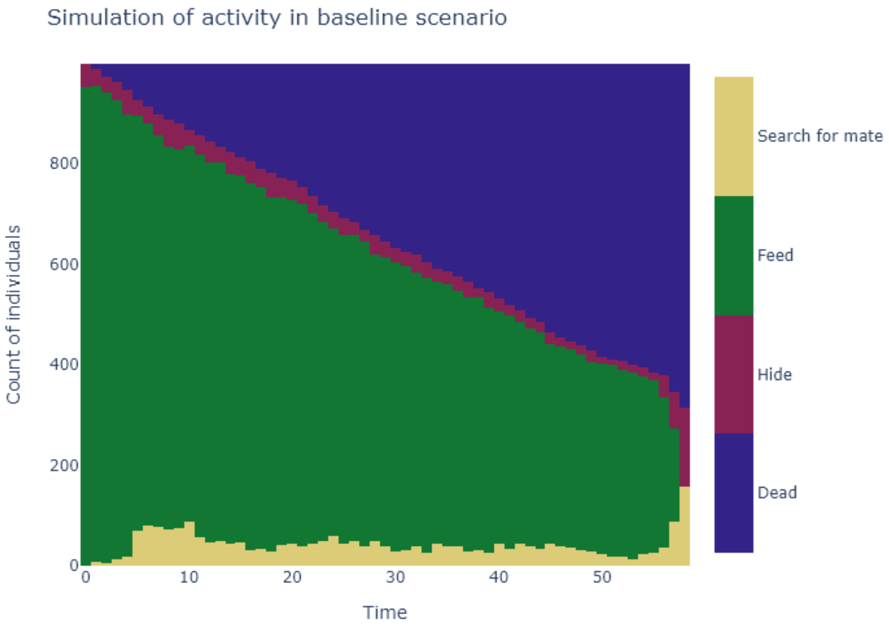


Figure 3.3: Simulation of activity for 1000 individuals in the baseline scenario. Every time step, the number of individuals being ”Dead” and choosing the different activities ”Hide”, ”Feed” and ”Search for a mate” is shown in different colours. Every individual experiences a random weather drawn from the probability distributions Z(z) and W(w) for each time step, the same probability distributions they are optimized for.

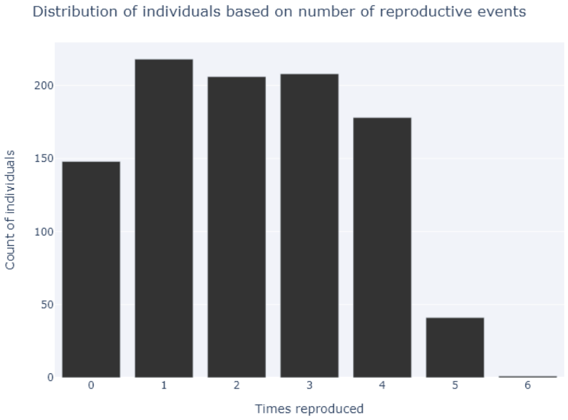


Figure 3.4: Distribution of number of successful reproductive events throughout the season for 1000 individuals in the baseline scenario.

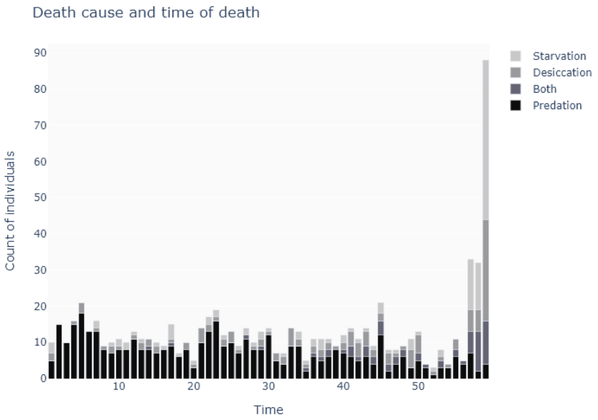


Figure 3.5: Mortality and death causes trough the season for simulations of 1000 individuals in the baseline scenario.

3.2 Effects of climatic conditions on optimal choices and realized patterns of behaviour and survival

Individuals are optimized for scenarios with other weather distributions than in the baseline scenario, which results in other optimal decision rules for the individuals to follow. Similar to the baseline scenario, there is an effect of terminal investment in all scenarios. The hot and dry scenario is considerably different, with searching for a mate being optimal in earlier time steps and for lower water and energy states compared to baseline. For which states and weathers the hiding alternative is optimal is also varying to some degree between the different scenarios.

Simulating individuals through scenarios with other weather distributions results in different fitness values (Table 3.1) as well as altered patterns for behavioral choices and death (Figure 3.6).

In terms of fitness, individuals in the wet scenarios does, on average better than individuals in the dry scenarios. When water availability conditions are similar, individuals in cold scenarios have, on average higher fitness than individuals in hot scenarios (Table 3.1). Comparing the fitness values for the different scenarios, the average fitness is found to be lowest for the ”hot and dry” scenario (Table 3.1). These individuals have high mortality from both desiccation and starvation (Figure 3.7). Compared to the baseline scenario, individuals choose to search for a mate in lower water and energy states (Figure 3.9), and this leads to fewer offspring from reproductive events. Searching being an optimal choice for many combinations of states can also be seen from the decision rule (Figure B.3). Despite the high mor-

Table 3.1: Accumulated fitness for 1000 individuals simulated in natal weather scenarios.

Scenario label	Mean	Standard deviation
Baseline	13	8.36
Cold and wet	10.75	6.53
Cold and dry	5.74	4.69
Hot and dry	1.36	1.5
Hot and wet	8.99	5.5

tality rate and the fact that most individuals die during the first 10 days and all are dead before mid-season, an overweight of individuals succeed in reproducing once (Figure 3.11) because their strategy is to start to reproduce early in the season (Figure 3.6), but very few individuals succeed in reproducing more than once.

Individuals in the "cold and dry" scenario follow a reproductive strategy that is quite similar to the baseline scenario, using some time to build up resources before starting reproducing. They have lower fitness due to higher mortality from starvation and desiccation (Figure 3.7 compared to Figure 3.5) and lower acquisition of resources. Fewer individuals succeed in reproducing and there is fewer reproductions for those who do (Figure 3.11 compared to Figure 3.4). Individuals in the "hot and wet" scenario follow an activity pattern similar to the baseline scenario as well (Figure 3.6), but with lower fitness due to more individuals dying from starvation (Figure 3.7).

Individuals in the "cold and wet" scenario have the highest fitness of the alternative climate scenarios. In this scenario, a higher proportion of individuals choose to hide than in any other scenario (Figure 3.6). Decision rule reveals individuals hiding in other combinations of internal states and in different weathers than the baseline (Figure B.4 compared to Figure 3.1).

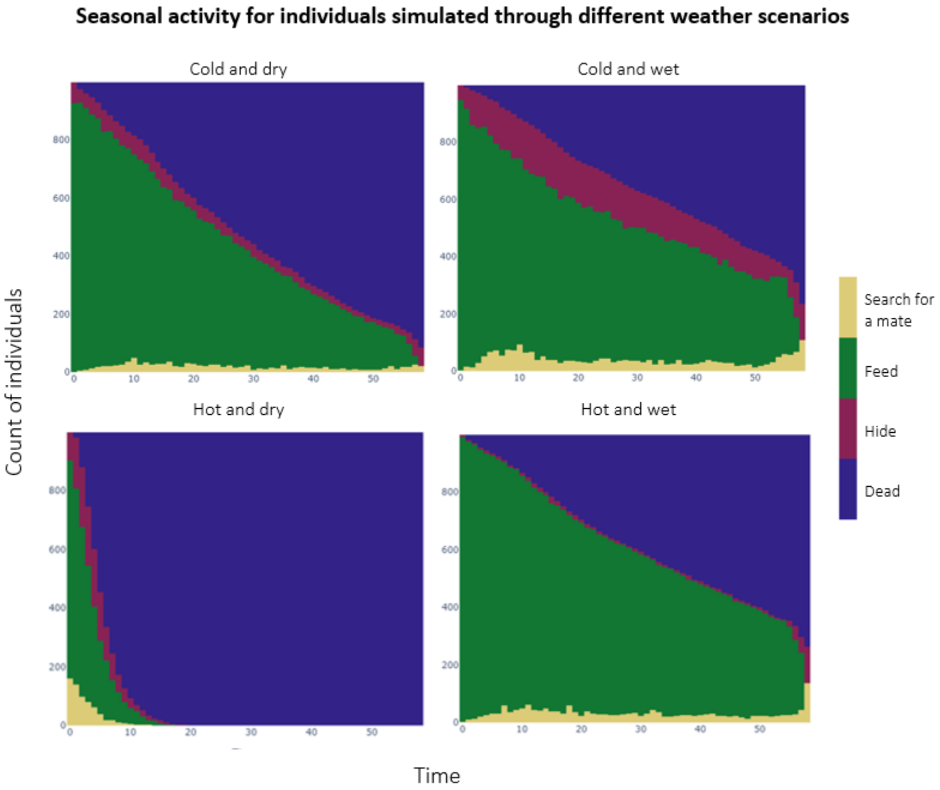


Figure 3.6: Simulation of activity for 1000 individuals for four different scenarios. Every time step, the number of individuals being "Dead" and choosing the different activities "Hide", "Feed", and "Search for a mate" is shown in different colours. Every individual experiences a random weather drawn from the probability distributions Z(z) and W(w) for each time step, the same probability distributions they are optimized for.

3.3 Individuals transplanted into other scenarios than what they are adapted to

As expected, when simulating individuals through a scenario, the individuals optimized for this scenario have higher fitness than individuals optimized for other scenarios (Table 3.2). How well different strategies do in environments they are not optimized for varies to some degree. The largest difference is still between climatic conditions rather than between differently optimized populations simulated through the same scenario.

Individuals optimized for a hot and dry scenario displayed a strategy in this environment that was to reproduce early even though they are not in or close to the

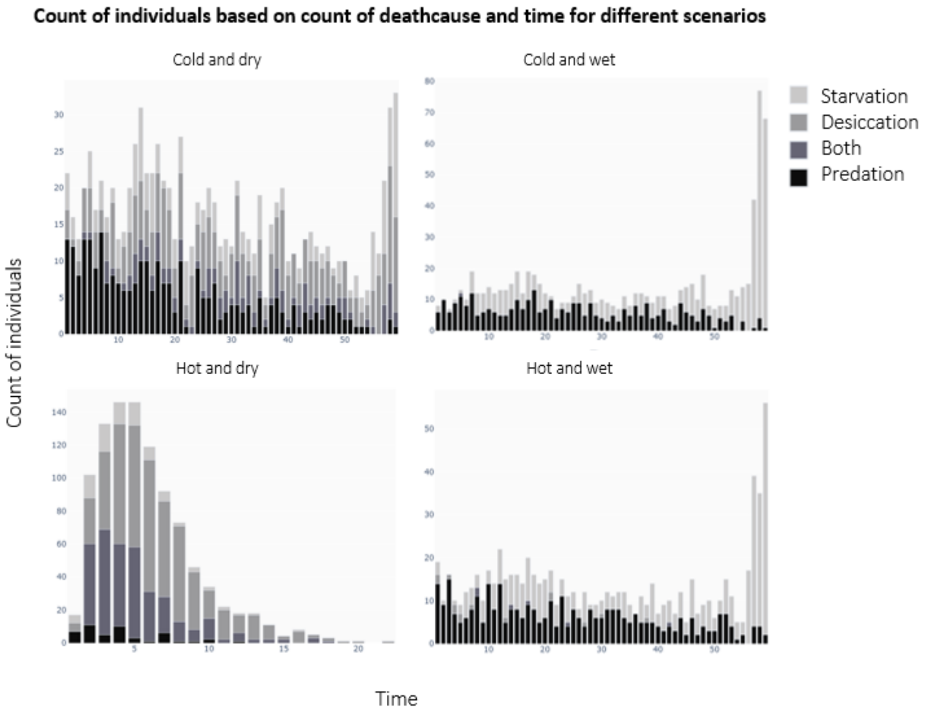


Figure 3.7: Count of individuals that die during each time step categorized based on death cause. Individuals simulated through scenarios they are optimized for.

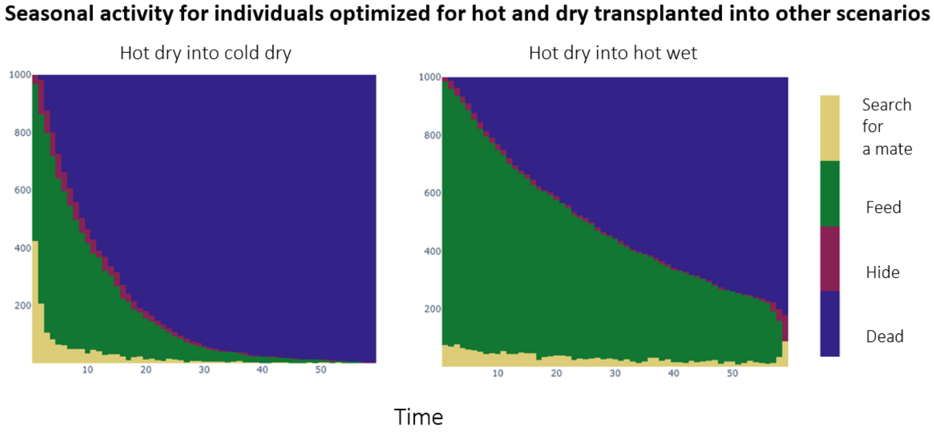


Figure 3.8: Count of individuals based on seasonal activity in scenarios they are not optimized for.

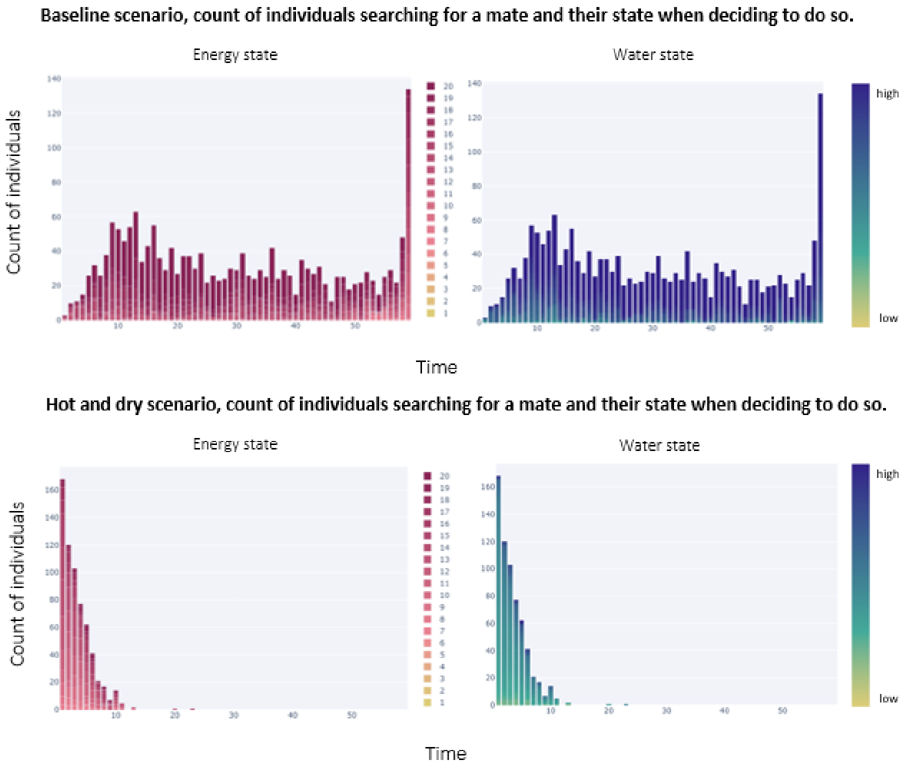


Figure 3.9: Comparing states for individuals searching in hot dry compared to baseline scenario.

max state of water or energy. When these individuals are transplanted into other scenarios they still tend to reproduce earlier than the individuals optimized for the scenario do (Figure 3.8 compared to Figure 3.6), in low states (Figure 3.9) and less individuals have zero reproductions (Figure 3.10) compared to the populations optimized for the respective scenarios (Figure 3.11). When other populations are transplanted into the hot and dry scenario, they do not reproduce from the beginning of the season, and almost none of the individuals reproduce before they die (Figure 3.12).

In wet conditions, an average accumulated fitness relatively close to the native population is achieved for the transplants as well, even though the individuals do not follow the optimized strategy. In dryer conditions, the fitness loss from not following the optimal strategy is more severe (Table 3.2). When ”hot and wet” and ”cold and dry” strategies are used in a ”hot and dry” environment, almost no individuals go searching for a mate, and most die before they get to reproduce (Figure 3.12).

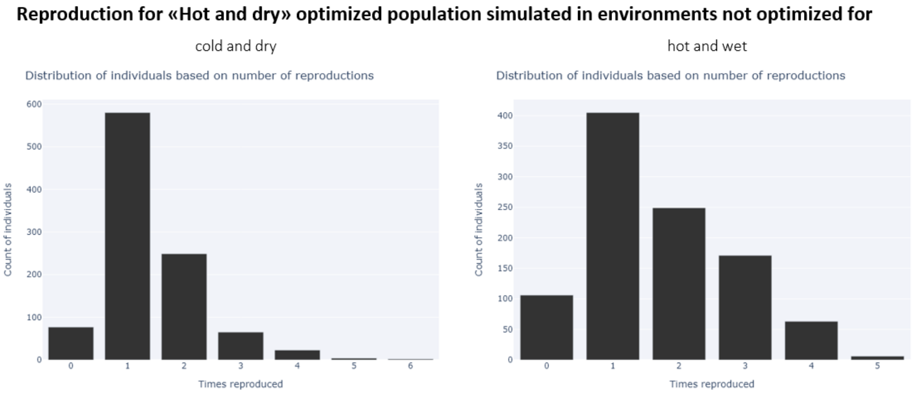


Figure 3.10: Count of individuals based on number of reproductions during the season for "hot and dry" optimized population simulated through "cold and dry" and "hot and wet" scenario.

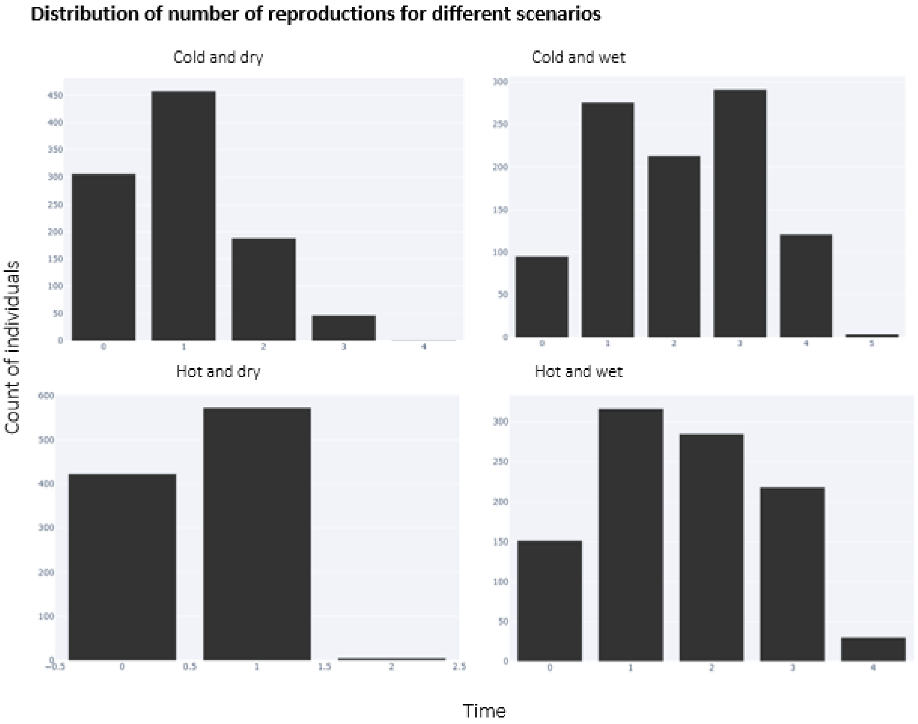


Figure 3.11: Distribution of individuals based on number of reproductions for the different weather scenarios. Individuals simulated through scenarios they are optimized for.

Table 3.2: Average accumulated fitness for individuals adapted to some conditions and simulated in different environmental conditions.

		Environmental conditions			
		cold dry	**cold wet**	**hot dry**	**hot wet**
Adaptation conditions	**cold dry**	**5.74**	10.41	0.08	-
	cold wet	4.89	**10.75**	-	8.17
	hot dry	3.1	-	**1.36**	8.24
	hot wet	-	10.11	0.26	**8.99**

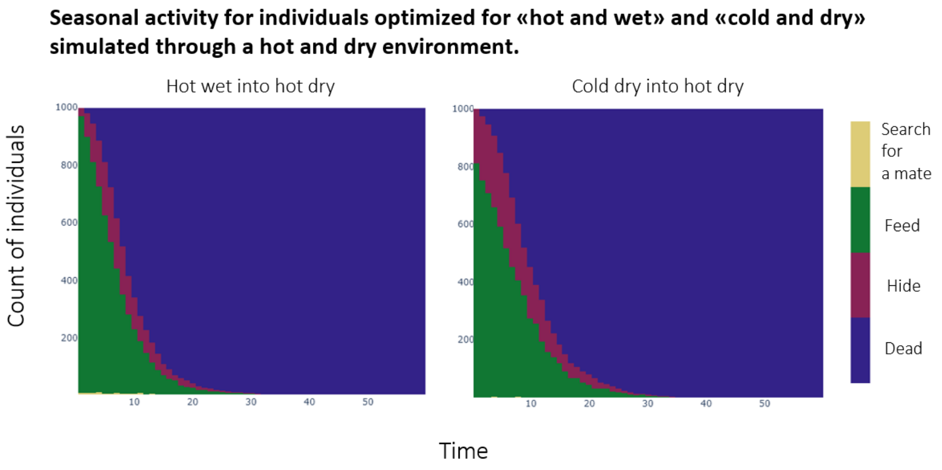


Figure 3.12: Count of individuals based on seasonal activity in scenarios they are not optimized for.

Discussion

A major question in global change biology is projecting how organisms will deal with the increasing multiple stressors associated with future climate change. For terrestrial ectotherms, the combined impacts of warmer temperatures and altered precipitation regimes represent a fundamental challenge. This challenge arises because organisms have the capacity to make decisions with regard to how they weigh the fitness costs and benefits of engaging in feeding, hiding, or mating behaviours under different internal and external states. Testing these ideas empirically is challenging because of the complex interactions between the various factors involved. Thus, the development of models provides a complementary approach to predicting how organisms might cope with multiple stressors. In this thesis, I take such a modelling approach.

The model developed for my thesis is an attempt at starting theoretically investigating the ecological effects of the double stressors of temperature and water availability through the lens of behaviour, life history and fitness optimization, following a generic female insect through one breeding season. The results from this model should be considered qualitative predictions rather than quantitative results. The results indicate that external environmental conditions of temperature and water interact with internal water and energy state in shaping the behavioural strategy. The strategies adapted to different temperature and water availability scenarios show some differences in activity choice. These results complement the more physiologically focused research, which tends to ignore behaviour, by indicating the importance of strategic behavioural choices and activity patterns that help or hinder individual's survival and reproduction in altered environmental conditions.

From simulations in environmental conditions that are similar to the condition an insect is adapted to, there are some similarities between different scenarios. From all scenarios, it is evident that most of the time budget is spent feeding, and just a small amount of time is spent hiding or searching for a mate. Individuals will only do the different activities for some combinations of weathers and internal conditions, and thereby we can say that both internal conditions of the individual and the external environment are important in deciding the optimal activity choice.

The behavioural strategies for the different scenarios are similar in that there is a tendency for individuals to reproduce when in higher states. Searching is costly in terms of water and energy loss, and the net reproductive output is higher if the organism reproduces when in high internal states. It is thereby reasonable that individuals spend only a small amount of time reproducing, even though it is only this activity that produces offspring and thus directly impacts fitness. Additionally, in the model, the chance of encountering a mate when deciding to search is set high, and the individuals are, therefore, likely to get the chance to reproduce if they decide to search for a sexual partner.

The different scenarios also share a tendency toward individuals reproducing in low temperatures; the temperature seems to be the most important factor when determining what weather to reproduce in. In low-temperature weather, individuals also reproduce for a more extensive combination of internal states than what they would do if they reproduced in other weather. This tendency could be because reproducing in low temperatures has lower energy loss, which in the model is assumed to be the most critical internal resource for reproductive output. An additional explanation is that temperature is important for both energy and water loss when searching for a mate. Low temperatures could therefore be preferred to ensure that the individual does not use too much resources on searching so that more resources can be invested in reproductive output.

The model captures that there might be a high cost of reproducing in high temperatures, but what the model does not capture, that might be of additional importance, is that in too low temperatures, mobility and speed might be reduced, and the search for a sexual partner and predator escape may be compromised (Berwaerts and Van Dyck, 2004). Thereby low temperature could negatively affect the searching success and predation risk and not just the energy gained from feeding. In addition to environmental conditions, the chance of encountering a sexual partner could be a determining factor for activity, although the effect might differ between the sexes (Peixoto and Benson, 2009). This chance of encountering a mate could also be different under different weather conditions. The chance of finding a mate is in the model, but it is a constant, and an argument could be made for modifying the model to have a weather-dependent mating probability.

Activity, microhabitat selection and foraging behaviours are considered shared behavioural components of thermo- and hydro regulation (Rozen-Rechels et al., 2020). In the model, these behaviours are incorporated as the quite general activities of feeding and hiding. For most scenarios, hiding is mainly done in high temperature and low humidity conditions. This is what we could expect from individuals choosing to hide as a way of sheltering from demanding weather as is proposed, though only from a thermoregulatory perspective (e.g. Huey and Tewksbury, 2009; Sunday et al., 2014). In addition to physiology, behavioural flexibility and the availability of shade and local micro-climates are predicted to be important to be able to survive high temperatures (Huey and Tewksbury, 2009; Kearney et al., 2009), and behavioural flexibility might be necessary when considering hydro regulation as well (Chown et al., 2011; Rozen-Rechels et al., 2019). However, despite the possibility of hiding being a refuge from costly weather, the hiding alternative is itself very costly in terms of lost opportunities to gain water and energy from feeding and searching for a mate. Feeding could often be the most beneficial because even though it is associated with higher costs in terms of energy and water loss compared to the hiding scenario, as is also providing energy and water gain and will therefor often be an alternative that maintains internal energy and water states.

When it comes to the small amount of time spent hiding, this could at least partially be explained by the conservative benefits of hiding incorporated in the model. Even though hiding is given lower water and energy costs, we can imagine the real costs being even more reduced compared to the other activities. The reason for this is that hiding could be less costly both due to a reduction of activity, but also as sheltering from costly weather provides a more favourable microhabitat. Hiding may be helpful for survival in this model, especially from a water perspective. However, as it takes away time from activities that could otherwise have contributed to fitness, it is rather costly. The hiding alternative probably also has additional benefits that are not included here. In the model, individuals are experiencing the same risk of predation, independent of the activity they choose. Predation risk is known to impact prey behaviour, which might therefore be important in explaining insect activity patterns in addition to weather (Ottesen, 1990; Sih et al., 2000). Thus, a more biologically realistic scenario could instead be a lower predation risk when hiding.

The decision to hide is not only determined by external weather conditions but also by the combination of internal states. For the strategies similar to the baseline scenario, there is a tendency for individuals in high temperature, low humidity conditions to hide when in low water state. Individuals in higher energy state will hide even when their water state is higher. This is interesting because from an energetic perspective, it will be more beneficial to feed in these scenarios. Therefore, the reason to hide in these scenarios must be to conserve water, which seems to be something the individuals can allow themselves when energy is not the limiting resource.

The cold and wet scenario differs from the other scenarios, with a higher proportion of individuals hiding each time step. Except for the baseline scenario, this is also the scenario with the highest fitness. The reason why the individuals hide more in this environmental scenario is not straightforward to understand. The decision rule reveals that individuals in this scenario hide in different weathers and states than in the baseline scenario. For some of the most probable weathers in this scenario, it is optimal to hide for a relatively large combination of states. For example, at the lowest temperature, it is optimal to hide when in a high water state. The tendency for hiding in at lowest temperature is also so that in lower energy state it is optimal to hide for lower water states than when in higher energy states. This scenario is thereby showing quite the opposite picture compared to the other scenarios.

One explanation for this altered strategy could be the relative importance of the two states under this climatic condition. It is also worth mentioning that hiding is the default option in the model when two options are considered with approximately equal fitness, such as when death is inevitable. A similar fitness could also be the explanation for why individuals in high water states are hiding in the lowest temperature weathers as individuals in these benign wet conditions should not be limited by water, and from an energetic perspective, it is in the model equally good to hide and feed in the lowest temperature.

Even though the reason why individuals hide more in this climate is not clear, it can still teach us something about the real world in that individuals choices is not straight forward to predict as they might depend on either internal state or external state or a combination of the two. In addition, the optimal choices are predicted to be different for organisms optimized for and living in different climates. A deeper investigation of the relevance of internal versus external states and choices of individuals living in different environments might be a way forward in complementing work aiming at understanding insects' activity patterns, such as the research of Chown et al. (2004a) and Peixoto and Benson (2009). The study of Chown et al. (2004a) reveals that in addition to habitat moisture and temperature, which is the focus of this model, other factors, such as wind and precipitation events, are found to be important in determining whether to hide or feed.

The hot and dry scenario is remarkably different from the other scenarios, differing in terms of high mortality, the timing of reproduction and states when deciding to reproduce. In the other scenarios, individuals spend some time at the beginning of the season building up resources before trying to reproduce. However, the individuals optimized for a hot and dry environment instead immediately start reproducing, and their optimal strategy is to reproduce under more of the weather conditions than in the other scenarios and for lower energy and water states. The comparison between the hot and dry scenario and the others is interesting from a life history theoretical perspective on semelparity and iteroparity and the differences in reproductive effort, time of reproduction and length of reproductive period (Hutchings, 2021). Individuals in the other scenarios start reproducing later in the season, spread their reproductive effort over a longer time period and have a high probability of iteroparity. On their hand, the individuals in the hot and dry scenario experience higher adult mortality, leading to earlier reproduction and a shorter reproductive period. In accordance with what is predicted from life-history theory, conditions leading to higher adult mortality favour a strategy where individuals reproduce early, with high reproductive effort and short reproductive period (Hutchings, 2021). The results thereby predict that adaptation to harsh hot and dry environments that increase adult mortality from desiccation and starvation can support a higher probability of semelparity. From the transplant experiments of "hot dry" into "cold dry" and "cold wet" it is interesting to see that when in less stressful conditions, individuals still have a clear tendency towards earlier reproduction, especially in the ”cold and dry” scenario. Many individuals succeed in having more reproductive events as the mortality is reduced in these environments.

The transplant experiments predict lower fitness of individuals when the temperature increases and when the water availability decreases. This emphasizes the need to account not only for temperature but also how water availability changes in the local habitats of the organism to be able to predict how well individuals will perform under altered climatic conditions.

When comparing the fitness of foreign and local individuals simulated through the same environment, there is a small difference in fitness in the wet environments. However, the fitness difference between the local and the foreign individuals simulated through dry environments is quite large. This is interesting for two reasons. First, the different performance of local and foreign individuals predicts an importance of behaviour. Foreign and locals have the same physiological tolerance in the model and differ only in terms of behavioural strategy. The differences in performance must, therefore, be due to them displaying different behaviours. The implications of this result is the importance of behavioural decisions in shaping performance, in addition to the physiological tolerance. Thermal physiological tolerance has already been associated with daily activity. Specifically, Gimenez Gomez et al. (2018) found different daily activity patterns for different beetle species with different thermal tolerances. My results predict that activity should not only be explained from a physiological tolerance perspective but be complemented by the importance of different behavioural strategies. Second, the results predict that it is not that important to follow the optimal strategy in benign wet conditions. However, it might be more crucial for performance to follow the optimal behavioral strategy in more demanding, dryer environments.

In the context of climate change, a large body of research has been concerned with the consequence of altered temperature. As an example, in the comprehensive review of ecological and evolutionary responses to climate change by Parmesan (2006) ”temperature” is mentioned 46 times, and ”precipitation”/”rainfall” only 3 times. To date, much research has looked into the relation between body temperature and fitness through the concept of thermal performance curves (Angilletta Jr, 2009), also with the aim of predicting climate consequences (Deutsch et al., 2008; Huey et al., 2012; Dowd et al., 2015; Sinclair et al., 2016). The results from this thesis are thereby an attempt at starting complementing this physiological research by investigating the possibility of behavioural strategy and activity choice to buffer or hinder individual’s survival and reproduction in altered climatic conditions. Temperature and water availability can affect the hydration state of the insects, and this project is an attempt to include not only a thermal perspective but a hydrational one as well when predicting performance. Even though climate change projections predict that precipitation patterns will be changing for many regions (IPCC, 2021; Tebaldi and Sans’o, 2009), we lack a complete understanding of how this aspect of climate change will affect the fitness of organisms. Altered precipitation patterns as a climate change effect still consist of a gap in our knowledge about the impact of climate change on biodiversity.

Comparing populations adapted to different environments provides a particularly interesting contrast to predict responses to different climate change scenarios. I found the difference between locals and foreigners seems to be biggest in dry environments, indicating that in areas where climate change is leading to less water availability in the local habitats, it is more valuable to be behaviorally adapted as it comes at a larger fitness cost not to be so. Looking at the transplant experiments of individuals adapted to "cold dry" and "hot wet" scenarios into "hot dry", we see that as these are not adapted to this scenario, most individuals do not succeed in reproducing before they die. Even though there is a fitness difference between locals and foreigners also in the wet conditions, behavioural adaptation is not of equal importance in these environmental scenarios.

It is interesting to see what is predicted for populations that experience novel environments, different from what they are optimized for. When looking at the "cold dry" and "cold wet" transplanted into a warmer environment, the water availability being the same, average accumulated fitness is reduced. Reduces fitness in a warmer climate is according to predictions from a physiological thermal perspective of what we could expect for tropical ectotherms (Deutsch et al., 2008; Dowd et al., 2015). Altering the water availability only, as for the "hot wet" and "cold wet" into "hot dry" and "cold dry" respectively, reveals the fitness is dramatically reduced, predicting more drought and reduced water availability can have severe fitness consequences. On the other hand, if climate change instead gives a dry environment a better water supply, it is predicted to increase fitness. The results thereby suggest that to predict the fitness consequences of climate change, it is essential to consider how climate change is altering habitat humidity.

My results predict that from a combined energetic and hydrational perspective, especially a warm and dry climate will be severe for the organisms. At the same time the results indicate that if organisms are able to adopt a strategy closer to the optimal strategy, altering the timing of reproduction and reproducing in lower states, it can buffer against some of the fitness loss by allowing most individuals to successfully reproduce once. The potential of behavioral thermoregulation to buffer ectotherms against climate warming, through timing of seasonal activity, reproduction and thermoregulate by the use of shade is highlighted by Huey and Tewksbury (2009), Kearney et al. (2009) and Sunday et al. (2014) among others. The results from this thesis add to these predictions by indicating the importance of behavioural strategy and timing of seasonal activity in tackling new and more stressful environmental conditions. Displaying the optimal strategy is predicted to be most important in the least benign dry environments. Nevertheless, it still remains a large question about the potential of behavioural thermo- and hydro regulation to buffer ectotherms against climate change.

4.1 Conclusion and further work

In this thesis, I have investigated the double effect of temperature and water availability on behavioural activity using a state-dependent approach. The results predict that behavioural strategy is affecting performance, when the physiological tolerance is the same. The results also predict that especially warm and dry conditions might be severe for the organisms from a hydrational and energetic perspective, but that a behavioural strategy adapted to these harsh conditions can be important to ensure performance in such environments. The value of an adapted behavioural strategy is predicted to be most valuable in harsh dry conditions.

A natural next step from this theoretical exploration is empirical time budget experiments monitoring some model insect species' daily activity during the breeding season to gain more knowledge about how different weather conditions impact their activity pattern. Inspiration can be found from this study of Chown et al. (2004a) investigating determinants of activity pattern for the *Bothrometopus brevis* beetle at Heard Island. This study demonstrates the importance of investigating more weather parameters, such as wind, as these could be important determinants of activity. In this thesis, the effect of altered precipitation is investigated through a quite general inclusion of humidity/water availability, but the effect of the actual precipitation event on activity is not included. To be able to predict the effect of altered temperature and rainfall patterns from climate change on activity, a broader range of weather parameters and more nuanced measures regarding precipitation and humidity should be investigated.

From the modelling process it has become clear that even though much is known on the many mechanisms and complex physiology of water loss in insects (Addo-Bediako et al., 2001; Chown et al., 2011; Edney, 1977; Woods and Smith, 2010) more knowledge on the more detailed relationships and magnitude of water loss with temperature, humidity and metabolism for insects would help understand the effect of altered temperature and humidity and the role of behavioural choice of activity and microhabitat selection in the maintenance of water balance and avoidance of desiccation. However, understanding the role of behavioural choice of activity and microhabitat selection in the maintenance of water balance and avoidance of desiccation may be a critical but overlooked factor in the vulnerability of insects to future climate change. Although this thesis is made from the desire for a more ecological perspective (Chown et al., 2011; Rozen-Rechels et al., 2019), gaining such insight would benefit from more knowledge from empirical physiological experiments on insect water loss.

This theoretical model is a first step into the investigation of the double effect of temperature and water availability on insect behaviour and fitness through the effect on state-dependent choices. Even though the model in its current form is not able to uncover the trade-offs in behavioural thermo- and hydro regulation, it is a start to implement energy and water as internal states, and include loss and gain depending on activity/metabolism and weather. Future research should aim to investigate the relations between temperature, water and energy as these are important to understand thermo- and hydro regulation in ectotherms (Rozen-Rechels et al., 2019) and thereby the effect of climatic change in temperature and water availability regimes on insects' fitness.

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Appendix A

The content of Table A.1 displays the expressions and parameters for the functions for energy and water gain and loss which results in the net state transitions displayed in Figure 2.1 and Figure 2.2. These relations are therefore already described in the method chapter, but in the following is an in-depth explanation of how they were implemented in the model.

$A_i(z)$ is the energy loss depending on activity (i), having an exponential increase with temperature (z). This continuous function's values are rounded to integer values for the different temperatures, as the model only uses discrete steps. The scaling parameter a is higher for feeding and searching compared to hiding. To give searching an increased cost compared to feeding, an energetic searching cost s_1 is added.

$C_(z)$ is the energy gain from feeding modelled as a logistic increase with temperature and with the parameter values shown in this table. These values are also rounded in the model to be discrete values.

$B_i(z, w)$ is the water loss depending on humidity and temperature. The water loss for hiding is displayed in the matrix $B_{1_{zw}}$ with rows and columns corresponding to the temperature and humidity, respectively. The water loss for feeding is doubled, and the water loss for searching is the water loss for feeding plus an additional water cost (s_2).

$E(w)$ is the water gain when feeding is linearly increasing with higher humidity/water availability.

Table A.1: This tables displays the expressions and parameters used for implementing energy and water relations into the model.

Function	**Expression**	**Parameters and values**
$A_i(z)$	$A_1(z) = e^{a_1 z}$ $A_2(z) = e^{a_2 z}$ $A_3(z) = e^{a_3 z}+s_1$	$a_1 = 0.2$, $a_2 = a_3 = 0.4$ $s_1 = 2$
$B_i(z, w)$	$B_2 = 2B_1$ $B_3 = B_2+s_2 \begin{bmatrix} 1 & 1 & 1 & 1 & 1 \\ 1 & 1 & 1 & 1 & 1 \\ 1 & 1 & 1 & 1 & 1 \\ 1 & 1 & 1 & 1 & 1 \\ 1 & 1 & 1 & 1 & 1 \end{bmatrix}$	$B_{1_{zw}} = \begin{bmatrix} 5 & 4 & 3 & 2 & 1 \\ 11 & 9 & 7 & 5 & 3 \\ 17 & 14 & 11 & 8 & 5 \\ 23 & 19 & 15 & 11 & 7 \\ 29 & 29 & 19 & 14 & 9 \end{bmatrix}$ $s_2 = 20$
$C_{(}z)$	$\frac{L}{1+e^{-k(z-x_0)}}$	$k = 2.2$, $x_0 = 1.8$, $L = 6$
$E(w)$		$E_w = \begin{bmatrix} 9 & 18 & 27 & 36 & 45 \end{bmatrix}$

Appendix B

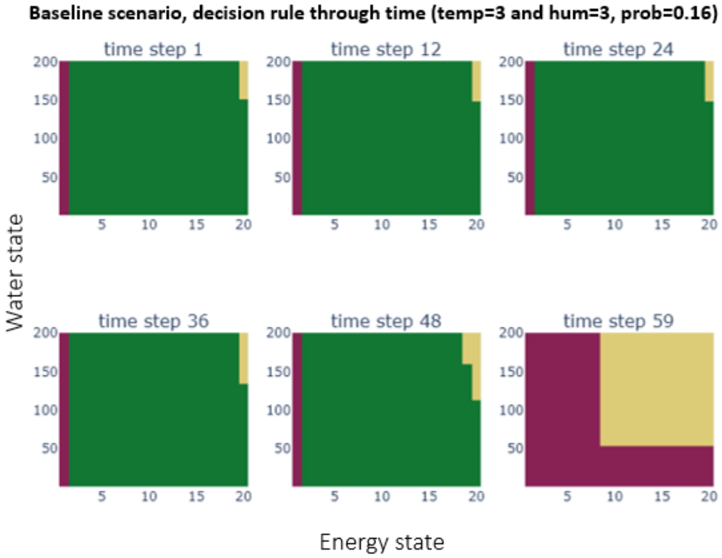


Figure B.1: Decision rule for baseline scenario showing the optimal choice of activity given for 6 time steps in intermediate weather. This is the most common weather in the baseline scenario.

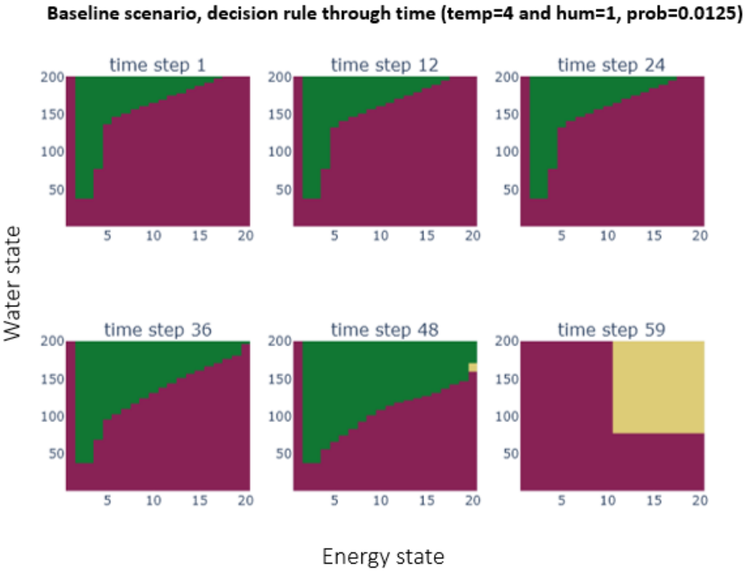
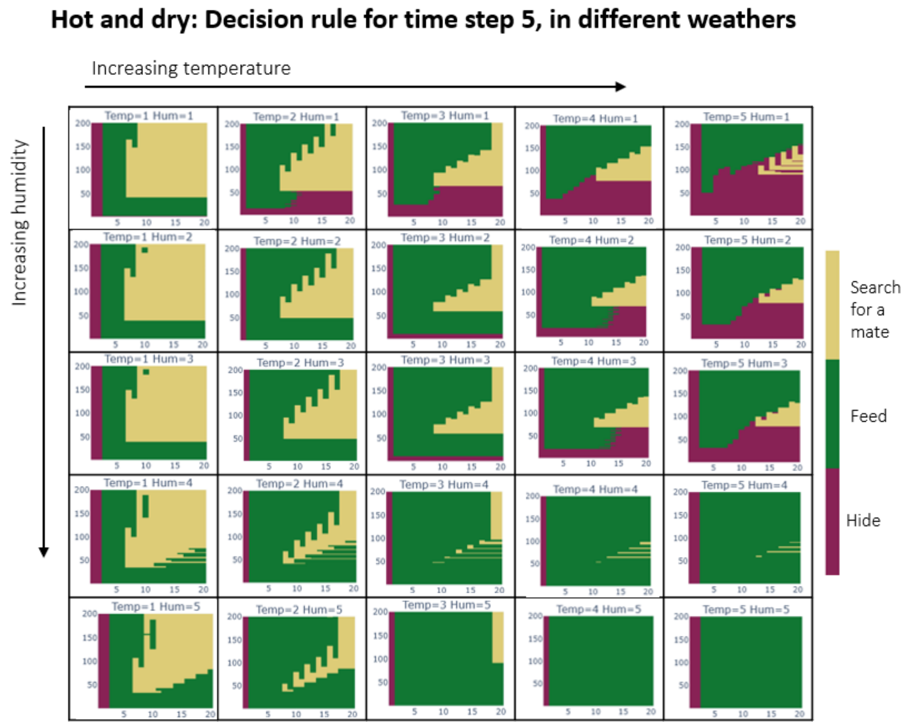
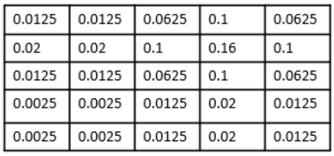


Figure B.2: Decision rule for baseline scenario showing the optimal choice of activity given for 6 time steps in relatively hot and dry conditions. This weather combination occurs with a low probability in baseline scenario.

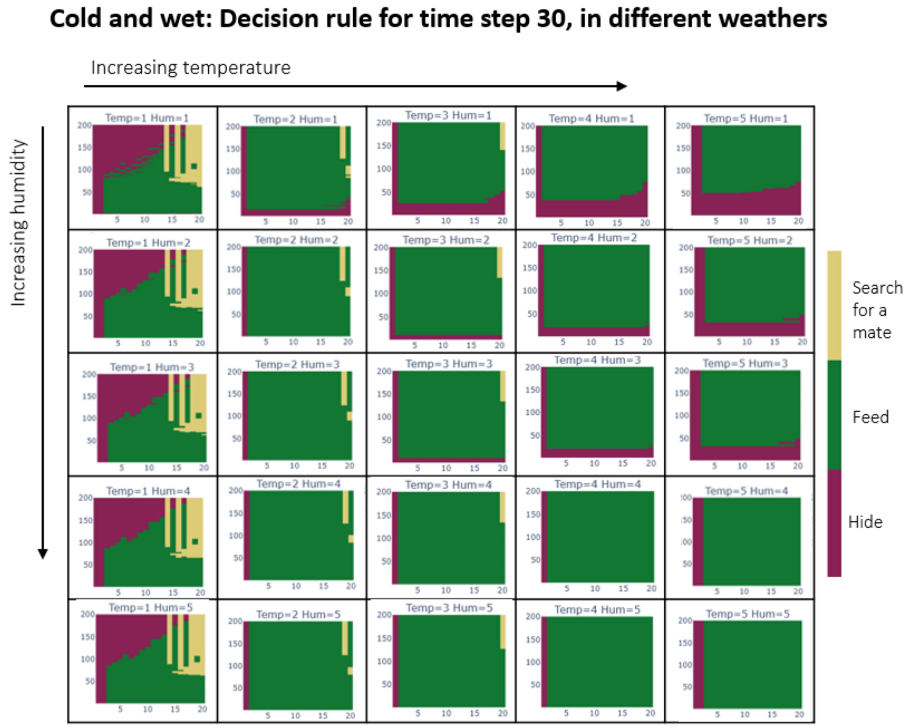


Weather probabilities



0.0125	0.0125	0.0625	0.1	0.0625
0.02	0.02	0.1	0.16	0.1
0.0125	0.0125	0.0625	0.1	0.0625
0.0025	0.0025	0.0125	0.02	0.0125
0.0025	0.0025	0.0125	0.02	0.0125

Figure B.3: Decision rule for hot and dry scenario showing the optimal choice of activity given state and weather for time step 5. For each subplot energy is on the x-axis and water on the y-axis. Mark that the weather combinations occur with different probabilities given in the table



Weather probabilities

0.0125	0.02	0.0125	0.0025	0.0025
0.0125	0.02	0.0125	0.0025	0.0025
0.0625	0.1	0.0625	0.0125	0.0125
0.1	0.16	0.1	0.02	0.02
0.0625	0.1	0.0625	0.0125	0.0125

Figure B.4: Decision rule for cold and wet scenario showing the optimal choice of activity given state and weather for time step 30. For each subplot energy is on the x-axis and water on the y-axis. Mark that the weather combinations occur with different probabilities given in the table

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