

UC Riverside

UC Riverside Electronic Theses and Dissertations

Title

Basking in the Warmth of the Red Queen: Novel Methods for Studying Rattlesnake Behavioral Strategies with Agent-Based Models

Permalink

<https://escholarship.org/uc/item/8d20h532>

ISBN

9798180114396

Author

Remington, Michael James

Publication Date

2026-05-09

Copyright Information

This work is made available under the terms of a Creative Commons Attribution-NonCommercial-ShareAlike License, available at <https://creativecommons.org/licenses/by-nc-sa/4.0/>

Peer reviewed|Thesis/dissertation

UNIVERSITY OF CALIFORNIA
RIVERSIDE

AND

SAN DIEGO STATE UNIVERSITY

Basking in the Warmth of the Red Queen:
Novel Methods for Studying Rattlesnake Behavioral Strategies
with Agent-Based Models

A Dissertation submitted in partial satisfaction
of the requirements for the degree of

Doctor of Philosophy

in

Evolutionary Biology

by

Michael James Remington

June 2026

Dissertation Committee:

Dr. Rulon Clark, Chairperson

Dr. Timothy Higham

Dr. Lorelee Larios

Dr. Xiaofeng Xu

Copyright by
Michael James Remington
2026

The Dissertation of Michael James Remington is approved:

Committee Chairperson

University of California, Riverside
San Diego State University

ACKNOWLEDGMENTS

I'd like to thank the people who gave me this opportunity to pursue this degree including Dr. Jeet Sukumaran, Dr. Rulon Clark, Dr. Timothy Higham, and the National Science foundation (Grant Number IOS 1856404) for funding this opportunity. Thanks as well to Dr. Lorelee Larios and Dr. Xiaofeng Xu for serving on my committee and all the advice they have given me to help form my dissertation.

I also would like to give personal thanks to Dr. Elizabeth Waters for all the administrative and emotional support. A special thanks to Dr. Ryan Hanscom and all the field crew for collecting the data used in my dissertation. Finally, thanks to my friends, Michael Tofflemier, Miranda Buckley, and Mayank Kashyap for all the laughs along the way.

ABSTRACT OF THE DISSERTATION

Basking in the Warmth of the Red Queen:
Novel Methods for Studying Rattlesnake Behavioral Strategies
with Agent-Based Models

by

Michael James Remington

Doctor of Philosophy, Graduate Program in Evolutionary Biology
University of California, Riverside and San Diego State University, May 2026
Dr. Rulon W. Clark and Dr. Timothy Higham, Co- Chairpersons

All chapters of this dissertation share two central themes: understanding predator–prey dynamics between kangaroo rats and rattlesnakes and developing standardized computational methods that are generalizable to other biological systems. In Chapter 1, I develop a game-theoretic agent-based model to simulate microhabitat use strategies in the kangaroo rat-rattlesnake system. Microhabitat choice shapes predator-prey interactions through differential selection pressures from aerial predators and sit-and-wait predators, as well as physical structure for refuge and camouflage. The results of our analysis show that when specialist predators occur at higher densities than generalist predators, both generalist predators and prey shift toward habitat specialization due to competition. In Chapter 2, I simulate microhabitat use from the perspective of an ectothermic predator that is thermoregulating to compare computational approaches to standard thermal ecology metrics used for determining how accurately ectotherms can maintain a preferred body temperature range. I find that rattlesnakes are not thermoconformers, but that models assuming regulation around a thermal preference boundary versus a thermal

preference optimum yield similar simulated body temperature profiles. My findings indicate that individual thermal preferences strongly influence thermoregulatory behavior. In Chapter 3, I develop an ensemble modeling framework linking agent-based simulations of foraging and thermoregulation to a mathematical predator–prey model to assess population dynamics under climate change. Together, these chapters demonstrate how agent-based models can link behavioral decision-making and physiological constraints to population-level consequences in nonlinear predator–prey systems.

TABLE OF CONTENTS

Chapter 1 - Uumarrty and the Nash Score: A Game theoretic, Agent-based Framework for Understanding Evolutionary Stability in Behavioral Traits.....	1
Abstract.....	2
Introduction	3
Methods.....	6
Construction of the Model.....	6
The Nash Score and Post Simulation Analysis.....	11
Kangaroo Rats and Rattlesnakes Demographic Parameters.....	15
Results.....	17
Case Study 1: Differing Foraging Energy Gains for Kangaroo Rats in Microhabitats	17
Case Study 2: Differing Strike Success of Rattlesnakes in the Bush Microhabitats	19
Case Study 3: Introducing Owls	21
Discussion.....	23
The Nash Score and Expanding Agent-based Modeling Methodology	23
Case Study 3: Introducing Owls	28
Conclusion and Future Work	31
Supplementary Material	32
Sensitivity Analysis	32
Figures.....	35
Tables.....	45
References.....	48
Chapter 2 - Thermal Dynamics of Ectotherm Behavioral Strategies: Insights from Agent-Based Simulations	51
Abstract.....	52
Introduction	53
Methods.....	56
Empirical Data.....	56
Simulation Model Description	57
Data Integration and Interpolation	59
Parameter Estimation with Gradient Descent.....	60

Thermal Indices.....	61
Time Series Comparison Analysis.....	62
Predicting Microhabitat Occupancy with Supervised Machine Learning	63
Results.....	64
Ecological Comparison of Thermoregulatory Strategy	64
Simulated Body Temperature Accuracy	66
Classifying Microhabitat Occupancy Accuracy	66
Discussion.....	68
Conclusion and Future Work	71
Tables.....	73
Figures.....	82
References.....	92
Chapter 3 - Climate Warming Reshapes Ectotherm–Endotherm Predator–Prey Interactions Through Temperature-Dependent Behavior.....	96
Abstract.....	97
Introduction	98
Materials and Methods	101
Purpose.....	101
Ecological Data and Analysis	104
Experimental Design	106
Suffugium Simulation Overview, Entities, and State Variables.....	108
Suffugium Sub-Models.....	110
Rosenzweig-MacArthur Mathematical Model.....	110
Estimating Annual Attack Rate and Handling time.....	112
Stability Analysis and Root Finding.....	113
Population Density Simulation	113
Sensitivity Analysis and Model Validation.....	114
Results.....	114
Behavior and Thermoregulatory Patterns	114
Predator-Prey Interactions	115
Population Dynamics and Stability	117
Discussion.....	119

Behavioral and Physiological Responses to Warming	119
Consequences for Predator-Prey Interactions Across a Latitudinal Gradient.....	120
Integrating ABM and Population Models: Implications, Limitations, and Future Directions	122
Conclusion and Future Work	124
Figures	125
Tables	132
Supplementary Material	137
Suffugium Sub-Models.....	137
Deriving the Jacobian Matrix	145
Model Validation	148
Sensitivity Analysis	152
Supplementary Figures	155
Supplementary Tables.....	163
References	165

LIST OF TABLES

Table 1.1: Constant experimental parameters. Cells titled “EXP” are parameters that are associated with experimental groups for a given case study. Parameters that state “per x cycles” indicate that the action is done once after x number of cycles in the associated cell have passed.....	46
Table 1.2: Experimental parameters for the case study of differing foraging energy gains in microhabitats for Kangaroo Rats.	46
Table 1.3: Experimental parameters for the third case study of differing strike success experimental groups.....	46
Table 1.4: Experimental parameters for the case study of introducing owls into the system experimental groups.....	47
Table 2.1: Parameter values for each of sub-model when parameters are not estimated via the gradient descent algorithm. For the preferred _{est} case, parameters for thermal minimum, thermal maximum, and thermal optima vary for each rattlesnake (see supplementary materials).	73
Table 2.2: Estimated thermal preference values used in the preferred _{est} sub-model. Data with a sampling frequency of 70 minutes was not imputed, whereas data with a sampling frequency of 15 minutes was imputed.	76
Table 2.3: Mean least square error (MSE) mixed linear regression results. MSE distances with thermoregulation strategy as a fixed effect explanatory variable and study site as a fixed effect. Individual snakes were treated as a random effect. Model coefficients were evaluated using z-statistics derived from maximum likelihood estimation. The results of this model suggest that the Boundary, Preferred, and Preferred _{est} strategies were significantly effective at reducing MSE.	77
Table 2.4: Mean Absolute Percentage Error (MAPE) mixed linear regression results. MAPE distances with the thermoregulation strategy as an explanatory variable and study site as a fixed effect. Model coefficients were evaluated using z-statistics derived from maximum likelihood estimation. Individual snakes were treated as a random effect. Based on this model, the simulated body temperatures with parameters estimated (Preferred _{est}) was the only thermoregulatory sub model that was significantly better at reducing MAPE compared to the random thermoregulatory sub model, which is represented by the intercept group. Overall, study site differences were more significant than the specific thermoregulation strategy sub-model, which could indicate there may be significant differences at the population and individual level in thermoregulation patterns.	78

Table 2.5: Mixed linear regression results correlating Dynamic Time Warping (DTW) distances with the thermoregulation strategy as an explanatory variable and study site as a fixed effect. Model coefficients were evaluated using z-statistics derived from maximum likelihood estimation. Individual snakes were treated as a random effect. Based on this model, the simulated body temperatures with parameters estimated (Preferred _{est}) was the only thermoregulatory sub model that was significantly better at reducing DTW compared to the random thermoregulatory sub model, which is represented by the intercept group. Overall, study site differences were more significant than the specific thermoregulation strategy, which could indicate there may be significant differences at the population and individual level in thermoregulation patterns.	79
Table 2.6: Results of the top 10 most accurate machine learning models predicting microhabitat occupancy of all models ran. Populations were subdivided by the study site and custom models were built from these sub populations marked by the column 'Study Site'. The first six columns are the model specifications, columns 7-10 showcase model performance, and c the results of our confusion matrix for each model and AUC which indicates model validity (11-15). Metrics such as accuracy, precision, recall, and F1 score are presented alongside additional performance metrics but accuracy is how we sorted the data set to evaluate our top models.	80
Table 2.7: The top 10 models from machine learning pipeline predicting microhabitat occupancy for all snakes sampled (study site = total population) under various model conditions. Filtering the data this way yields us models where we assume that intraspecific differences among populations can be generalized with a single model. The first five columns are the model specifications, columns 6-9 showcase model performance, and columns 10-14 are further details to how performance metrics were calculated. In our analysis we primarily focused on the accuracy of the model over metrics such as precision, recall, and F1 Score.	81
Table 3.1: Summary of predator behavioral states with corresponding microhabitat, metabolic state (Standard Metabolic Rate SMR/Active Metabolic Rate AMR), and active foraging status.	132
Table 3.2: Key parameters used in the simulation and analytical models.	135
Table 3.3: Results of regression models showing the effects of body mass, warming level, and brumation length on (A) total prey consumption and (B) survivorship. Study site is included as a control or random effect as indicated. Robust (HC3) standard errors are reported for OLS model.	136
Table 3.4: Descriptive statistics for empirical rattlesnake body temperatures from telemetry data grouped by study site, with mean reported with standard error.	163

Table 3.5: Descriptive statistics for empirical rattlesnake body temperatures from telemetry data grouped by meteorological season and study site. Mean values are reported with standard error. 163

Table 3.6: Validation statistics comparing hourly simulated and empirical body temperatures across study sites. Bias is defined as $\text{mean}(T_{\text{sim}} - T_{\text{emp}})$. RMSE stands for Root mean squared error which measures the average magnitude of error. Kolmogorov–Smirnov (KS) statistic quantifies the maximum discrepancy between the cumulative distributions of simulated and empirical body temperatures, with values near 0 indicating close agreement and values approaching 1 indicating strong divergence. KS p is the p-value determined from the Kolmogorov–Smirnov test. 164

LIST OF FIGURES

- Figure 1.1:** Conceptual diagram showcasing the logic of an individual simulation. This logic is applied to both the kangaroo rat population and the rattlesnake population of all simulations. 35
- Figure 1.2:** Conceptual diagram of the simulation workflow for how to generate the results of one experimental group of a case study. This workflow was applied to all 6 experimental groups of all 3 case studies. 36
- Figure 1.3:** Both graphs are the mean microhabitat preference for the kangaroo rat population per generation during an individual simulation. A microhabitat preference of 1 is a complete preference toward bush microhabitats while a microhabitat preference of 0 is a complete preference toward the open. (A) is a single simulation for the owl experiment from experimental group one. (B) is a single simulation for experimental group 6. The metric λ_0 is the difference between the microhabitat preference of an optimal point and the previous optimal point in the time series which represents the magnitude of the strategy flip, shown by the red dotted line. The metric β_0 is the number of generations from one optimal point to the previous one. When λ and β are zero this means there are no optimality points and the microhabitat preference of the population is in equilibrium which can be seen in (B). Point class represents whether an optima point is a maximum or a minimum point. The arrow indicates how from experimental group 1 to experimental group 6, the microhabitat preference of the kangaroo rat population reached an equilibrium due to the introduction of owls. 37
- Figure 1.4:** Results of the Tukey Post Hoc ANOVA test. Values in each cell are the differences of the means between experimental groups. A positive increase (red) demonstrates an increased preference to the bush, while a negative mean difference indicates an increased preference for the open. Stars represent whether the experimental groups have statistically significantly different means. *** $p < 0.001$, ** $p < 0.01$, * $p < 0.05$ 38
- Figure 1.5:** Mean microhabitat preference of the populations for all experiments with pure microhabitat usage strategies. The y-axis shows the experimental groups with pie charts representing how the experimental parameter of interest is being changed. The x-axis is the mean microhabitat preference of the population over all generations sampled from the simulation. The sum of the open preference bar graph (red) and the bush preference bar graph (blue) in all figures is equal to 1. (A) shows the microhabitat preferences of kangaroo rats for the differing foraging gains experiment for the kangaroo rat population. (B) is the same as (A) but for the rattlesnake population. Pie charts are of the values in Table 1.2. Figure (C) is the microhabitat preferences of kangaroo rats in the rattlesnake strike probability experiment. Pie charts are of the values in Table 1.3. Figure (D) is the same as (C) but for the rattlesnake population. (E) are the microhabitat

preferences of the kangaroo rat population under different experimental designs for the owl experiment. Pie charts are of the values in Table 1.4. (F) is the same as (E) but for the snake population. 39

Figure 1.6: Mean microhabitat preference of the populations for all experiments with mixed microhabitat usage strategies. The y-axis shows the experimental groups with pie charts representing how the experimental parameter of interest is being changed. The x-axis is the mean microhabitat preference of the population over all generations sampled from the simulation. The sum of the open preference bar graph (red) and the bush preference bar graph (blue) in all figures is equal to 1. 40

Figure 1.7: Analysis of metrics produced by the point classification algorithm applied to simulations of pure strategies across all case studies, including total number of strategy flips, the mean number of generations before a strategy flip, and the mean magnitude of a strategy flip.β 41

Figure 1.8: Analysis of metrics produced by the point classification algorithm applied to simulations of mixed strategies across all case studies, including total number of strategy flips, the mean number of generations before a strategy flip, and the mean magnitude of a strategy flip. 42

Figure 1.9: Results of the Nash Score analysis where each cell represents the Nash Score for that specific experimental group associated with the experimental simulations. The Nash Score is the ratio of simulations that reached equilibrium over the total number of simulations run for a given experimental design. A Nash Score of 1 means that 100% simulations completely reached equilibrium and the associated microhabitat preference strategy is an evolutionarily stable strategy and cannot be invaded by other strategies throughout evolutionary time. (A) shows Nash Score values for the kangaroo rat population and (B) shows the same information but for the rattlesnake population. 43

Figure 1.10: Results of sensitivity analysis of the microhabitat preferences of kangaroo rats and rattlesnakes. Each point is the mean microhabitat preference of ten simulations for the population with the given parameter being changed. Color represents the parameter being changed and the value it is being changed to. Circles indicate results for kangaroo rats (krats) while x's represent rattlesnake results. See Table 1.1 for the base parameters that are being manipulated. 44

Figure 2.1: Workflow of the simulation analysis conducted. ThermaNewt, is the name for the simulation model based on Newton's law of cooling. Random, Boundary, and Preferred represent our three thermoregulation sub-models..... 82

Figure 2.2: Behavioral response functions shown with black lines for our three thermoregulatory sub-models. The x axis is the organism's internal body temperature and the y axis is the probability of an agent switching to the optimal thermal refugia. Red

lines represent the thermal preference range we set for the snakes. A) Represents the random model, where our modeled organism flips states at random regardless of internal body temperature. B) The boundary model where the organism changes state if it is no longer in the thermal preference range. C) The preferred model represents an organism trying to maintain its body temperature along a thermal optima (shown in blue)...... 83

Figure 2.3: Both graphs showcase microhabitat usage metrics by thermoregulation strategy. Figure A, the y-axis represents the probability of being in the open, where 1 is 100% probability of being in the open and 0 is 100% probability of being in the burrow. Figure B is the average count of state flips from being in the open to back to the burrow or vice versa per snake. 84

Figure 2.4: Plot matrix to showcase simulated body temperature of the various thermoregulation strategies (blue) plotted alongside empirical rattlesnake body temperature (orange) for the month of September. Thermal preference zone marked by red lines. The x axis is the date and the y axis is body temperature. The first row is a snake (EDCRVI003) collected in Canada, the second row is a Nebraska snake (NVC RVI030), and the third is a snake collected in Texas (MGCRVI021). This was with non-imputed data which has a sampling frequency of 70 minutes. 85

Figure 2.5: This figure presents a time series distance analysis using Mean Squared Error (MSE), Mean Absolute Percentage Error (MAPE), and Dynamic Time Warping (DTW) for each thermoregulatory strategy. The top row displays the mean and standard error of the time series distance metrics, illustrating the precision and variability of each metric across thermoregulatory sub-models. The bottom row features kernel density distribution plots of the distance values, providing a visual representation of the accuracy distribution for each thermoregulatory strategy. This analysis allows for a quantitative assessment of the effectiveness and consistency of different thermoregulatory sub-models in simulating real-world body temperature dynamics 86

Figure 2.6: Probability of being in the open by hour. The y-axis represents the probability of being out of the burrow, where 1 is 100% probability of being in the open and 0 is 100% probability of being in the burrow. 87

Figure 2.7: Thermal accuracy for snakes caught in the field, with simulated agents included. Thermal accuracy (db) is a metric that measures the difference between an organism's body temperature (T_b) from its thermal preference zone. High values of thermal accuracy indicate poor thermal accuracy [13, 21, 27]. 88

Figure 2.8: Thermal quality by microhabitat and for simulated snakes. Thermal quality (de) is a metric that measures the difference between environmental temperature (T_e) from the thermal preference zone [13, 21, 27]. Thermal quality traditionally cannot be estimated for snakes caught in the field due to not knowing what microhabitat (T_e) they

may be sampling. However, we can assess this for simulated agents to gain a better understanding of the thermal conditions snakes may experience in field conditions..... 89

Figure 2.9: Plot grid of four thermal indices calculated by hour of the day. Figure A showcases thermal quality (de) is a metric that measures the difference of the thermal operative temperature (T_e) from the thermal preference zone. So high values of de indicate low quality thermal habitat. Thermal accuracy (db) which is a metric that measures the difference between an organism's body temperature (T_b) from its thermal preference zone. High values of db indicate poor thermal accuracy. Figure C showcases thermal effectiveness (E) which is one minus the ratio of mean db and mean de. Values of one indicate careful and precise thermoregulation; zero indicates the animal does not need to thermoregulate and is thermoconforming, while values approaching negative one indicates periods of where the organism is in poor habitat and are actively avoiding thermoregulation. Finally, Figure D is the thermal exploitation index (Ex) which is the percentage of time spent in the thermal preference zone. Higher values indicate more time spent in the thermal preference zone. 90

Figure 2.10: Kernel density plots of the accuracy results for all machine learning models built. Figure A is the results grouped by the sample population (Study Site) and Figure B is the results grouped by the thermoregulatory sub-model used to simulate training labels. 91

Figure 3.1: Rattlesnake sub-model conceptual diagram. 125

Figure 3.2: Brumation periods for each site and climate condition showcasing the schedule of brumation days. We used data from free ranging snakes to derive a brumation rule for simulated agents. Brumation is initiated when, on any given day, at least one hourly burrow temperature falls below 5°C and the mean of burrow and open microhabitat temperatures is also below 5°C. 125

Figure 3.3: Descriptive statistics for thermal ecology metrics of the nominal set of the 1-year Suffugium simulation during the active season. The nominal is initiated at a prey density of 7 small mammals per hectare. Average body temperature (A) of snake agents increases with warming at all sites. Thermal Accuracy (C) is the difference between thermal optima (29°C) and body temperature. Thermal quality (E) is the absolute difference between environmental temperature and thermal optima. Right panels display behavioral profiles for the snakes adjusted by the length of the brumation period to make them directly comparable. Warming temperatures at all three sites decreases the need to thermoregulate (B) but only minimally increase the need to forage (D), resulting in more time spent in non-foraging ("rest") states (F). 126

Figure 3.4: Results of prey density map simulations measuring mean prey consumed (A) and snake survivorship (B) with respect to the prey density parameter. Under warming

conditions prey consumption increases at all sites, but snake agent survivorship remains similar. 127

Figure 3.5: Fitting prey consumption rates to the Holling type II model shows that the saturation point (the maximum number of meals) is expected to grow at a larger magnitude than the attack rate, indicating that predators are not necessarily getting more efficient at prey capture but will have more time in the year to consume prey. 128

Figure 3.6: Population density simulations using the Rosenzweig-MacArthur Model show some variation across sites. Canada (A) populations tend to have lower prey densities but more rapid oscillations, while Texas (C) exhibits less frequent oscillations but higher prey densities. Nebraska (B) is intermediate between the two. 129

Figure 3.7: Estimated prey and predator densities across sites and climate scenarios. Our model indicates that warming temperatures lead to reductions in overall prey density at all 3 of the sites and across all climate scenarios. 130

Figure 3.8: Stability maps of estimated attack rates ($\hat{a}$) and handling times ($\hat{h}$) by predator and prey carrying capacities. In figures (A) and (C), we hold handling time constant at 0.15 to see how variation in attack rate ($\hat{a}$) interacts with predator (K_{pred}) and prey (K_{prey}) carrying capacities, respectively. Figures (B) and (D) show the corresponding relationships for handling time ($\hat{h}$) while holding attack rate constant at 2. Black regions indicate parameter combinations leading to unstable oscillations, gray regions represent saddle equilibria, and white regions denote stable coexistence equilibria. Colored vertical lines mark site-specific parameter estimates, while line styles denote experimental warming scenarios. Overall, stability regions are narrow, suggesting that predator-prey coexistence at local spatial scales may be sensitive to small changes in $\hat{a}$, $\hat{h}$, and carrying capacities. 131

Figure 3.9: Distributions of body size for our three study sites. We found that body masses tend to be greater in northern populations. 155

Figure 3.10: Scatter plots of open and burrow temperatures aggregated from an array of operative temperature models deployed at each study site. This is the base environmental data used for Experiment 0. This data was experimentally increased by 1, 2, and 3°C to simulate the experimental groups. 155

Figure 3.11: Mean hourly temperatures for burrow, open, and rattlesnakes for each site and season. During the brumation behavioral state, we set the snake agents body temperature to 10°C based on live snake body temperatures in the winter months. 156

Figure 3.12: The rate of prey consumption as a function of prey density across simulations. Fitting this data to the Holling type II foraging model (Green) closely matching with average prey consumption rates (Red). The parameter $\hat{a}$ is the estimated

attack rate, $\hat{h}$ is the estimated handling time, and R^2 is how well the model fits the data. Across all three sites, we see similar trends of warming temperatures leading to increased attack rates and decreased handling times. 157

Figure 3.13: A qualitative comparison between simulated snake body temperatures and field active snake body temperatures. Column 1 (Figure A, D, and G) showcases body temperatures of a single snake versus a simulated snake at that site for the month of July. Column 2 (Figure B, E, H) is the same data as column 1 but over the course of a full year. Column 3 (Figure C, F, I) is a comparison of the average body temperature each month of the populations of simulated versus field snakes. 158

Figure 3.14: The distribution of body temperatures of simulated versus field snakes body temperatures during the active season. 159

Figure 3.15: Median days between a successful prey capture for simulated snakes across each climate scenario. 160

Figure 3.16: One factor at a time (OFAT) sensitivity analysis of simulations from the Suffugium agent-based model. We summarized the output by taking the mean of the prey consumption rates. For this analysis, we leveraged Texas site data at baseline experimental temperatures (Exp 0). The x-axis shows the manipulated variable and values input into simulations. The nominal set (orange) is baseline parameters we leveraged in the nominal set simulation analysis (see results section). Blue bars are deviations in the parameter of interest. Numbers on top of bars denote the measured influence metric which is the ratio of the percent change in prey consumed over the percent change in the parameter value with respect to the nominal (See Table 3.2 for nominal set variables). Overall, simulations had little parameter sensitivity as no influence value exceeds 1 and prey consumption rates tend to vary between 4 – 6..... 161

Figure 3.17: Sensitivity analysis (OFAT) of mean prey density and predator density simulated in the Rosenzweig-MacArthur Model. For the nominal set (orange), we set an attack rate of 2 and a handling time of 0.15. Figures (A, C) are direct parameters in the Rosenzweig-MacArthur Model. Figures (B, D) are parameters used to calculate the intrinsic growth rate of the prey population (See Table 3.2). Numbers above bars indicate the influence. The color of the influence value represents if the simulation was stable equilibrium (black), a saddle point equilibrium (purple), or unstable equilibria (red). .. 162

Chapter 1 - Uumarrty and the Nash Score: A Game theoretic, Agent-based Framework for Understanding Evolutionary Stability in Behavioral Traits

Michael Remington^{1*}, Rulon W. Clark¹, Ryan J. Hanscom¹, Timothy E. Higham², Jeet Sukumaran¹

¹ Dept. of Biology, San Diego State University, San Diego, California, USA. ² Department of Evolution, Ecology, and Organismal Biology, University of California, Riverside, California, USA.

* mremington3369@sdsu.edu

Abstract

This paper introduces a new in silico framework for testing hypotheses relating to behavioral strategies in predator-prey systems. To this end, we present two tools for simulating and analyzing behavioral trait dynamics: The Nash Score, a novel metric for evaluating evolutionary stability, and Uumarrty, a Python-based framework for simulating predator-prey interactions using game theory. These tools provide a new approach for assessing the temporal co-evolution of behavioral traits within agent-based models, with a particular focus on predator-prey dynamics, though the framework is generalizable to other ecological interactions. The Nash Score functions as an analog to the Evolutionarily Stable Strategy (ESS) from classical game theory, offering a quantitative index to assess the relative stability and resilience of behavioral traits under selection. We demonstrate the utility of these tools through a case study focusing on the microhabitat preferences of kangaroo rats and rattlesnakes. Specifically, we explore the emergence and stability of optimal strategies across scenarios with: (1) heterogeneous energy yields among microhabitats, (2) differential predator attack success rates by microhabitat, and (3) the presence of a second, specialist predator. Our results highlight how microhabitat specialist predators can drive generalist predators in the system to exhibit specialization due to competition, leading to behavioral strategy stability in the system. Our case studies also show how behavioral trait dynamics can greatly vary depending on whether the trait is modeled as a pure strategy versus a mixed strategy. Collectively, this framework enhances our ability to explore ecological and evolutionary

responses to environmental change, supporting more robust and comparable simulation-based research in eco-evolutionary dynamics.

Introduction

When modeling predator-prey behavioral interactions, explicitly accounting for the co-evolution of both populations is important for accurately understanding the system, as opposed to modeling one of the populations as a fixed entity [1, 5, 15]. This phenomenon is due to the fitness landscape of both populations being interdependent on the behavioral strategy of the other species, leading to a coupling effect [9]. However, modeling the co-evolution of both populations can be difficult from a computational perspective as it introduces more variables and parameters, and increases the complexity of the model output. In this paper, we propose a new method in this paper that we term the “Nash Score”, which is a post-hoc evolutionary stability analysis we use to summarize the temporal co-evolutionary effects of behavioral trait evolution in an agent-based system.

The Nash Score functions as an analog to the concept of the evolutionarily stable strategy (ESS) in evolutionary game theory [24], but for an agent-based modeling framework. This new method will give researchers a standardized metric to assess the evolutionary stability of traits in an arbitrarily complex, co-evolving, simulated systems under various conditions. The Nash Score also can be utilized as a measure of the degree of divergence from the stable point, as it is a continuous metric. This provides a standardized, quantifiable description of the system under a given set of conditions. From

a theoretical perspective, the Nash Score can be used to tell whether the system is either periodic or bi-stable, which is typical of evolutionary arms races, versus the system state reaching the ESS.

Taking tools from evolutionary game theory and integrating them into an agent-based system addresses several different gaps in the field of modeling predator-prey interactions. First, utilizing agent-based models addresses critiques of game theory being too simplistic and unable to capture the complexity of real-world systems, especially across biological scales [16]. Second, computational simulations can provide a standardized post-hoc analysis of agent-based systems which allows for the ability to contrast the results of simulation studies and non-linear systems among researchers, the lack of which has been a critique of agent-based modelling [3, 8, 12]. Finally, agent-based simulations allow researchers to assess the emergent consequences of shifts in ecological conditions, which is useful for modeling the long-term consequences of rapidly changing environmental conditions [11].

To demonstrate how our methods can contribute to studying the evolution of optimal behavioral strategies, we apply our approach to a predator-prey system of a habitat generalist prey (kangaroo rats) and a habitat generalist sit-and-wait predator (rattlesnakes) to assess how they influence one another's microhabitat preferences under various experimental designs. The dynamics of microhabitat usage in rattlesnakes and kangaroo rat systems have been studied in both empirical [4, 10, 6, 14, 22] as well as theoretical contexts, including an influential predator-prey game theory model [5], an

agent-based model [21], and other mathematical frameworks [7]. This makes this system suitable for comparing our methodology to a rich body of previous research.

We incorporated the game theory logic into an agent-based simulation model we entitled “Uumarrty” along with the Nash Score to re-create a previous mathematical game theory model which analyzed the same system [5]. Following this original game theory model, we also incorporate a second predator, a habitat specialist, to determine how its presence affects the microhabitat use of the generalist kangaroo rats and snakes. The original model found that ESS conditions occurred when the risk from owls in the open microhabitat was larger than the risk from snakes present in the bush microhabitat, and under these conditions all snakes and all rodents should select the bush microhabitat. Thus, by adding a specialist predator (owls) into our system, we expect to observe similar qualitative findings of the optimal behavior strategy and ESS conditions.

In conjunction with our case study of introducing a specialist predator into the system, we explore two other experimental conditions; first, we assess the influence of increasing heterogeneity in energy gains from kangaroo rats foraging in different microhabitats. This case study could be viewed as a bottom-up effect, as the selection pressure only directly impacts the prey. Secondly, we analyze the impact of increasing heterogeneity between predator attack success in different microhabitats, as this condition is analogous to a top-down effect.

A long-standing debate in the predator-prey literature revolves around whether the microhabitat preferences of prey are primarily driven by risk aversion caused by predator decisions [7], or by decisions made by prey to maximize foraging yields [25].

One primary objective of all our experimental designs is to determine which ecological factors most influence shifts and stability in the microhabitat preferences of a predator-prey system. We also sought to confirm the validity of the use of the Nash Score, as well as to showcase how researchers can utilize the Nash Score for novel analysis of community dynamics. Comparing the Nash Score analysis results across our set of case studies allows us to examine the importance of factors driving the behavior of organisms across the system.

Methods

Construction of the Model

Agent-based Modelling and the Genetic Algorithm

Our model is an agent-based, stochastic predator prey model written in Python 3.8 [26]. The basic model has two main populations of agents: the kangaroo rat agent (prey) and the rattlesnake agent (predator). We applied an evolutionary genetic algorithm to both populations that acts on a microhabitat preference trait that is assigned to individuals of the population at birth (Figure 1.1). Agents move in a virtual landscape composed of individual cells representing microhabitats based on a random decision that is weighted by the behavioral preference trait for one microhabitat over another. This microhabitat preference trait is an inherited, mutable trait assigned at birth of the new agent. These virtual organisms are modeled as asexual populations with discrete, non-overlapping generations.

During an agent's generation time, agents accrue payoffs by successfully foraging without dying from either predation or energy depletion. Organisms move based off their preference which is treated as a constant trait within a generation but evolves within the population over the course of the simulation. There are three parameters set by the user (owl movement frequency, snake movement frequency, and kangaroo rat movement frequency) which indicates how many cycles pass before agents move to a new location. See Table 1.1 for parameter values.

Individuals that accrue a higher sum of payoffs compared to others in the population leave more offspring with the same microhabitat preference unless a random mutation occurs. At the end of each generation time, the payoff scores from the set of agents who survived are aggregated by their microhabitat preference type. The proportion of the sum of payoff scores of the individuals with a given microhabitat preference trait over the total sum of payoff scores of all agents in the species class is then the proportion of agents in the next generation that will retain the same trait. Each population persists on the landscape for a set number of feeding and/or movement cycles which is also referred to in the model as a generation (Figure 1.1).

The payoff score is a proxy for fitness that is parameterized by the user of the software. In our model, the only populations that can reproduce are the kangaroo rats and the rattlesnakes. However, when the trait is assigned to the individual of the next generation, there is some probability that the trait will mutate into another microhabitat preference strategy based on a set probability by the user. The kangaroo rat and rattlesnake populations interact for a set number of feeding cycles set by the user before

the simulation is terminated and the results are aggregated into a format to be summarized (Figure 1.2).

Population sizes are semi constant. At the start of each generation, populations with the genetic algorithm applied to them start at an initial population size parameterized by the user. Over the generation time, individuals are removed from the simulation if they are successfully predated or starve. The user may also set a variable for a random chance of dying to model the other ecological processes that may affect this population outside the scope of the simulation such as predation or disease. For example, we set a parameter in our case study called “Snake Death Probability Per Cycle” which is a 0.1% chance per cycle that a snake agent dies (Table 1.1). At the end of the generation, pay off scores are aggregated among the surviving individuals and the next generation is reset back to the initial population size, with the population’s proportions of traits being dependent on the success of the individuals of the previous generation.

Landscape

Many species of kangaroo rats and rattlesnakes predominately reside in sparsely vegetated arid environments with significant open space. To simplify this environment in silico, we modelled the landscape as a two-dimensional grid composed of two classes of cells that represent open or vegetated microhabitats, we termed the bush and the open. The bush microhabitat represents any habitat that gives an aerial canopy cover such as creosote (*Larrea tridentata*) or mesquite (*Prosopis spp.*). The open microhabitat represents areas with sparse vegetation, such as grasses or dune fields, with no aerial

cover. All microhabitat cells of the same class are equal in terms of parameterization and agents operate and interact in these cells. The interactions in a given microhabitat vary based on the classification of the cell and the input parameters of the model. Payoffs for foraging in these microhabitats are then accrued by a prey individual based on the microhabitat they occupy during a feeding event. The specific parameters we use in our model can be seen in Table 1.1. Experimental parameters are set as initial conditions of the model (Table 1.2, 1.3, 1.4) and included factors such as the number of owls (specialized aerial predators that only forage in the open), differential energy gain by prey foraging in a given microhabitat, and the probability of a predator's strike being successful in a microhabitat.

Classes of Agents

There are two classes of agents for our model, predator and prey. For both classes, the goal of the agent is to maximize their payoff score and avoid dying. The payoff score for each class of agent is a running score that accrues throughout its lifetime per cycle. Equation 1.1 represents how the energy score is calculated each cycle for each individual. In Equation 1.1, p_n is the current energy score of the individual, α represents the energy cost per cycle, and ω represents the energy gain. For both classes of agents, α is a constant. Energy gain ω , differs between the two classes of agents and for prey agents, can also vary by microhabitat.

$$p_{n+1} = p_n + \omega - \alpha \quad (1.1)$$

For predators, ω is dependent on an interaction with a prey agent and an attack success probability (for snakes in our model this was termed “strike success”) set as a parameter by the user that can differ based on microhabitat. If a attack is successful, the prey agent is removed from the landscape and an energy amount ω accrues to the predator agent’s score. For prey agents, ω is a constant that is dependent on the type of microhabitat the organism occupies. For both classes of agents, at the beginning of each cycle, if p_n is less than 0, then the agent is considered to have starved and is removed from the environment. In our simulations, values for energy gain and cost values for both predator and prey were based on a previous game theory model analyzing the same system [5].

Pure and Mixed Strategies

Uumarrty is capable of modelling the microhabitat preference of an individual as a pure strategy or a mixed strategy [24]. Under a pure strategy an individual agent exclusively prefers one microhabitat over another, while agents with a mixed strategy have a weighted preference for one microhabitat over another, but can still utilize both microhabitats for foraging over the course of their lifetime.

Equation 1.2 represent the probability of an individual moving into a given cell in a landscape. Terms in this equation correspond to (mp) is the individual’s agent’s weighted preference of a given microhabitat (mp), bc is the total number of bush microhabitats in the landscape (bc), oc is the number of open cells in the landscape (oc), I is an individual bush cell in the landscape (I), and j is an individual open microhabitat cell (j). Both the pure and the mixed strategies use these sets of equations for movement;

however, the parameter mp is binary when microhabitat preference is modeled as a pure strategy, and continuous from 0 to 1 (rounding to two decimal places) when microhabitat preference is modeled as a mixed strategy. The mp value of 1 represents a complete preference for the bush and a mp value of 0 represents a preference for the open. This value is passed down to the offspring with a probability of mutating. If a mutation even occurs, the magnitude of the mutation is sampled from a Gaussian distribution with a standard deviation set as a parameter of the model.

$$\begin{aligned}
 Pr_i(bush) &= mp\left(\frac{1}{bc}\right) \\
 Pr_j(open) &= (1 - mp)\left(\frac{1}{oc}\right) \\
 \sum_{i=1}^{bc} Pr_i(bush) + \sum_{j=1}^{oc} Pr_j(open) &= 1
 \end{aligned} \tag{1.2}$$

The Nash Score and Post Simulation Analysis

After 50 simulations for each experimental group, our model summarizes data for both the total run and per generation (Figure 1.2). The data for the total run is a global mean of all the microhabitat preference traits of all individuals of a population at every time cycle. These means are compared across experimental groups to evaluate strategy choices. This value is the optimal strategy of the population under the set experimental conditions. A one-way ANOVA and Tukey post hoc test for multiple comparisons are implemented to establish statistically significant differences between experimental groups of a case study. Statistical tests were conducted using the statsmodels package in Python [23].

The simulation software also summarizes mean microhabitat preference of a population aggregated by each feeding cycle. To convert this to per generation, only the last cycle of the generation time is used and the other data mid generation is filtered out. Under certain selection conditions for a given simulation, microhabitat preference per generation will fluctuate in a stochastic, oscillating manner (Figure 1.3A), or may become constant (Figure 1.3B). We developed a novel method to classify the local optima points of the per generation microhabitat preference strategies in order to obtain metrics for stability analysis.

Our local optima point classification algorithm works by using a central approximation of the first derivative, and the second derivative of the per generation data with a window size of three generations. Because both vectors are highly chaotic, we applied a Savitzky Golay smoothing function [20] with a window size of three.

We used two methods to classify local optima points; the first is a traditional calculus method where minimums are defined when the first derivative of a point is equal to zero and the second derivative is positive. Maximums are classified if the second derivative is negative. However, this can be unreliable due to portions of the data that rapidly oscillate between positive and negative values. If the first method does not classify local optima point at a given time step, the algorithm checks if the first derivative changes from being negative at the current time step to being positive at the next time step with a magnitude greater than a set sensitivity, classifies such points as minimum local optima point, and the inverse would be a maximum. A sensitivity parameter of the absolute value of the second derivative being greater than 0.1 was used

in the classification algorithm to only classify one local maxima point per strategy flip as rapid small changes of the data could produce a false local optimum. From a biological context, local optima points would represent populations undergoing a shift toward a different microhabitat preference strategy, likely as a result of interspecific competition or predation.

From the local optima point classification algorithm, three descriptive statistics are generated to understand the dynamics of strategy flip oscillations: the total count of strategy flips, the mean number of generations before a strategy flip, and the mean magnitude of a strategy flip (Figure 1.3A). Unstable microhabitat preferences are characterized by having a large number of strategy flips, a low value for mean generations before a strategy flip, and a larger value for the mean magnitude of strategy flips. We classify a completely evolutionary stable strategy for microhabitat preference as having zero local optima points and being a constant trend. However, general stochasticity from the model can lead to occasional false positive local optima points. To account for this, the algorithm has sensitivity conditions. If there are less than five local optima points, and a mean magnitude before strategy flip value of less than 0.05, then the results of the per generation data of a given simulation is classified as stable.

Due to the stochastic nature of an agent-based framework, there can be variance in the results of simulations run using the same set of experimental parameters. To quantify the stability of the microhabitat preference strategies for a given experimental design, we used the Nash Score. The Nash Score is the ratio of simulations classified as stable over the total number of simulations of an experimental group. A Nash Score of 1

would be analogous to the evolutionarily stable strategy used in game theory, as it demonstrates a consistent outcome of in all simulations at all generations of an experimental group, and mutant behavioral strategies cannot invade the fixed microhabitat preference adopted by a population. The advantage of the Nash Score is that it is a continuous metric and can be used to assess and compare relative “evolutionary stability” across different simulation conditions. Stability is not likely to be a consistent property of most evolutionary systems in nature, as they are subject to stochasticity from changing abiotic and biotic conditions, and a metric for evolutionary stability that is continuous is arguably more useful for cross-system comparisons than a categorical metric. A Nash Score of less than one but greater than zero would indicate the system is approaching an ESS and is semi-stable under a given set of experimental conditions.

From a theoretical perspective, these conditions match the definition of the ESS because, under the genetic algorithm, new mutants will always arise in the population. In cases where behavioral trait strategies are constant and no inflection points can be identified, all mutants that deviate from the optimal strategy have such comparatively low fitness or survivability that their microhabitat preference has no effect on the populations mean preference due to strong selection against mutant traits. A Nash Score of 1 would indicate that no mutant strategies can invade the optimal behavioral preference strategy, and thus it can be classified as an ESS. A Nash Score of less than one but greater than zero would indicate the system is approaching the ESS. This gives the user of the model a sense of how certain selection pressures lead to behavioral traits becoming evolutionarily stable strategies.

Kangaroo Rats and Rattlesnakes Demographic Parameters

For each experimental group of all case studies described below, we modelled the interaction between kangaroo rat and rattlesnake populations with the goal of first identifying optimal microhabitat usage strategies in a basic predator-prey scenario and then introducing more complexity into the system in subsequent experimental conditions. Each set of experiments is also run with a control group with consistent experimental parameters across all the case studies. In the experimental groups, model parameters are systematically altered, and outcomes are compared to the control group to evaluate the evolution of microhabitat preferences of the population and how they may diverge from the expected frequency seen in the control group.

Input parameters for kangaroo rat and rattlesnake population agents were derived from ecological data. Rattlesnakes live about 5 times longer than kangaroo rats, so in our model kangaroo rat agents reproduced after 50 foraging events while rattlesnakes reproduce after 300 foraging events. Rattlesnake strike success probability (1 in 4 encounters result in death of kangaroo rat) are from empirical data [27]. Energy gain parameters are from a game theory model [5] that was in turn based on empirical field observations and experiments [4]. Parameters used in case studies are listed in Table 1.1.

Case Study 1: Differing Foraging Energy Gains for Kangaroo Rats in Microhabitats

Different microhabitats may provide more nutritious or abundant food resources to the kangaroo rats, which is likely to influence microhabitat preference. To see the

effect of how food resource levels may influence the microhabitat preference of the prey and predator, we increase the energy gain for the kangaroo rats in one microhabitat over the other (Table 1.2). This experimental design is meant to simulate the ecological impact of a bottom-up regulation of energy gain from prey foraging influences the microhabitat preference of both the predator and prey.

Case Study 2: Differing Strike Success of Rattlesnakes in Bush Microhabitats

Although empirical data is lacking, it is possible that the increased structural complexity of vegetated microhabitats helps conceal ambush-hunting rattlesnakes, thus leading to increased strike success toward prey. To simulate this scenario, we increased the strike success of rattlesnakes in the bush by 1% increments across scenarios, while decreasing the strike success in the open by 1% increments, thereby holding total selection pressure constant, but varying risk across microhabitats (Table 1.3).

Case Study 3: Introducing Owls

There have been several studies on the effects of owls on kangaroo rat and small mammal foraging that generally show owl predation results in kangaroo rats decreasing foraging time in open habitats, where they are susceptible to aerial attacks [4, 5, 10]. In this experiment, we introduce a risk of predations from owls, specialist predators that only utilize the open microhabitat for foraging. We assume they are microhabitat specialists due to the canopy cover providing protection to kangaroo rats in bush microhabitats. We also assume that rattlesnakes are not subject to owl predation. Owls are modeled as a static threat, with their total number held constant, but our experimental

simulations alter the ratio of snakes to owls in a landscape to see how this influences the kangaroo rat and rattlesnake microhabitat preference (Table 1.4).

Results

For each experimental group, we obtain results from an ANOVA test and a Tukey-post hoc test (Figure 1.4) for both the rattlesnake and kangaroo rat population, and for pure and mixed microhabitat preferences. The model output also summarizes mean microhabitat preference (Figure 1.5-1.6), the total amount of microhabitat usage strategy changes (Figure 1.7-1.8A,D,G), mean generations before a strategy change (Figure 1.7-1.8B,E,H), and the mean magnitude of the severity of strategy changes (Figure 1.7-1.8C,F,I). Finally, we visualize Nash Score results as a heat map (Figure 1.9). For all the case studies, the ANOVA test resulted in a significant p-value, indicating that all of our experimental designs had significant effects on changing the microhabitat preferences of both populations compared to the control group. However, the results of the Tukey-post hoc test indicate that some experimental groups were more similar than others (Figure 1.4).

Case Study 1: Differing Foraging Energy Gains for Kangaroo Rats in Microhabitats

This set of simulations involved progressively increasing the amount of energy individual kangaroo rats gain from foraging in the open compared to the bush microhabitat (Table 1.2), while keeping the effects of predation constant. When modeling microhabitat preference as a pure trait, as the disparity of energy gain in the open microhabitat versus the bush grows large enough (experimental groups 4, 5, and 6;

Table 1.2), prey preference shifts completely toward the open (Figure 1.5A). However, before this tipping point (experimental groups 1, 2, and 3; Table 1.2), the resource disparity has no effect kangaroo rat microhabitat preference (Figure 1.4A), and kangaroo rat agents are distributed evenly in both microhabitat types (Figure 1.5A).

In contrast, the rattlesnake agents showed a more gradual transition to preferring the open in experimental groups 1, 2, and 3, and then show complete preference for the open in conditions where kangaroo rats also mostly prefer the open (groups 4, 5, and 6). Experimental groups 4, 5, and 6 are statistically identical (Figure 1.4B). The rattlesnake population microhabitat preference in this case study showed high levels of evolutionary stability, with a Nash Score greater than 0.5 (Figure 1.9B), meaning that over half of the simulations reached an equilibrium state. In contrast, the kangaroo rat populations in this case study have a Nash Score of 0 (Figure 1.9A), with a large number of strategy flips and high variance for experimental groups 3-6 (Figure 1.7A). The kangaroo rat mean number of generations before a strategy flip and the mean magnitude of the strategy flip (Figure 1.7B, C) are relatively low in experimental groups 3, 4, 5, and 6 compared to experimental groups 1 and 2, further demonstrating frequent strategy changes.

The results of simulations when modelling microhabitat preference as a mixed trait were generally similar, with both kangaroo rats and rattlesnakes adopting an increased preference for the open in experimental groups with a higher disparity in food resources but maintaining a limited preference for bush microhabitat across all experimental groups (Figure 1.6A, B). Nearly all experimental groups are statistically different than one another for the kangaroo rat population, except for experimental group

1 and 2 (Figure 1.4C). The Nash Score analysis shows that neither condition approximate an ESS in this case study, as all experimental groups have a Nash Score of 0 (Figure 1.9A, B).

The only notable differences in simulations modeling pure versus mixed strategies were in experimental groups 3-6 (Table 1.2), wherein kangaroo rats retained a greater preference for the bush habitat in the mixed strategy simulations (Figure 1.5A, B, 1.6A, B). Additionally, the mean number of generations before a strategy flip for kangaroo rats is lower in the mixed strategy simulations (Figure 1.8), indicating that the kangaroo rat population is not altering microhabitat preference over time as drastically.

Case Study 2: Differing Strike Success of Rattlesnakes in the Bush Microhabitats

To explore the impact of differential predator attack success, we created experimental groups with a gradually increase in the probability of strike success in bush microhabitats and a decrease in the open (Table 1.3). When microhabitat preference is modelled as a pure trait, kangaroo rats gradually shift preferences toward the open across experimental groups, with the mean difference between experimental group 1 to experimental group 6 of -0.188 (Figure 1.4E). Rattlesnakes, in contrast, shifted preferences toward the bush, but by a lesser degree, as the largest difference between experimental groups is from group 1 to 5 with an approximately 0.05 preference shift toward bush microhabitats. Neither the kangaroo rat population or the rattlesnake population strategy was evolutionary stable as the Nash Score of all experimental groups is 0 (Figure 1.9). Both populations also have a high mean magnitude of strategy flips

(Figure 1.7F) and the mean generations before a strategy flip are constant which indicates both populations are switching strategies often through evolutionary time and the rattlesnake strike success probability has little effect on driving microhabitat usage toward equilibrium.

This same set of conditions resulted in very different outcomes when microhabitat preference was modeled as a mixed trait. Rather than trending slightly toward a bush preference (Figure 1.5D), the mixed trait rattlesnake population tends to prefer the open (Figure 1.6D), with a mean difference of -0.138 between experimental groups group 1 and 6 (Figure 1.4H). This increased preference toward the open appears to reach a limit, as the mean difference between experimental group 5 and 6 is only -0.008 and is less statistically significant compared to the differences of the other experimental groups (Figure 1.4H). In contrast, kangaroo rat preferences were similar when modelled as either mixed or pure traits, although they did show an increased propensity for the open at higher experimental groups in the mixed strategy simulations (Figure 1.6C). For both populations, these strategies are not evolutionary stable (Figure 1.9). There is evidence that increasing the strike success probability does have a somewhat stabilizing effect on microhabitat preference, as the mean magnitude of strategy flips does decrease in subsequent experimental groups for both populations (Figure 1.8F). Experimental group 5 and 6 have an increased mean generations before a strategy flip (Figure 1.8E), meaning populations are not switching strategies as often compared to the control group (experimental group 1).

Case Study 3: Introducing Owls

Introducing owls into the system had a large and significant effect on the microhabitat usage patterns of rattlesnakes and kangaroo rats. For the pure microhabitat usage strategy, both kangaroo rats and rattlesnakes had similar responses to the introduction of owls (Figure 1.5E, F). When owl numbers were relatively low (experimental group 1, 2, 3), both kangaroo rats and rattlesnakes showed a gradual shift in microhabitat preference toward the bush (Figure 1.4). Once the proportion of owls was equal to or higher than rattlesnakes (experimental groups 4, 5, 6), both agents showed strong preferences for the bush (Figure 1.4). In terms of evolutionary stability, kangaroo rats' preference toward the bush starts approaching equilibrium in experimental group 4 with a Nash Score of 0.58 and then becomes an ESS with a Nash Score of 1.0 for experimental groups 5 and 6 (Figure 1.9A). The rattlesnake population does not reach equilibrium in any of the experimental groups. Experimental group 4 has a Nash Score of 0.26, meaning that the population was approaching equilibrium, but the subsequent experimental groups 5 and 6 did not (Figure 1.9B). For the rattlesnake population, the total number of strategy flips (Figure 1.7G) dramatically drops from experimental group 3 to 4, but then increases again for experimental group 5 and 6. The mean generations before a strategy flip (Figure 1.7H) decreases from experimental group 4 to 5, indicating that there are more fluctuations in microhabitat usage strategies over time as the total number of rattlesnakes in the population decreases (Table 1.4).

Modelling microhabitat preference as a mixed strategy trait yields similar results; when owls are more abundant than snakes (groups 4, 5, 6) this causes both snakes and

kangaroo rats to heavily prefer bush microhabitats; however, there are subtle differences in these two experiments. In the pure owl experiment, both populations adopted a 100% preference for the bush when owls are the more abundant predator (Figure 1.5E, F). In contrast, in the mixed experiment, when owls are dominant, kangaroo rats will prefer to use bush habitats approximately 90% of the time and rattlesnakes prefer the bush about 83% of the time. Experimental groups 4, 5, and 6 are not significantly different in microhabitat preference (Figure 1.4L).

Another difference between the pure and mixed experiment is that in the mixed experiment, kangaroo rat microhabitat preference reaches an evolutionary stable equilibrium in later experimental groups. Experimental group 5 has a Nash Score of 0.68 and reaches complete equilibrium at experimental group 6 with a Nash Score of 1 (Figure 1.9A). The rattlesnake population again showed no evidence of approaching an evolutionary stable equilibrium. The total number of strategy changes for the rattlesnakes has a non-linear trend and there is an increase in strategy flips when comparing experimental group 4 and 5 (Figure 1.8G) and a slight increase in the mean magnitude of strategy flips from experimental group 4 to 5 and 5 to 6 (Figure 1.8I), indicating that rattlesnakes become more unpredictable in landscape usage at these higher experimental groups.

Discussion

The Nash Score and Expanding Agent-based Modeling Methodology

One of our primary modeling objectives was to integrate a well-known analysis techniques from evolutionary game theory into an agent-based framework to increase the standardization and interpretability of future simulation studies using agent-based models. Concepts such as behavioral strategies, pay off scores, pure or mixed strategies, and the ESS are all derived from classical game theory and were integrated as inputs into our agent-based framework. Our model outputs summarize the optimal behavioral strategy in a given set of conditions, and formulated a new method for determining when the system reaches an ESS.

Conceptually, the Nash Score is analogous to the ESS as it describes when a behavioral trait transitions from cycling through many strategies over evolutionary time due to frequency-dependent selection, to being completely stable from generation to generation. The dynamic of cyclical fluctuations of behavioral strategies over time has been observed in other agent-based predator prey models [21] and is due to predator and prey interacting and coevolving with one another. This is also known as an evolutionary “chase” [1], as both predators and prey display bi-stable cyclical trends, with an evolutionary time lag in the predator population.

The notion of an ESS finds application in agent-based systems when genetic algorithms are used to parameterize the simulation. When a population’s behavioral trait remains constant over the run time of a simulation, it signifies that any potential mutant strategies are suboptimal and unable to become fixed within the population. In

mathematical terms, the ESS in an agent-based framework categorized by the Nash Score is quantified by a system transition from a bistable equilibrium to a unstable equilibrium for a given population. Because it is a continuous metric, the Nash Score also allows us to quantify if the system is approaching equilibrium and provides methods to assess equilibrium of populations independently of one another as certain selection pressures may impact one population's behavioral strategies more than others.

However, one key difference between the Nash Score and traditional ESS analysis is that, for agent-based simulations, the behavioral strategies of the two species (kangaroo rats and snakes) are evaluated independently; thus, one population may reach an ESS but the other may not. This is a key difference, our method depicts more whether the strategies used by predator or prey are likely to be evolutionarily stable for either or both species, whereas the ESS in traditional game theory assesses the stability for both populations together. Thus, the two concepts could have different application purposes and are not mutually exclusive.

Our modeling approach may be particularly useful for understanding frequency dependent behavioral strategies, as the system will oscillate when the behavioral trait of one population is dependent on what strategy the other agents in the other population are adopting. A Nash Score of < 1 indicates that the payoff (or fitness) of a trait will be dependent on the choices made in the antagonist population, and that there will be oscillating proportions of trait values rather than a stable equilibrium. For the kangaroo rats, our simulations indicate the payoff for microhabitat preference is generally negatively frequency dependent as more kangaroo rats adopt a certain strategy, this

increases the fitness of the rattlesnakes that adopt the same microhabitat preference which then makes the rare trait have higher fitness, leading to oscillating trait values. This is inversely true for the rattlesnakes. If too many snakes adopt a certain microhabitat preference, it will cause the kangaroo rats to switch their preference.

However, under certain ecological conditions the fitness impacts of a strategy choice will be stable, meaning that optimal microhabitat preference does not shift with changes in the antagonist population. This showcases the utility of the Nash Score as it can provide more detailed information on situations where cyclical arms race dynamics dominate the system. When the Nash Score is 0, the frequency dependent predator prey arms race is the primary dynamic in the system, whereas under other ecological conditions (such as the presence of a microhabitat specialist predator like owls) microhabitat choice may stabilize and move away from the cyclical dynamic (Nash Score = 1) (Figure 1.9A).

This modeling framework gives researchers a new computational tool to describe the stability and trajectories of many simulations that would be difficult to analyze visually. For the case studies described, we ran a total of 1800 simulations and the Nash Score and the other metrics provided by the point classification algorithm provide a tool for understanding simulation trajectories without having to analyze each simulation individually which greatly reduces the analysis complexity. This makes it easier to assess the implications of how changes in ecological conditions impact overall community dynamics and behavioral trait evolution for future studies and formulate an objective narrative based on the results of many simulations.

Case Study 1: Differing Foraging Energy Gains for Kangaroo Rats in Microhabitats

One of the objectives of all our experimental simulations was to determine the ecological factors that most influence shifts and stability of microhabitat preferences in a classic predator-prey system. For the first case study, increased energy gain heterogeneity, our findings add nuance to the general principle that predator microhabitat preferences track prey preferences, and prey balance predation risk with energy gain. In our analysis, we were able to identify a tipping point in the system between these two dynamics, suggesting environmental conditions shift the balance between safety and energy gain in terms of microhabitat preferences. A tipping point is generally defined as when small changes in external environmental conditions cause large and abrupt changes to individuals' behaviors, interactions among group members, and therefore how the group functions of the system [17]. Thus, our analysis shows that there is a duality between these two hypotheses rather than a general rule of all systems.

For kangaroo rat agents simulated using a pure strategy, we found that when there is a small difference in energy gain between the microhabitats, but both still provide a net energy gain, there is little to no behavioral changes for kangaroo rats at the population level, but we do observe behavioral changes in the rattlesnakes in that they prefer the microhabitat that provides kangaroo rats the most payoff. This can also be observed from the Nash Score analysis as after this tipping point is reached, as the Nash Score begins to approach 1 for the rattlesnake population under the pure strategy. The Nash Score for the kangaroo population remains at 0 for all experimental groups.

From an ecological perspective this indicates that kangaroo rats are becoming predictable in their microhabitat usage as one of the microhabitats becomes much less profitable than the other, leading to stability in predator microhabitat usage strategies as they always prefer the more valuable microhabitat (open). This may seem counter intuitive because the energy gain function of the microhabitats applies only to kangaroo rats, yet stable strategy that emerges applies only to the snakes. This finding underscores the importance of prey using both microhabitats that may yield energy and those that may provide temporary spatial refuge from predators, even at the cost of less or no energy gain.

Overall, what this case study indicates is that, under certain conditions, prey microhabitat preferences predominately drive the behavioral strategies of the system, and the predator tracks their landscape usage, leading to cyclical frequency-dependent patterns, whereas conditions that lead to prey behavior being highly predictable can lead to stability of behavioral traits in the system.

Case Study 2: Differing Strike Success of Rattlesnakes in Bush Microhabitats

From the Nash Score analysis, increased strike success heterogeneity only led to increased cyclical dynamics with not stable equilibria, as all Nash Score values across this case study remained at zero. When modeled as pure strategies, increasing the probability of rattlesnake strike success in bush microhabitats did not increase preference toward the bush. When modeled as a mixed strategy, the same dynamic occurred, except rattlesnakes would switch microhabitat usage strategies frequency often through

evolutionary time despite the being at a disadvantage in the open microhabitat. These simulations indicate that rattlesnakes can be successfully when preferring the open microhabitat because their increased efficiency in the bush microhabitat drives kangaroo rat preferences toward open microhabitat. Thus, increased predator performance in one microhabitat, without some outside ecological pressure such as owls or increased energy gain, can, counterintuitively, lead to higher rates of preference for hunting in the other microhabitat.

Case Study 3: Introducing Owls

The results from this case study indicate that the introduction of another predator specializing in foraging in open microhabitats (owls) will cause a shift in preference for both kangaroo rats and rattlesnakes toward using the bush. Our results also imply that there can be a microhabitat preference tipping point when the number of owls exceeds that of rattlesnakes. If the trait is a pure strategy, then preference for bush microhabitats becomes an ESS for the kangaroo rats. The snakes adopt the same strategy, but it is not an ESS for snakes, suggesting that it is occasionally optimal for snakes to forage in the open, thus increasing selection pressure to drive kangaroo rats toward the bush.

One of the main goals of our study was to confirm the validity of our model by comparing it to a previous game theory model on kangaroo rat and rattlesnake predator prey interactions [5]. Our findings were similar to the traditional game theory model, which found that it is an ESS for both kangaroo rats and rattlesnakes preferring the bush when the probability of being captured by an owl in the open outweighs the probability of being captured by a snake in the bush. However, the rattlesnake population in our

model never reaches equilibrium, which could be because of low population sizes in conditions that should be evolutionary stable as the population briefly starts approaching equilibrium in experimental group 3 (Figure 1.9B). When the population size is low, even one member of the population having a different microhabitat preference will have a larger effect on the population's mean microhabitat preference due to a low sample size, thus making equilibrium harder to reach.

When microhabitat preference is modeled as a mixed strategy, the owl simulations suggest there is a limit for the rattlesnake population's bush preference regardless of the number of owls present. These results do not indicate that rattlesnakes and owls work synergistically [10] but rather support the idea that it is rattlesnakes to distribute selection pressure across microhabitats. This supports the idea that predators work to distribute "fear" across a landscape [7, 13, 14], however, owls will shift the theoretical fear distribution. It is evolutionary advantageous for rattlesnakes to switch behavioral strategies after a certain number of generations (Figure 1.8H) to increase the probability of a strike from either a rattlesnake or an owl against a kangaroo rat in the open, showcasing the benefits of being a generalist predator compared to a specialist. When this probability is larger than the probability of a strike in the bush, this drives the kangaroo rat population primarily using the bush to be an evolutionary stable strategy. This means that owls primarily benefit rattlesnakes, rather than vice versa, as kangaroo rats reach an ESS for preferring bush microhabitats due to two predators in the open versus only having one type of predator in the bush.

As with any model, our simulations incorporate somewhat simplistic assumptions that may reduce ecological realism, such as the assumption that owls are incapable of catching kangaroo rats under bushes (i.e., bush provide perfect canopy protection) [10]. Other assumptions of our model that are likely overly simplistic are that owls cannot predate rattlesnakes, and incorporating some level of predatory pressure from owls on rattlesnakes would likely have an impact on their microhabitat preference [19].

Across all our case studies, our study supports the hypothesis that predators generally exhibit foraging behaviors that diffuse the probability of predation across a landscape [7], and predators and prey will display cyclical strategies (i.e., arms race dynamics) over evolutionary time [1]. Predator microhabitat preferences diffuse risk across the landscape even when predators are directly disadvantaged in a microhabitat, as seen in the strike success experiment. Although these predator-prey dynamics have been recovered in other models and empirical studies, our modeling approach provides a nuanced understanding of how these dynamics are dependent on ecological circumstances, and our simulation analyses can identify tipping points in which the behavior of a population drastically shifts. Overall, the overarching conclusion from the case study our analysis suggests is that there are environmental conditions where predator-prey systems are driven by prey decisions, and conditions where predators drive system trajectories. This point can be seen as analogous to other complex behavioral system relationships such as employer-employee relations in economics where the scale of negotiating power is based on the economic conditions and supply and demand [2].

Conclusion and Future Work

The most practical extension of our game theoretic simulator may be to leverage these methods as a way of building a bridge between hypotheses developed during field studies, further integrating empirical data to estimate parameters, and hypotheses formed from theoretical or computational analyses. Our modeling approach also allowed us to develop metrics that illustrate how microhabitat preferences shift through evolutionary time such as the mean generations before a strategy flip, mean magnitude of the strategy flip, and the Nash score. Our model can also be applied to other frequency-dependent biological systems, and other types of traits to develop a deeper understanding of predator-prey dynamics.

Future work could focus on developing several complementary extensions of our modeling approach. For example, our modeling framework would allow for randomly setting parameters to apply a regression-based approach to understanding how these ecological forces interact with one another and impact microhabitat preference. Some of the case studies showed non-linear trends in microhabitat preference shifts across the experimental groups due to tradeoffs between predation risks and foraging gain. Some of these limits may be shifted or overcome when introducing additional ecological factors. For example, in our strike success study, rattlesnakes show only a modest increase in preferences for bush microhabitat, despite their greatly increased strike success. Their preference could be greatly increased if we also introduced owls into the landscape, or increased foraging gain potential in the bush for kangaroo rats at the same time.

Another potential ecologically relevant extension would be to include within-generation behavioral learning of predator and prey to model the impact of behavioral experience in these populations. This has been successfully accomplished in other models and would better incorporate how ontogeny effects landscape usage over evolutionary time [28]. Applying genetic algorithms or a learning algorithm to the owl population as well would perhaps provide a more accurate model of predator interference and would address the potentially limiting assumption that owls cannot hunt in bush microhabitats.

The benefit of developing an agent-based modeling approach is that it is relatively easy to incorporate more complexity. The design and analysis of our initial case studies provide a standardized framework to obtain several important insights into how microhabitat preferences of predator and prey population shift as a result of ecological complexity. Our approach allows us to measure the magnitude of trait shifts and their evolutionary stability. These tools, in conjunction with empirical studies, can help better understand how ecology influences the evolution of certain traits and can be applied to many other biological systems.

Supplementary Material

Sensitivity Analysis

We conduct an “One-factor-at-a-time” (OAF) protocol for sensitivity analysis of our model [18]. The base parameter being manipulated can be found in Table 1.1 and the values they are changed to can be found in the legend of Figure 1.10 next to the

parameter name. Ten simulations are run and the mean microhabitat preference is calculated for both kangaroo rats and rattlesnakes. From this analysis, we find that overall, the system is the most sensitive to changes in landscape parameter “open to bush microhabitat proportion” compared to other parameters, especially in the mixed model (Fig 1.10 B). This makes sense as preference would likely be correlated with the abundance of a given microhabitat. Both the mixed and the pure model are relatively robust to parameters involving game theoretic components such as energy cost and energy gain, population sizes, and overall landscape size in the x and y direction (Fig 1.10).

Optimal Point Classification Accuracy

To obtain metrics such as number of strategy flips, mean generations before a strategy flip, mean magnitude of a strategy flip, and Nash Score we developed an algorithm developed to classify points as local maxima or local minima in the per generation time series from single simulations. To evaluate the performance of this algorithm, I manually classified local optimality points from a subset of two different time series and then applied the classification algorithm to form a confusion matrix and calculate metrics such as accuracy, precision, and recall.

The first was the snake population generations 1500 – 1665 from simulation 0 of pure owl experimental group 2 (Table 1.4) which had 63 optimal points. The algorithm had an accuracy of 0.95, a precision of 0.92, and a recall of 0.94. The second subset was from the kangaroo rat population of the mixed owl experimental group 1 (Table 1.4)

from generations 9500 – 9998 which had 19 optimal points. Our algorithm had an accuracy of 0.95, a precision of 0.17, and a recall of 0.05. This showcases that the algorithm in some time series has propensity for false negatives in certain time series regions. Overall, our algorithms performance can range greatly, and further work may be to make the algorithm less conservative as it can miss optima points in some time series. Despite this, we still see clear trends in our metrics provided by this algorithm as seen in Figure 1.7 and Figure 1.8. This is likely due to the sheer number of simulations run and the large number of generations for each simulation which could be statistically compensating for regions where the algorithm does poorly.

Figures

Single Sim Workflow

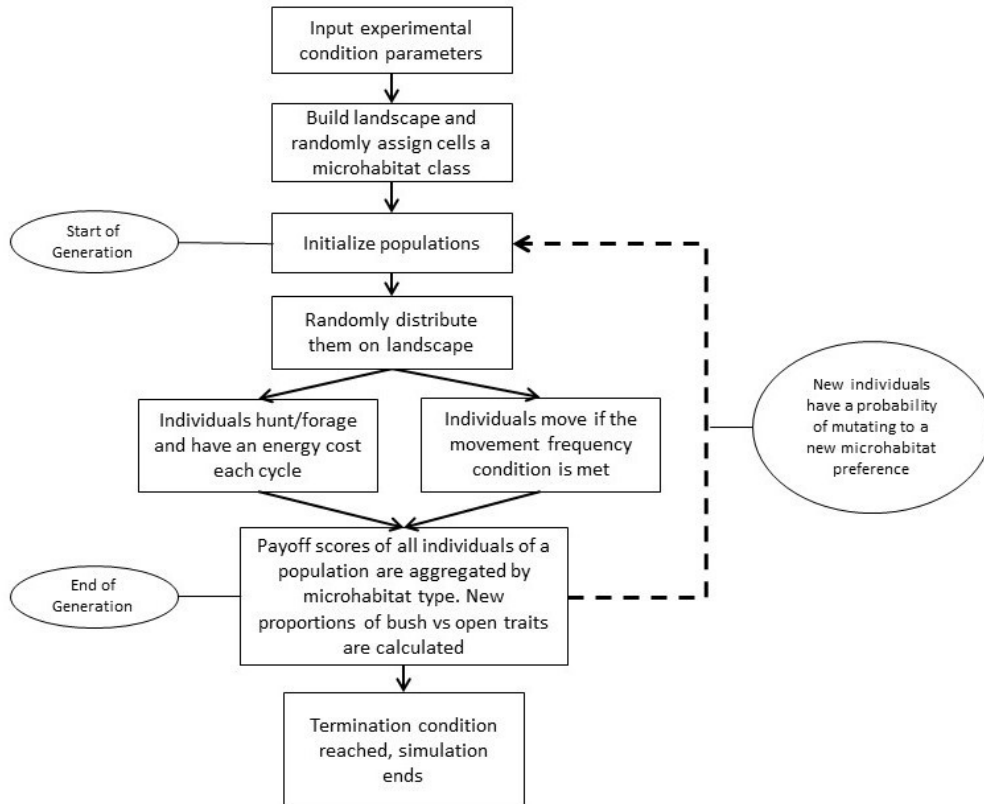


Figure 1.1: Conceptual diagram showcasing the logic of an individual simulation. This logic is applied to both the kangaroo rat population and the rattlesnake population of all simulations.

Workflow for Experimental Group Data

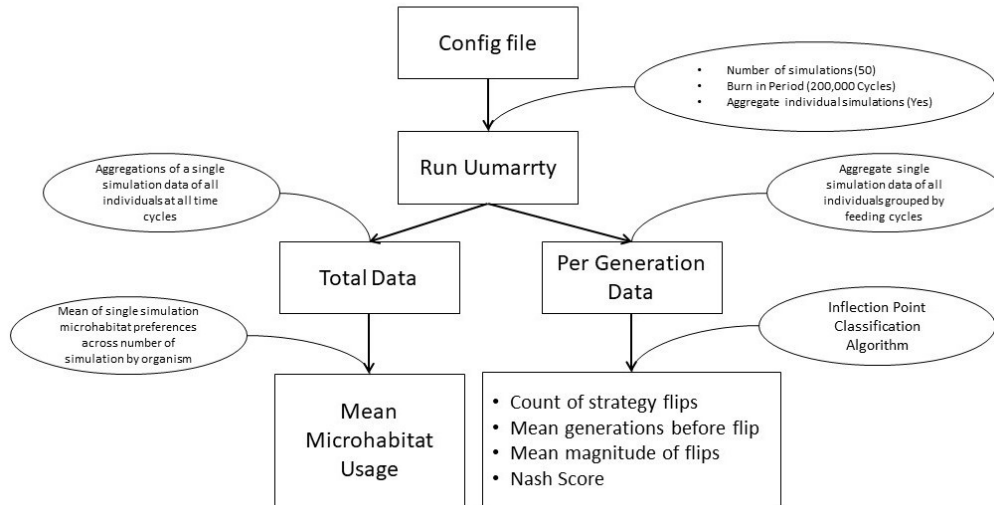


Figure 1.2: Conceptual diagram of the simulation workflow for how to generate the results of one experimental group of a case study. This workflow was applied to all 6 experimental groups of all 3 case studies.

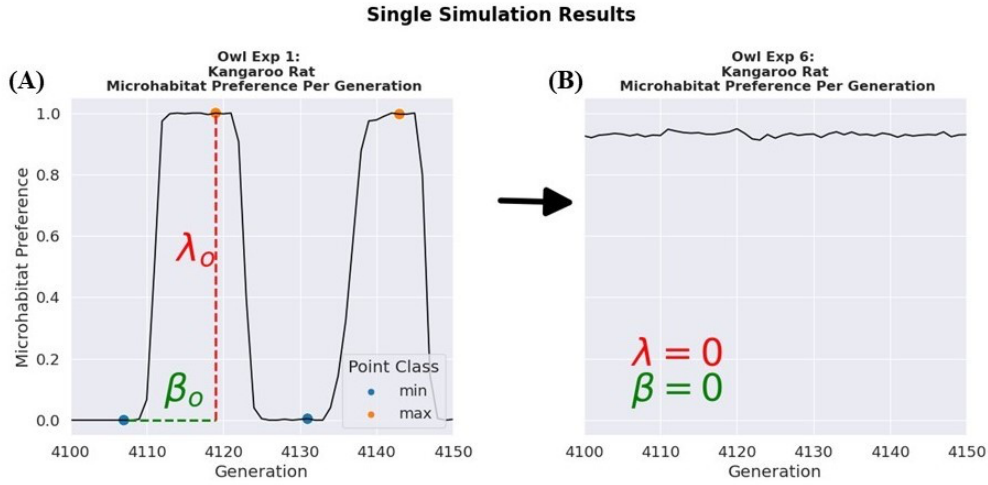


Figure 1.3: Both graphs are the mean microhabitat preference for the kangaroo rat population per generation during an individual simulation. A microhabitat preference of 1 is a complete preference toward bush microhabitats while a microhabitat preference of 0 is a complete preference toward the open. (A) is a single simulation for the owl experiment from experimental group one. (B) is a single simulation for experimental group 6. The metric λ_0 is the difference between the microhabitat preference of an optimal point and the previous optimal point in the time series which represents the magnitude of the strategy flip, shown by the red dotted line. The metric β_0 is the number of generations from one optimal point to the previous one. When λ and β are zero this means there are no optimality points and the microhabitat preference of the population is in equilibrium which can be seen in (B). Point class represents whether an optima point is a maximum or a minimum point. The arrow indicates how from experimental group 1 to experimental group 6, the microhabitat preference of the kangaroo rat population reached an equilibrium due to the introduction of owls.

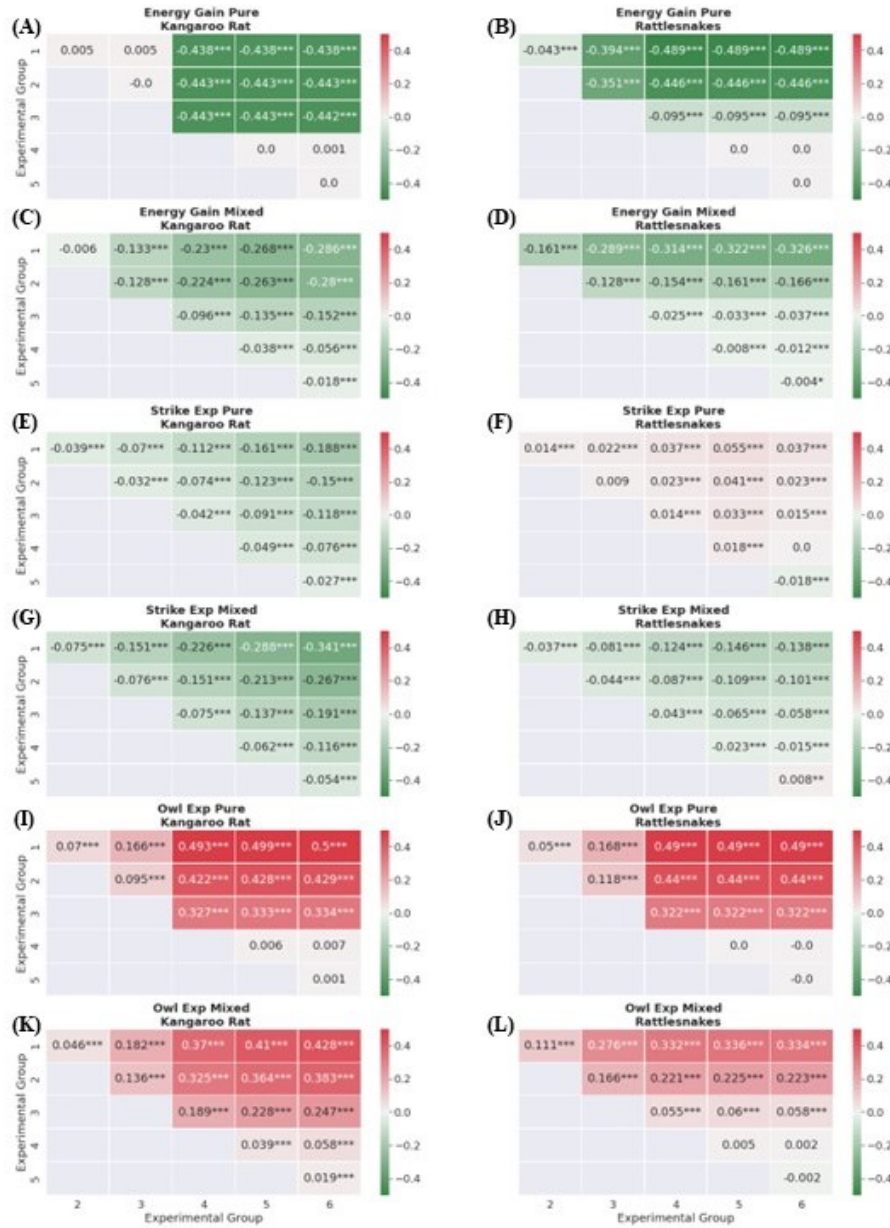


Figure 1.4: Results of the Tukey Post Hoc ANOVA test. Values in each cell are the differences of the means between experimental groups. A positive increase (red) demonstrates an increased preference to the bush, while a negative mean difference indicates an increased preference for the open. Stars represent whether the experimental groups have statistically significantly different means. *** $p < 0.001$, ** $p < 0.01$, * $p < 0.05$.

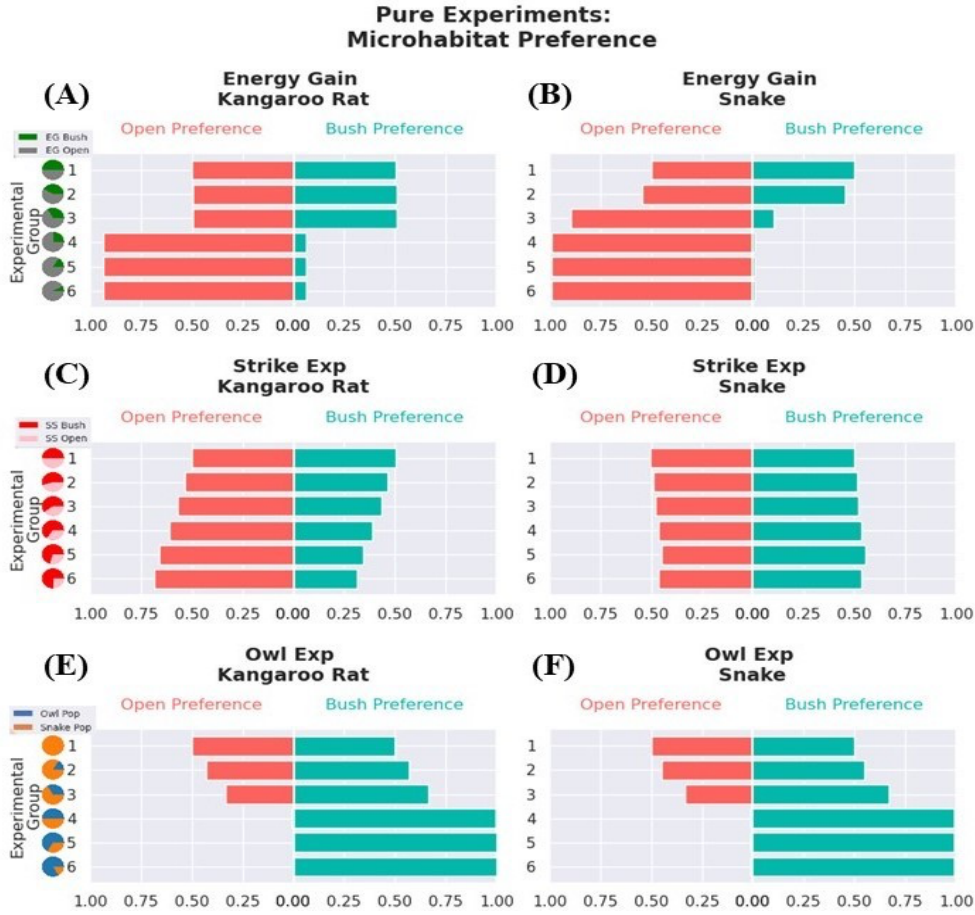


Figure 1.5: Mean microhabitat preference of the populations for all experiments with pure microhabitat usage strategies. The y-axis shows the experimental groups with pie charts representing how the experimental parameter of interest is being changed. The x-axis is the mean microhabitat preference of the population over all generations sampled from the simulation. The sum of the open preference bar graph (red) and the bush preference bar graph (blue) in all figures is equal to 1. (A) shows the microhabitat preferences of kangaroo rats for the differing foraging gains experiment for the kangaroo rat population. (B) is the same as (A) but for the rattlesnake population. Pie charts are of the values in Table 1.2. Figure (C) is the microhabitat preferences of kangaroo rats in the rattlesnake strike probability experiment. Pie charts are of the values in Table 1.3. Figure (D) is the same as (C) but for the rattlesnake population. (E) are the microhabitat preferences of the kangaroo rat population under different experimental designs for the owl experiment. Pie charts are of the values in Table 1.4. (F) is the same as (E) but for the snake population.

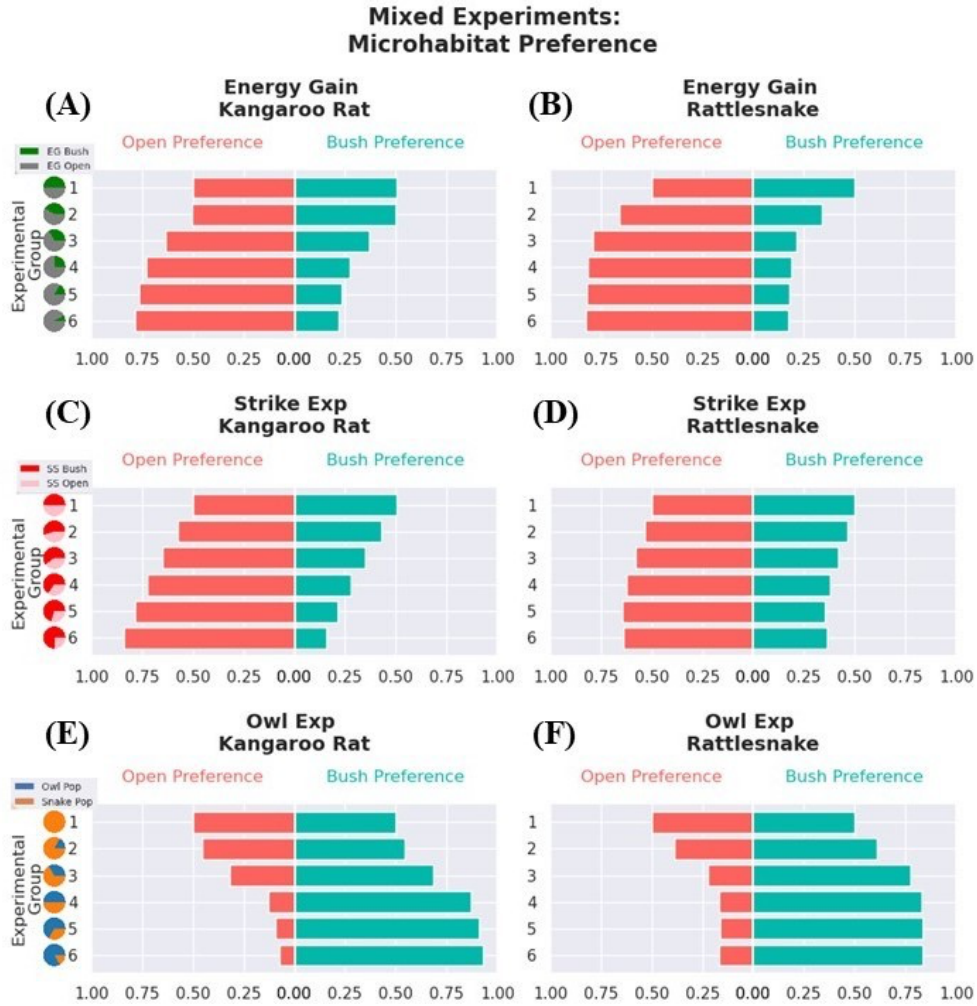


Figure 1.6: Mean microhabitat preference of the populations for all experiments with mixed microhabitat usage strategies. The y-axis shows the experimental groups with pie charts representing how the experimental parameter of interest is being changed. The x-axis is the mean microhabitat preference of the population over all generations sampled from the simulation. The sum of the open preference bar graph (red) and the bush preference bar graph (blue) in all figures is equal to 1.

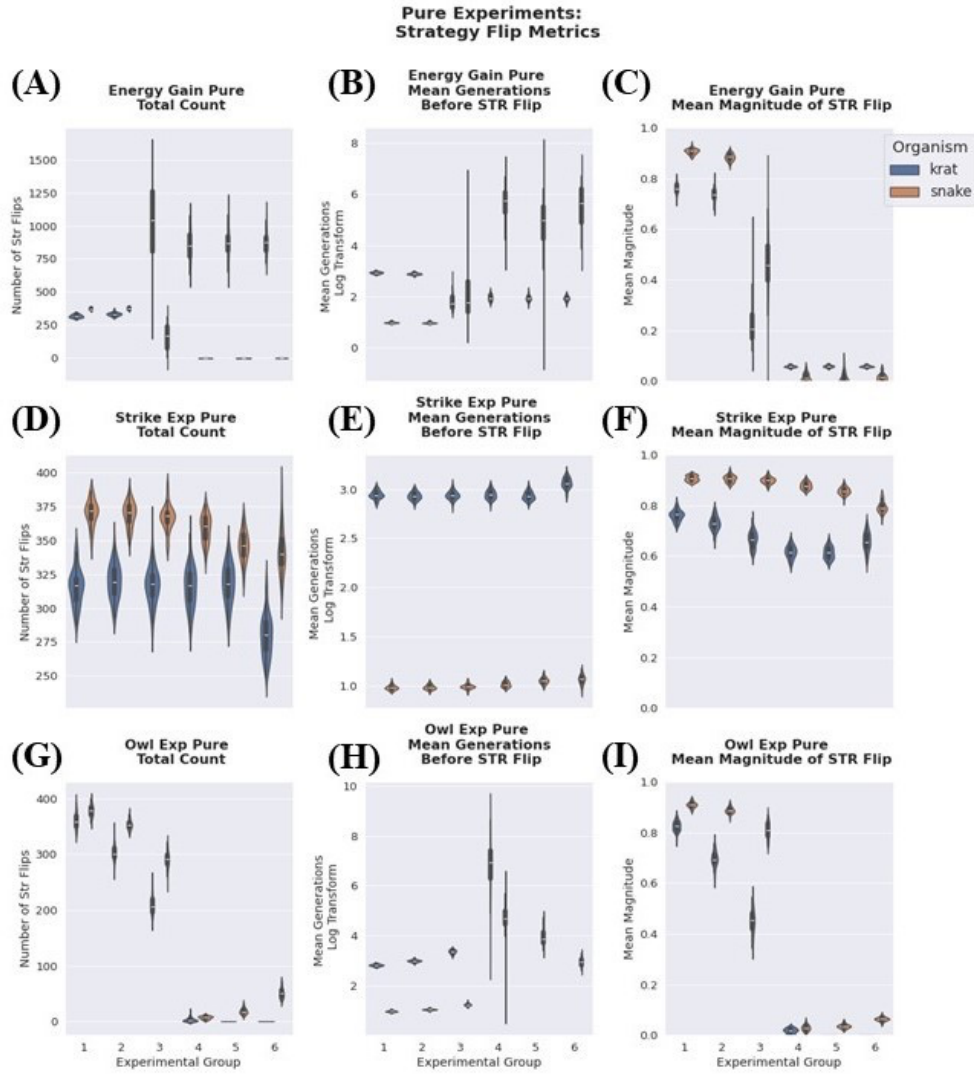


Figure 1.7: Analysis of metrics produced by the point classification algorithm applied to simulations of pure strategies across all case studies, including total number of strategy flips, the mean number of generations before a strategy flip, and the mean magnitude of a strategy flip (β).

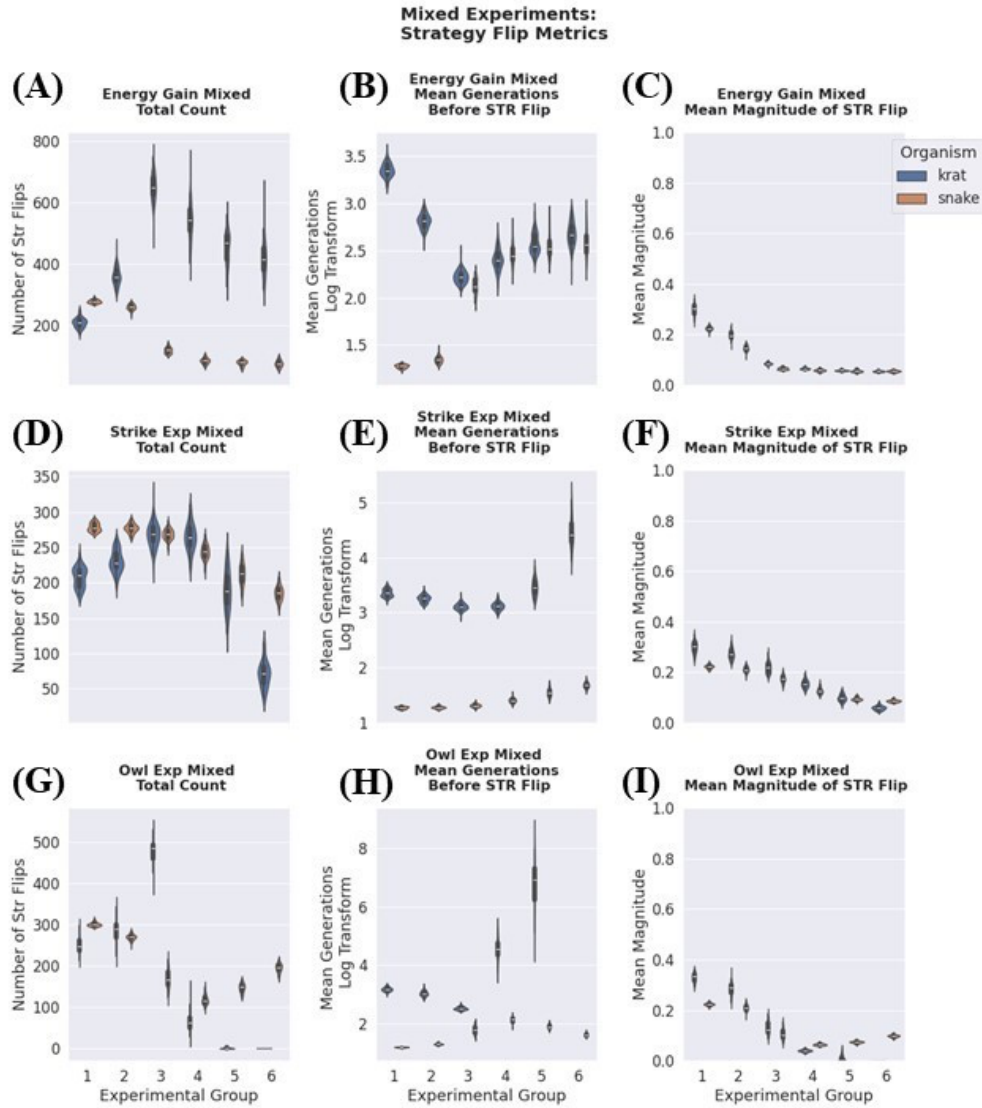


Figure 1.8: Analysis of metrics produced by the point classification algorithm applied to simulations of mixed strategies across all case studies, including total number of strategy flips, the mean number of generations before a strategy flip, and the mean magnitude of a strategy flip.

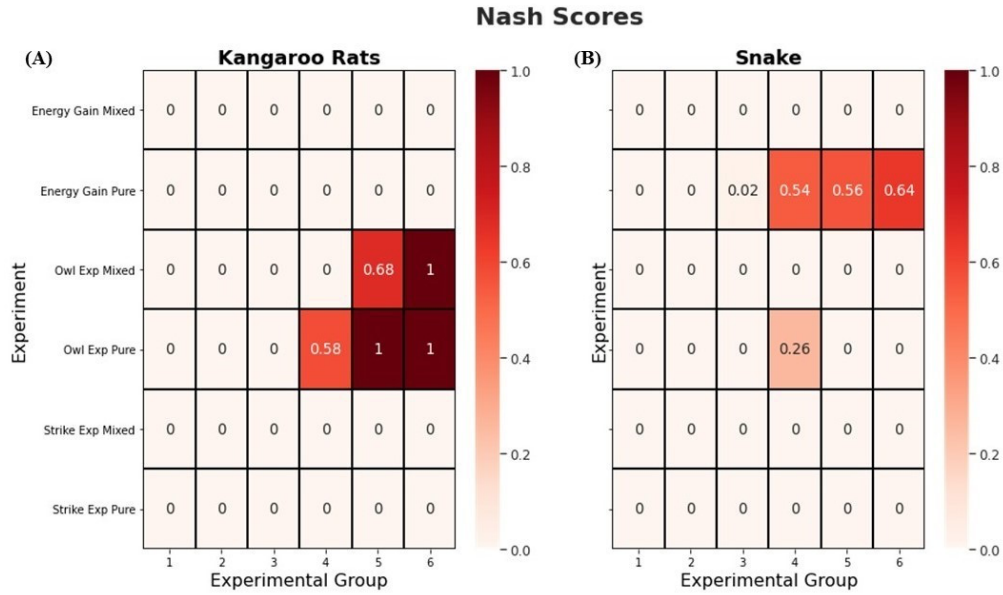


Figure 1.9: Results of the Nash Score analysis where each cell represents the Nash Score for that specific experimental group associated with the experimental simulations. The Nash Score is the ratio of simulations that reached equilibrium over the total number of simulations run for a given experimental design. A Nash Score of 1 means that 100% simulations completely reached equilibrium and the associated microhabitat preference strategy is an evolutionarily stable strategy and cannot be invaded by other strategies throughout evolutionary time. (A) shows Nash Score values for the kangaroo rat population and (B) shows the same information but for the rattlesnake population.

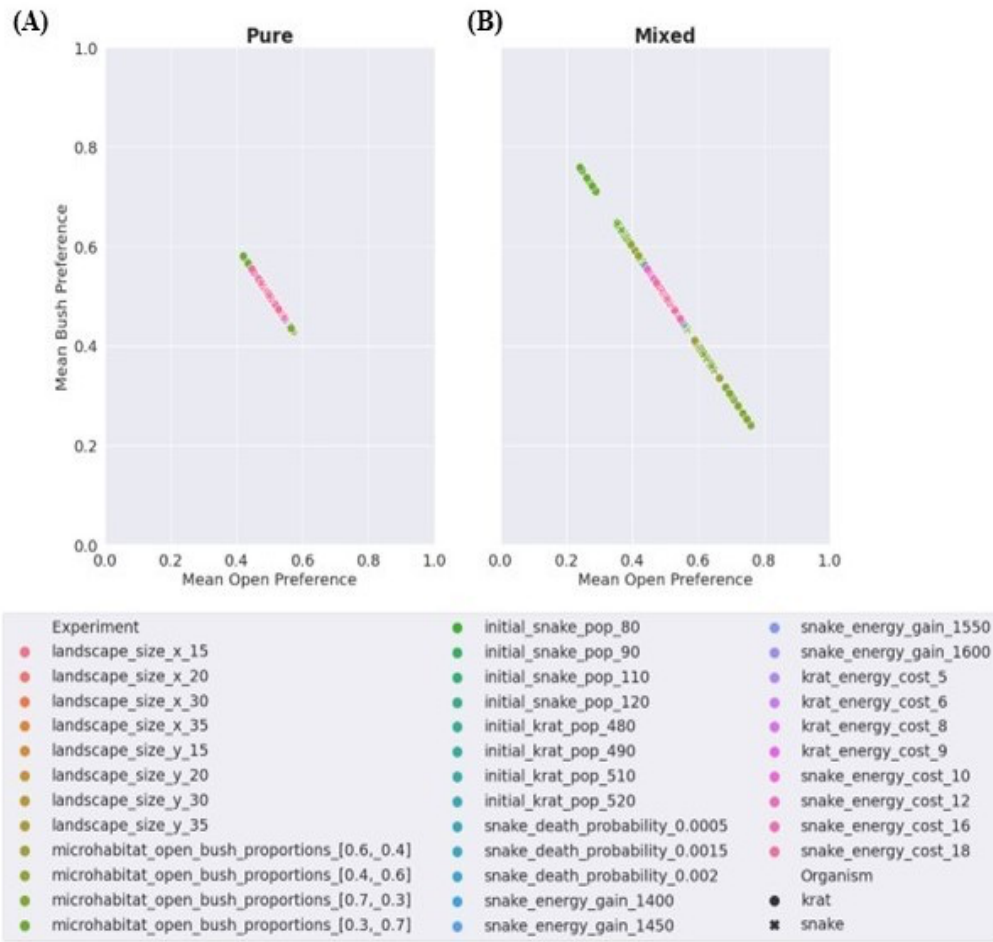


Figure 1.10: Results of sensitivity analysis of the microhabitat preferences of kangaroo rats and rattlesnakes. Each point is the mean microhabitat preference of ten simulations for the population with the given parameter being changed. Color represents the parameter being changed and the value it is being changed to. Circles indicate results for kangaroo rats (krats) while x's represent rattlesnake results. See Table 1.1 for the base parameters that are being manipulated.

Tables

Parameter	Owl Exp	Energy Gain Exp	Snake Strike Exp
Cycles	500,000	500,000	500,000
Landscape Size X Direction (cells)	25	25	25
Landscape Size Y Direction (cells)	25	25	25
Proportion Open Habitat	50%	50%	50%
Proportion Bush Habitat	50%	50%	50%
Kangaroo Rat Population Size	500	500	500
Rattlesnake Population Size	EXP	100	100
Owl Population Size	EXP	0	0
Snake Death Probability Per Cycle	0.001	0.001	0.001
Snake Strike Success Probability (Bush)	0.21	0.21	EXP
Snake Strike Success Probability (Open)	0.21	0.21	EXP
Owl Strike Success Probability (Bush)	0.0	NA	NA
Owl Strike Success Probability (Open)	0.21	NA	NA
Kangaroo Rat Energy Gain (Bush)	12	EXP	12
Kangaroo Rat Energy Gain (Open)	12	EXP	12
Snake Energy Gain	1500	1500	1500
Kangaroo Rat Energy Cost	7	7	7
Snake Energy Cost	14	14	14
Kangaroo Rat Movement Frequency (per x cycles)	1	1	1
Snake Movement Frequency (per x cycles)	8	8	8
Owl Movement Frequency (per x cycles)	1	NA	NA
Kangaroo Rat Mutation Probability	0.01	0.01	0.01
Snake Mutation Probability	0.01	0.01	0.01
Kangaroo Rat Reproduction Frequency (per x cycles)	50	50	50
Snake Reproduction Frequency (per x cycles)	300	300	300

Table 1.1: Constant experimental parameters. Cells titled “EXP” are parameters that are associated with experimental groups for a given case study. Parameters that state “per x cycles” indicate that the action is done once after x number of cycles in the associated cell have passed.

Experiment	Energy Gain (Open)	Energy Gain (Bush)
Group 1	12	12
Group 2	14	10
Group 3	16	8
Group 4	18	6
Group 5	20	4
Group 6	22	2

Table 1.2: Experimental parameters for the case study of differing foraging energy gains in microhabitats for Kangaroo Rats.

Experiment	Strike Success Probability (Bush)	Strike Success Probability (Open)
Group 1	0.21	0.21
Group 2	0.231	0.189
Group 3	0.252	0.168
Group 4	0.273	0.147
Group 5	0.294	0.126
Group 6	0.315	0.105

Table 1.3: Experimental parameters for the third case study of differing strike success experimental groups.

Experiment	Kangaroo Rat Population	Snake Population	Owl Population
Group 1	480	120	0
Group 2	480	100	20
Group 3	480	80	40
Group 4	480	60	60
Group 5	480	40	80
Group 6	480	20	100

Table 1.4: Experimental parameters for the case study of introducing owls into the system experimental groups.

References

1. Peter A Abrams. Habitat choice in predator-prey systems: Spatial instability due to interacting adaptive movements. *The American Naturalist*, 169:581–594, 11 2007.
2. Daron Acemoglu and David Autor. Chapter 12 - skills, tasks and technologies: Implications for employment and earnings. volume 4 of *Handbook of Labor Economics*, pages 1043–1171. Elsevier, 2011.
3. Li An, Volker Grimm, Abigail Sullivan, B. L. Turner II, Nicolas Malleson, Alison Heppenstall, Christian Vincenot, Derek Robinson, Xinyue Ye, Jianguo Liu, Emilie Lindkvist, and Wenwu Tang. Challenges, tasks, and opportunities in modeling agent-based complex systems. *Ecological Modelling*, 45710 2021.
4. Amos Bouskila. Interactions between predation risk and competition: A field study of kangaroo rats and snakes. *Ecology*, vol. 76, no. 1, pp. 165–78, 1995.
5. Amos Bouskila. A habitat selection game of interactions between rodents and their predators. *Finnish Zoological and Botanical Board*, 38:58–70, 2001.
6. Joel S Brown. Patch use as an indicator of habitat preference, predation risk, and competition. *Sociobiology*, Volume 22, pages 37–47, 1988.
7. Joel S Brown, John W Laundre, and Mahesh Gurung. The ecology of fear: Optimal foraging, game theory, and trophic interactions. *Journal of Mammology*, 80:385–399, 1999.
8. Donald L. DeAngelis and Stephanie G. Diaz. Decision-making in agent-based modeling: A current review and future prospectus. *Frontiers in Ecology and Evolution*, 6, 2019.
9. Emily Dolson and Charles Ofria. Digital evolution for ecology research: A review. *Frontiers in Ecology and Evolution*, 9: 11 2021.
10. Keren Embar, Ashael Raveh, Ishai Hoffmann, and Burt P. Kotler. Predator facilitation or interference: A game of vipers and owls. *Oecologia*, 174:1301–1309, 4 2014.
11. Lynn Govaert, Emanuel A. Fronhofer, Sébastien Lion, Christophe Eizaguirre, Dries Bonte, Martijn Egas, Andrew P. Hendry, Ayana De Brito Martins, Carlos J. Melián, Joost A.M. Raeymaekers, Irja I. Ratikainen, Bernt Erik Saether, Jennifer A. Schweitzer, and Blake Matthews. Eco-evolutionary feedbacks—theoretical models and perspectives. *Functional Ecology*, 33:13–30, 1 2019.
12. Volker Grimm, Uta Berger, Finn Bastiansen, Sigrunn Eliassen, Vincent Ginot, Jarl Giske, John Goss-Custard, Tamara Grand, Simone K. Heinz, Geir Huse, Andreas Huth, Jane U. Jepsen, Christian Jørgensen, Wolf M. Mooij, Birgit Müller, Guy Pe'er, Cyril Piou, Steven F. Railsback, Andrew M. Robbins, Martha M. Robbins, Eva Rossmannith, Nadja Rüger, Espen Strand, Sami Souissi, Richard A. Stillman, Rune Vabø, Ute Visser, and Donald L. DeAngelis. A standard protocol for describing individual-based and agent-based models. *Ecological Modelling*, 198:115–126, 9 2006.

13. D. M. Hugie and Lawrence M. Dill. Fish and game: a game theoretic approach to habitat selection by predators and prey. *Journal of Fish Biology*, 45:151–169, 1994.
14. Burt P Kotler. Risk of predation and the structure of desert rodent communities. *Ecology*, 65:689–701, 1984.
15. Steven L Lima. Putting predators back into behavioral predator-prey interactions. *TRENDS in Ecology & Evolution*, 17:581–590, 2002.
16. John M. McNamara. Towards a richer evolutionary game theory. *Journal of the Royal Society Interface*, 10:88, 11 2013.
17. Jonathan N. Pruitt, Andrew Berdahl, Christina Riehl, Noa Pinter-Wollman, Holly V. Moeller, Elizabeth G. Pringle, Lucy M. Aplin, Elva J.H. Robinson, Jacopo Grilli, Pamela Yeh, Van M. Savage, Michael H. Price, Joshua Garland, Ian C. Gilby, Margaret C. Crofoot, Grant N. Doering, and Elizabeth A. Hobson. Social tipping points in animal societies. *Proceedings of the Royal Society B: Biological Sciences*, 285, 2018.
18. Saman Razavi and Hoshin V. Gupta. What do we mean by sensitivity analysis? the need for comprehensive characterization of "global" sensitivity in earth and environmental systems models. *Water Resources Research*, 51:3070–3092, 5 2015.
19. Matthew P Rowe, Richard G Coss, and Donald H Owings. Rattlesnake rattles and burrowing owl hisses: A case of acoustic batesian mimicry. *Ethology*, 72:53–71, 1986.
20. Abraham Savitzky and Marcel J.E. Golay. Smoothing and differentiation of data by simplified least squares procedures. *Analytical Chemistry*, 36:1627–1639, 1964.
21. Inon Scharf. The interaction between ambush predators, search patterns of herbivores, and aggregations of plants. *Behavioral Ecology*, 32:6, pages Pages 1246–1255, 8 2021.
22. Gene D Schroder. Mechanisms for coexistence among three species of dipodomys: Habitat selection and an alternative. *Ecology*, 68:1071–1083, 1987.
23. Skipper Seabold and Josef Perktold. statsmodels: Econometric and statistical modeling with python. In *9th Python in Science Conference* 2010.
24. John Maynard Smith. *Evolution and the Theory of Games*. Cambridge University Press, New York, 1982.
25. Annalee M. Tutterow, Andrew S. Hoffman, John L. Buffington, Zachary T. Truelock, and William E. Peterman. Prey-driven behavioral habitat use in a low-energy ambush predator. *Ecology and Evolution*, 11:15601–15621, 11 2021.
26. Guido Van Rossum and Fred L. Drake. *Python 3 Reference Manual*. CreateSpace, Scotts Valley, CA, 2009.
27. Malachi D. Whitford, Grace A. Freymiller, Timothy E. Higham, and Rulon W. Clark. Determinants of predation success: How to survive an attack from a rattlesnake. *Functional Ecology*, 33:1099–1109, 6 2019.

28. William A. Mitchell. Multi-behavioral strategies in a predator-prey game: An evolutionary algorithm analysis. *Oikos*, 118:1073–1083, 11 2009.

Chapter 2 - Thermal Dynamics of Ectotherm Behavioral Strategies: Insights from Agent-Based Simulations

Michael J. Remington^{a,b}, Rulon W. Clark^a, Ryan J. Hanscom^{a,b}, Timothy E. Higham^b,
Jeet Sukumaran^a

*^aDepartment of Evolutionary Biology, San Diego State University, 5500 Campanile
Dr, San Diego, California, 92182, USA*

*^bDepartment of Evolution, Ecology, and Organismal Biology, University of
California, Riverside, 900 University Ave, Riverside, California, 92521, USA*

Abstract

Terrestrial ectotherms use dynamic behavioral thermoregulation strategies that typically depend on finding thermal refugia to avoid unfavorable conditions. Traditional analytic approaches rely on analysis of thermal indices to describe thermal conditions organisms may or may not choose, though computational simulations could potentially be used to analyze thermoregulatory behavior explicitly. Here, we leverage a novel simulation framework that integrates data from operative thermal models deployed in microhabitats available to ectotherms in order to showcase the trade-offs between two basic thermoregulatory strategies: maintaining a thermal optimum or attempting to keep body temperature within a preferred thermal range. We assess the output from simulations of these behavioral strategies to understand their influence on body temperature regulation and occupancy of thermal refugia, and then compare our findings to an empirical case study. Results from our analysis suggest that these two general strategies do not impact materially alter thermoregulation behavior as strongly as previously assumed. We also found that occupancy of thermal refugia appeared to be driven by environmental conditions rather than the thermoregulation strategy. Although our case study showed promise in providing insights into predicting use of thermal refugia, understanding microhabitat occupancy from thermal data alone may require finer scale temporal data, or the integration of other factors such as foraging dynamics or predation avoidance.

Introduction

Behavioral thermoregulation is critical for ectothermic organisms, which regulate their body temperature using external heat sources and are highly susceptible to environmental temperature fluctuations. Microhabitats in the landscape may vary in thermal conditions across both space and time, and thus ectotherms employ dynamic behavioral strategies to find thermal refugia that best maintain their body temperature. For example, terrestrial ectotherms that are semi-fossorial, make or use underground burrows that serve as both thermal and physical refugia that protect them from unfavorable biotic and abiotic conditions [18]. Since body temperature regulates enzymatic processes [17] and muscle function [3], behavioral thermoregulation is essential for optimizing performance in activities like foraging and predator avoidance.

Although some ectotherms exhibit little or no behavioral thermoregulation, most species maintain body temperatures within a preferred thermal range, and some may regulate body temperature more precisely near a thermal optimum [6, 13, 21]. The spectrum of behavioral strategies involved in thermoregulation has numerous consequences on evolutionary fitness and ecological interactions. Because hiding in refugia almost always involves a trade-off with other fitness critical activities (e.g., finding food or mates), the movement of individuals back and forth between refugia and more open microhabitats is a central aspect of the daily behavioral cycle of terrestrial ectotherms.

Research on ectotherm thermal ecology has primarily relied on mathematical models, including dynamic energy budget theory or another niche-based models.

However, these approaches typically focus on population-level trends, potentially overlooking behavioral variability at the individual level [25]; furthermore, some mathematical models have been criticized for their lack of capacity to capture fine-scale spatio-temporal temperature conditions [16]. Additionally, an ectotherm's body temperature condition is not only dependent on its current microhabitat but also is affected by microhabitats that the individual sampled previously [12]; thus, aggregating thermal conditions across microhabitats may fail to capture dynamics related to behavioral thermoregulation.

While traditional field-based methods such as camera traps and field surveys provide valuable ecological insights, they are labor-intensive and limited in their ability to capture large volumes of temporally granular behavioral data [23, 31]. Another prominent approach in thermal ecology involves characterizing thermoregulatory behavior using operative temperature models (OTMs), which continuously sample temperatures across available microhabitats. These data are then used to calculate heuristic thermal indices such as thermal accuracy, thermal quality, and thermal effectiveness [27].

OTM-based methods rely on operative temperature (T_e) to infer thermal environments experienced by ectotherms. Understanding how ectotherms sample various microhabitats with different T_e values can be approached through mathematical models [10] or summarized in reference to specific microhabitats [8]. However, rather than aggregating across microhabitats, reducing multidimensional T_e vectors through simulation into a single dynamic trajectory could provide deeper insights into individual

thermal refuge selection. For example, the thermal conditions of a basking lizard can be represented as T_{rock} (rock surface temperature) versus T_{shade} (shade temperature). A simulation model could simulate the lizard's chosen environment at any given time point, resulting in a vector of T_{lizard} , which reflects the thermal conditions it experiences based on its behavioral choices.

Here, we explore the utility of a novel agent-based thermoregulatory simulation framework designed to explicitly model the behavioral strategies ectotherms use to navigate thermal variability in their habitat. Our analysis proceeds along two lines: first, we conceptually quantify the thermal trade-offs that arise from different thermoregulatory strategies; second, we demonstrate the utility of our approach through a case study, applying the framework to empirical data and showing how it can supplement current OTM based studies. By doing so, we demonstrate our tool has the potential not only to predict individual body temperature patterns and microhabitat occupancy, but also to offer thermal ecologists a more comprehensive means of understanding and quantifying behavioral strategies. Ultimately, this framework can help classify which strategies ectotherms may adopt under varying environmental conditions and potentially estimate the rates at which they occupy thermal refugia, thereby improving our insight into daily activity patterns and habitat thermal quality.

Methods

Our simulation software is an agent-based simulation model (entitled ThermaNewt, as it relies on Newton's Law of Cooling) that simulates body temperature changes and microhabitat occupancy using time series data from temperature loggers placed in key microhabitats available to ectotherms. To see the full analysis pipeline, refer to Figure 2.1. The model simulations and post simulation analysis were implemented in Python 3.8.5 [29].

Empirical Data

For an empirical application of our approach, we used a field study of three populations of Prairie Rattlesnakes (*Crotalus viridis*) located at North American sites across a latitudinal cline (Canada site: South Eastern Alberta Canada in the Palliser Triangle; Nebraska site: Northern Nebraska near the Niobrara River in the Central Great Plains ecoregion; Texas Site: Near the city of Marathon in the Chihuahuan Desert). Individual snakes at these sites were surgically implanted with radio transmitters (Wildlife Materials, SOPI-2380-MVS) and Thermochrom iButtons DS1922L- F5, accuracy = $\pm 0.5^{\circ}\text{C}$, Maxim Integrated Products Inc., Rio Robles, San Jose, CA), which recorded field-active body temperatures (T_b) every 70 minutes. Snakes were released 1-2 days following surgery at the location of capture. Snakes were recaptured after one year of monitoring and the iButton and radio transmitter were surgically removed.

Our model incorporated 10 snakes from the Canada site, 2 from the Nebraska site, and 9 from the Texas site. At each site we also placed three replicate physical Operative

Thermal Models (OTMs) in each of four different microhabitats typically used by this species (inside burrow, at entrance of burrow, under vegetation, and on open ground); however, to generate this initial case study, we simplified this array of microhabitats to the two extremes (i.e., the two microhabitat most likely to differ in temperature): in burrow, and in open. OTMs consisted of hollow copper tubes that replicate thermal qualities of snake bodies [1].

We were also able to intermittently validate microhabitat occupancy of snakes from fixed videography and direct observation via iradio telemetry tracking to monitor snake behavior. This provides sparse, semi-continuous time series observations of whether the focal snake was in the burrow or out in the open. This data was used to evaluate the accuracy of our simulated microhabitat occupancy classification output from our model.

Simulation Model Description

The simulation model is based on a discrete, time-dependent version of Newton's Law of Cooling (Equation 2.1), which describes the change in body temperature over time due to heat exchange with the environment. The framework uses thermal time series data from temperature loggers that are exposed to the direct sun or placed in thermal refugia that could potentially be occupied by a focal species, then simulates body temperature changes and occupancy of thermal refugia. During each cycle, the internal body temperature of the agent is calculated via Newton's law of cooling equation with respect to time.

Equation 2.1: Newton's Law of Cooling

$$t_{\text{body},n+1} = t_e + (t_{\text{body},n} - t_e) \cdot e^{-k \cdot \delta t} \quad (2.1)$$

where:

- t_e is the environmental temperature
- $t_{\text{body},n}$ is the body temperature of the organism at time step n
- $t_{\text{body},n+1}$ is the body temperature of the organism at the next time step
- δt is the time interval between consecutive steps
- k is a constant representing the cooling rate
- e denotes the base of the natural logarithm, Euler's number

Newton's law of cooling has a rich history in the study of organismal thermal ecology [24, 26, 9]. Because T_e often differs between potential microhabitats, we developed behavioral response functions as sub-models that relate the agent's internal body temperature to the probability of the organism switching microhabitat occupancy (open or refuge) to infer which microhabitat temperature the organism occupies at any given time step.

We developed three basic thermoregulatory sub-models: *random*, *boundary*, and *preferred* (Figure 2.2), and a fourth sub-model as a variant of the *preferred* sub-model (*preferred_{est}*). The *random* sub-model serves as a null model where agents switch microhabitat occupancy randomly, regardless of their internal temperature. In the *boundary* sub-model, agents change occupancy when their internal temperature falls outside a defined thermal preference range. Finally, in the *preferred* sub-model, agents try to maintain their body temperature near a defined thermal optimum, with the

probability of switching states increasing as their temperature deviates from this optimum. The preferred_{est} is a variant of the preferred sub-model which models intraspecific differences in thermal preferences by estimating thermal preference variables from empirical data (see Parameter Estimation with Gradient Descent section for more details).

Empirical T_{set} measurements (i.e., the range of body temperatures within which an ectotherm exhibits optimal physiological performance) for the focal populations of our case study *Crotalus viridis* were not available from a controlled experimental, but most observations indicate that their summer body temperatures range between 20–30°C [22]. Experimental data for a closely related species (*C. oreganus*) indicate that minimum T_{set} values can vary by population but typically lie between 11–16°C for voluntary minimum values, and between 36–38°C for voluntary maximum values (Crowell et al. (2021)). Based on this information and under the assumption an ectotherms thermal preference range is a subset of its T_{set} , we assumed a conservative minimum thermal preference of 18°C and a maximum thermal preference of 32°C for our model. Parameters for the random, boundary, and preferred sub-models are provided in Table 2.1. Estimated thermal preference parameters for the preferred_{est} sub-model are listed in Table 2.2.

Data Integration and Interpolation

All data analysis and cleaning were conducted using Pandas, a python library for dataframe manipulation [28]. We averaged the microhabitat temperature data across OTMs placed in replicate microhabitats to the nearest hour, and matched it to the

corresponding snake body temperature timeline using Pandas' *merge asof* function with the forward-filling method. This approach creates a unified timeline for all temperature variables at each site, associating snake body temperatures with climate observations that occurred within a 70-minute window.

Data from cooler months (October through April) when snakes are inactive were excluded from the analysis. Snake body temperatures during overwintering remain nearly constant and are often higher than near-surface conditions because snakes use deeper underground refugia during these months.

Parameter Estimation with Gradient Descent

One assumption of our base analysis is that there is no intraspecific variation in thermal preferences between populations of rattlesnakes. This assumption may not reflect real world conditions as evidence exists that individuals of some species of ectotherms can vary in thermal preferences [19]. To evaluate the impact of accounting for individual variation, we relaxed this assumption and conducted a separate preferred sub-model (preferred_{est}). This analysis fits our model to observed rattlesnake body temperature data and estimates the minimum, maximum, and optimal thermal preferences of each individual using a gradient descent algorithm.

If this model fits the empirical data significantly better than our other models, it would suggest that individual differences in thermal preference play a greater role in driving thermoregulation dynamics than the specific thermoregulatory strategy itself. Conversely, if the model performs similarly or worse, it would imply that individuals

across the population adopt static strategies, with thermal preferences being less influential in thermoregulation.

We used a bounded limited memory BFGS 'L-BFGS-B' optimization algorithm with an approximated gradient with a step size of 0.01 to estimate parameters. We found this method outperformed the Adam optimization algorithm at recovering simulated parameters. Estimated parameters used in analysis can be seen in Table 2.2. Note that this sub-model was constructed to demonstrate the potential utility that a simulation approach has for considering individual variation in thermoregulatory strategies, and that future use of this approach would need to incorporate estimates of individual variation in body temperature preferences that were independent from field-collected data (i.e., collected from animals occupying a thermal gradient under controlled conditions).

Thermal Indices

The effectiveness of ectotherm thermoregulation has historically been evaluated through heuristics based on thermal indices. Our simulation software outputs simulated ectotherm body temperature (T_b), and the environmental conditions of the agent as a function of microhabitat occupancy (open or burrow). For each of our thermoregulatory sub-models, we evaluate four thermal indices traditionally used in thermal ecology studies: thermal quality (de), thermal accuracy (db), thermal effectiveness (E), and the thermoregulatory exploitation index (Ex) [13, 27].

Thermal accuracy (db) is a metric that measures the difference between an organism's body temperature (T_b) and its thermal preference zone. High values of db indicate poor thermal accuracy. Thermal quality (de) is a metric that measures the

distance of the thermal operative temperature (T_e) from the thermal preference zone, with high values of d_e indicating low quality thermal habitat. Thermal effectiveness (E) is one minus the ratio of mean d_b and mean d_e . Values of 1 indicate careful and precise thermoregulation, and 0 indicates that the animal is thermoconforming (body temperature always matches the environmental temperature). Values approaching negative 1 or lower indicate periods of where the organism is in poor habitat and is experiencing thermal stress. Finally, the thermal exploitation index (Ex) is the percentage of time spent in the thermal preference zone, with higher values indicating more time spent in the thermal preference zone [13, 21, 27].

Time Series Comparison Analysis

One of the primary objectives of our simulation is to evaluate which thermoregulatory sub-model best approximates the body temperatures observed in empirical data. To assess the similarity between empirical and simulated data, we conducted a time series comparison analysis. This involved calculating three key distance metrics for each snake: mean squared error (MSE), mean absolute percentage error (MAPE), and dynamic time warping distance (DTW) [4]. MSE quantifies average squared differences between simulated and empirical temperatures, highlighting large deviations. MAPE measures prediction accuracy as a percentage, offering interpretability across scales. DTW captures temporal alignment by comparing time series with potential shifts in timing, making it ideal for assessing sequences with time lags or irregular patterns. These metrics collectively provide a comprehensive evaluation of both prediction accuracy and temporal correspondence.

We assume that the sub-model which minimizes this set of distance metrics represents the most probable thermoregulatory strategy adopted by free-ranging rattlesnakes. For each distance metric, we applied a mixed linear model to statistically determine whether a behavioral sub-model significantly reduced these metrics compared to a random sub-model. The study site location was included as a fixed effect, and individual snakes were treated as random effects in each model.

Predicting Microhabitat Occupancy with Supervised Machine Learning

We used a supervised machine learning pipeline to assess which sub-model best approximates empirical data and determine if we could accurately predict microhabitat occupancy (burrow usage) using our simulation framework. We performed an exhaustive search of different machine learning parameter combinations to evaluate the accuracy of our method in predicting ectotherms' occupancy of thermal refugia. If our pipeline consistently achieves high accuracy, it could become a valuable tool for predicting population-level patterns such as daily activity times or phenology.

Two machine learning algorithms were evaluated, a random forest (RF) approach [5] and a recurrent neural network (RNN) approach [11]. We chose these two methods because RNNs are specifically designed for sequential data, making them well-suited for time series forecasting. While RFs are not inherently designed for sequential data, they can still be effective in time series analysis when temporal features are explicitly engineered.

For the RF approach, we used the month, hour, open temperature, and burrow temperature as our explanatory features and used simulated burrow occupancy labels

from the thermal model as our response variable for the classification algorithm. Hyper parameters were estimated via a randomized hyper-parameter optimization algorithm called *RandomizedSearchCV* [20]. Hyper-parameters are parameters that do not have biological relevance but impact model fit. Data were partitioned into a training and a test set (80/20).

The RNN pipeline parsed our training and test data into sequences. We tested window sizes (3-10) to see which window size was optimal. Empirical behavioral validation data from video analysis was also parsed into sequences to make them directly comparable.

For both models, we evaluate accuracy, precision, recall, and F1 scores against an empirical validation set outside of the training and test sets of the machine learning model, using functions provided by the scikit-learn library [20]. We apply both models to all combinations of our simulation pipeline including imputing versus not imputing data, each of the thermoregulatory sub-models, and parameters estimated (yes or no).

Results

Ecological Comparison of Thermoregulatory Strategy

Among our thermoregulatory study groups (random, boundary, preferred, and preferred_{est}), we found that the boundary thermoregulatory sub-model led to the highest rate of exposure (agents occupying open habitat), while also having more state changes compared to the preferred. Both the preferred and the preferred_{est} models resulted in lower exposure rates and fewer state changes than the random model (Figure 2.3A, B).

Our analysis of 24-hour exposure rates revealed distinct patterns across three agent models. Agents with the boundary, preferred, and preferred_{est} all demonstrated crepuscular activity patterns, with the probability of being in the open peaking near dawn and dusk. Agents with the boundary model spend more time exposed in the open at all times of a diel cycle compared to the preferred model. Agents encoded with the preferred sub-model show somewhat similar temporal trends, but to a lesser degree, and the preferred_{est} agents were intermediate between the two (Figure 2.6).

Thermal index analysis across different times of the day corroborates the idea that simulated agents favor crepuscular activity. During the morning and evening times of the day, thermal quality and thermal accuracy are minimized while thermal exploitation is maximized (Figure 2.9). These times also correspond to the highest probabilities of being active (Figure 2.6). This indicated that crepuscular activity is optimal for snakes in reference to maintaining preferred body temperatures, regardless of behavioral strategy. Colder nighttime conditions compel agents to warm up during the morning, but as the day rapidly heats up, they must retreat to thermal refugia to avoid overheating. In the evening after spending the day sheltered in a burrow, they can become more surface active again.

Comparison to empirical data from free-ranging snakes indicates that simulated agents were more likely to occupy open microhabitat than free-ranging snakes. At the Nebraska and Texas study site, the thermal accuracy values of the boundary agents tended to underestimate the thermal accuracy of free ranging snakes while the preferred sub-model tended to match actual snakes' thermal accuracy at those sites (Figure 2.7 B,

C). However, at the Canada site, simulated snake thermal accuracy values more closely matched measures from free-ranging snakes for all sub-models except the random sub-model (Figure 2.7A).

Simulated Body Temperature Accuracy

Due to the number of snakes and the length of our time series, visually assessing the similarity of all our simulated conditions can be difficult (Figure 2.4). This subset of data highlights the general finding that the position of the oscillations is accurate, but the overall magnitude of simulated body temperatures does not match actual temperatures.

The results of a linear mixed model assessing MSE, MAPE, and DTW between thermoregulatory strategies found the boundary, preferred, and preferred_{est} all significantly reduced the 3 time series measures compared to the random model, meaning they were more similar to the actual data (Table 2.3, 2.4, 2.5). The preferred sub-model was slightly more effective at minimizing MSE and DTW than the boundary sub-model (Figure 2.5A, C), while the boundary performed better than the preferred at minimizing MAPE (Figure 2.5B). The preferred_{est} performed the best at minimizing time series (Tables 2.4, 2.5).

Classifying Microhabitat Occupancy Accuracy

An exhaustive search of different pipeline combinations to evaluate the accuracy of our method in predicting ectotherms' occupancy of thermal refugia found that our most accurate simulation used the preferred thermoregulatory sub-model for the Texas-Marathon study site and yielded an accuracy of 0.717 (Table 2.6). However, when we

analyze the distribution of model accuracy grouped by training data population used (Figure 2.10A), the Texas population has a bimodal distribution while all other accuracy result distributions for the study site and the thermoregulatory sub-models were primarily normally distributed around 0.5 accuracy (i.e., similar to random) (Figure 2.10A,B). When we assessed the top 10 models using the total population of individuals sampled our best model yielded an accuracy of 0.61 using the random thermoregulatory sub-model (Table 2.7).

Discussion

Our primary objective in this study was to examine the utility of a computational simulation framework for studying and quantifying the thermal effects of thermoregulatory behavioral strategies. Secondary goals were to evaluate potential trade-offs in thermal conditions associated with different algorithms and explore the potential for our framework to classify patterns of microhabitat occupancy over time. From our analyses, both the boundary and preferred sub-models were relatively equivalent at reproducing real world conditions, while the preferred_{est} consistently outperformed the other sub-models in time series similarity metrics (Table 2.3, 2.4, 2.5). This could indicate that individuals may adopt a mix of strategies depending on the environmental conditions, and thermoregulation strategy should not be treated as a static trait of the individual. Secondly, the superior performance of preferred_{est} group indicates a potentially substantial role of individual variation when modeling thermal preferences.

Further evidence that thermoregulation strategies may be mixed can be qualitatively assessed by comparing simulated thermal accuracy to field snake values (Figure 2.7). At the Canada field site, both the preferred and boundary thermal accuracy values align with field conditions, with the preferred value corresponding to the lower thermal accuracy range and the boundary value matching snakes at the upper bounds. The thermal accuracy of the preferred and the preferred_{est} models better match field conditions compared to the boundary model at the Nebraska and Texas Site. One explanation for this pattern is that the Canada site had the poorest burrow thermal quality compared to the other two sites (Figure 2.8) which indicates individuals would need to spend more time

thermoregulating in order to maintain preferred body temperatures. This would in turn lead to real conditions matching model assumptions more closely, as simulated snakes in our model only thermoregulate and do not hunt or rest, so a poorer average thermal quality would result in individuals prioritizing thermoregulation more than other behaviors. From our thermal refugia analysis, the preferred sub-model has the fewest number of state flips (Figure 2.3) so from the perspective of an organism minimizing energetic costs, ectotherms in thermally favorable conditions would likely adopt the preferred strategy over the boundary strategy.

From a thermoregulatory perspective, organisms must maintain a balance between minimizing the energetic costs of switching microhabitat states and minimizing (db) under dynamic spatial-temporal temperature conditions. The main ecological trade-offs we identified between the boundary and preferred sub-models were during midday hours when thermal quality was at its worst, regardless of strategy. Under these conditions, the boundary thermoregulatory sub-model experienced the worst thermal quality (de); however, the boundary sub-model did not switch microhabitat states as often, which may minimize energy expenditure from a movement perspective in a living organism. All models had relatively equivalent thermal exploitation index values, even at midday, although the boundary thermoregulatory model resulted in the lowest thermal accuracy (Figure 2.9B). However, as the thermal exploitation index is relatively equivalent across models (Figure 2.9C), the boundary strategy may be the most advantageous in the context of foraging as organisms following this strategy could spend more time exposed under thermally challenging conditions.

How ectotherms navigate these trade-offs may partially explain why many ectotherms become cathemeral under certain conditions, meaning environmental conditions primarily drive activity times of the organisms, rather than the diel cycle [2]. Results from our machine learning pipeline further corroborate this as our attempt to build supervised machine learning models to predict microhabitat occupancy from environmental variables proved largely unsuccessful (Figure 2.10). Our best model yielded an accuracy of only 0.71 at one site, indicating that this modeling framework could have potential, but would likely require further integration of biotic and ecological phenomena such as predation risk, prey availability, or movement dynamics.

Fitness outcomes often hinge on trade-offs involving movement cost, energetics, and predation risk, none of which are currently included in our model. Although our model does allow us to identify the behavioral and temporal trade-offs of thermoregulatory patterns, it does not explicitly model fitness, which would be required for developing an understanding of how dynamics such as movement cost, energetics, spatial thermal heterogeneity, and other risks play into thermoregulatory decisions. This is also likely the explanation for why our sub-models produce relatively accurate body temperature values, but we had inconclusive results for predicting microhabitat occupancy as occupancy may be shaped primarily by selection pressures and a variety of environmental conditions rather than solely temperature and thermoregulation.

Conclusion and Future Work

The notion that ectothermic organisms adopt strategies to balance the physiological cost of poor thermal accuracy and the energetic costs of thermoregulation (e.g., seeking thermal refuges) is a long-established idea [15, 30]. Our framework aims to find application with this theory to provide a methodology that elucidates how, when, and why ectotherms choose various behavioral thermoregulation strategies.

This research highlights the potential of a simulation framework for understanding more nuanced thermoregulatory behavior but also indicates that simulations of thermoregulatory behavior or microhabitat use may be more accurate if they can incorporate more behavioral and ecological complexity. Future iterations of our model could explicitly model fitness as a function of not only thermal accuracy, but also incorporate factors such as movement cost, hunger, and risk to analyze how individuals navigate these trade-offs and quantify the emergent patterns at the population level.

Our simulation modeling approach and overarching modeling pipeline (Figure 2.1) provide researchers with a tool to analyze these conditions at both fine temporal resolutions and site-specific scales—without necessarily requiring the collection of live organisms. Such an analysis would be invaluable for predicting how organisms may adapt to climate change, as plasticity in thermoregulatory behavior will almost certainly mediate how ectotherm survival and reproduction are affected by shifting temperatures [7]. In conjunction, our method could be leveraged as a pre-hoc OTM analysis leveraging just microhabitat data to inform field site selection and assess whether functional differences in thermoregulation are likely among different populations of ectotherms.

Lastly, future work could expand on the potential of simulation frameworks for understanding individual variation in thermal ecology. The best performing sub-model (preferred_{est}) assumed individuals differed in thermal preference, suggesting that there is significant intraspecific variation in body temperature dynamics of the individual snakes in our study. Intraspecific variation in thermal traits has also been linked to personality traits in poikilotherms, suggesting that modeling certain thermoregulatory characteristics (e.g., low thermal accuracy) is correlated with bolder (high-risk taking strategies) behavioral syndromes in lizards [14]. In our simulation framework, the boundary sub-model may be conceived of as a bold strategy, as it results in higher exposure rates at the cost of poorer thermal accuracy. Thus, a promising direction for future work would be to make thermoregulatory behavior selection a function of “shy” (the preferred sub-model) versus “bold” (the boundary sub-model) personality types.

Tables

Sub-Model	t_{initial}	k	$T_{\text{pref min}}$	$T_{\text{pref max}}$	T_{opt}
Random	25	0.01	-	-	-
Boundary	25	0.01	18	32	-
Preferred	25	0.01	18	32	28
Preferred _{est}	25	0.01	-	-	-

Table 2.1: Parameter values for each of sub-model when parameters are not estimated via the gradient descent algorithm. For the preferred_{est} case, parameters for thermal minimum, thermal maximum, and thermal optima vary for each rattlesnake (see supplementary materials).

Sampling Frequency (min)	Study Site	Snake ID	Thermal Pref. Min (°C)	Thermal Pref. Max (°C)	Thermal Optimum (°C)
15	Canada	EDCRVI003	18.0	32.0	28.0
15	Canada	EDCRVI004	18.0	32.0	28.0
15	Canada	EDCRVI001	18.0	32.0	28.0
15	Canada	EDCRVI002	17.8	34.7	20.0
15	Canada	EDCRVI015	18.0	31.8	28.7
15	Canada	EDCRVI013	18.0	32.0	28.0
15	Canada	EDCRVI005	18.1	32.1	29.8
15	Canada	EDCRVI006	18.1	32.0	27.8
15	Canada	EDCRVI016	18.0	31.9	27.7
15	Canada	EDCRVI010	18.0	32.0	28.1
15	Nebraska	NVCRVI037	18.0	31.9	28.5
15	Nebraska	NVCRVI030	18.0	32.0	28.0
15	Texas- Marathon	MGCRVI021	15.1	30.8	20.0
15	Texas- Marathon	MGCRVI015	18.2	31.4	26.1
15	Texas- Marathon	MGCRVI014	10.0	25.7	20.0
15	Texas- Marathon	MGCRVI013	22.7	32.4	23.5
15	Texas- Marathon	MGCRVI011	18.1	31.9	28.4
15	Texas- Marathon	MGCRVI010	10.2	32.3	20.0
15	Texas- Marathon	MGCRVI008	10.7	28.4	20.0
15	Texas- Marathon	MGCRVI003	18.0	32.0	28.0

Sampling Frequency (min)	Study Site	Snake ID	Thermal Pref. Min (°C)	Thermal Pref. Max (°C)	Thermal Optimum (°C)
15	Texas- Marathon	MGCRVI009	19.0	30.3	20.1
70	Canada	EDCRVI003	18.0	32.0	28.0
70	Canada	EDCRVI004	18.0	32.0	27.7
70	Canada	EDCRVI001	18.0	32.3	20.9
70	Canada	EDCRVI002	18.0	32.0	28.0
70	Canada	EDCRVI015	20.0	32.0	20.0
70	Canada	EDCRVI013	17.4	30.9	24.4
70	Canada	EDCRVI005	18.0	32.0	28.6
70	Canada	EDCRVI006	18.0	32.0	28.1
70	Canada	EDCRVI016	18.0	32.0	28.0
70	Canada	EDCRVI010	18.1	31.9	28.2
70	Nebraska	NVCRVI037	18.2	31.8	28.2
70	Nebraska	NVCRVI030	19.8	32.0	23.4
70	Texas- Marathon	MGCRVI021	15.8	31.2	20.4
70	Texas- Marathon	MGCRVI015	10.1	25.4	20.7
70	Texas- Marathon	MGCRVI014	10.8	20.3	20.0
70	Texas- Marathon	MGCRVI013	17.9	32.0	20.4
70	Texas- Marathon	MGCRVI011	20.0	30.9	21.7
70	Texas- Marathon	MGCRVI010	10.0	27.6	20.0
70	Texas- Marathon	MGCRVI008	17.9	32.0	22.7

Sampling Frequency (min)	Study Site	Snake ID	Thermal Pref. Min (°C)	Thermal Pref. Max (°C)	Thermal Optimum (°C)
70	Texas- Marathon	MGCRVI003	13.3	21.7	20.0
70	Texas- Marathon	MGCRVI009	18.0	32.0	28.0

Table 2.2: Estimated thermal preference values used in the preferred_{est} sub-model. Data with a sampling frequency of 70 minutes was not imputed, whereas data with a sampling frequency of 15 minutes was imputed.

MSE	Imputed:		
	False		
Fixed Effects	Coefficients	Std.Err.	P-value
Intercept	53.582	3.949	0.000***
Strategy: Boundary	-25.383	2.197	0.000***
Strategy: Preferred	-28.814	2.197	0.000***
Strategy: Preferred _{est}	-32.647	2.197	0.000***
Study Site: Nebraska	-0.032	9.094	0.997
Study Site: Texas-	5.825	5.395	0.280
Marathon			
Group Var	125.174	7.358	-

Table 2.3: Mean least square error (MSE) mixed linear regression results. MSE distances with thermoregulation strategy as a fixed effect explanatory variable and study site as a fixed effect. Individual snakes were treated as a random effect. Model coefficients were evaluated using z-statistics derived from maximum likelihood estimation. The results of this model suggest that the Boundary, Preferred, and Preferred_{est} strategies were significantly effective at reducing MSE.

MAPE	Imputed:		
	False		
Fixed Effects	Coefficients	Std.Err.	P-value
Intercept	28.166	1.572	0.000***
Strategy: Boundary	-4.718	0.625	0.000***
Strategy: Preferred	-3.833	0.625	0.000***
Strategy: Preferred _{est}	-6.389	0.625	0.000***
Study Site: Nebraska	-5.433	3.734	0.146
Study Site: Texas-	-5.668	2.215	0.010**
Marathon			
Group Var	22.214	4.363	-

Table 2.4: Mean Absolute Percentage Error (MAPE) mixed linear regression results. MAPE distances with the thermoregulation strategy as an explanatory variable and study site as a fixed effect. Model coefficients were evaluated using z-statistics derived from maximum likelihood estimation. Individual snakes were treated as a random effect. Based on this model, the simulated body temperatures with parameters estimated (Preferred_{est}) was the only thermoregulatory sub model that was significantly better at reducing MAPE compared to the random thermoregulatory sub model, which is represented by the intercept group. Overall, study site differences were more significant than the specific thermoregulation strategy sub-model, which could indicate there may be significant differences at the population and individual level in thermoregulation patterns.

DTW	Imputed:		
	False		
Fixed Effects	Coefficients	Std.Err.	P-value
Intercept	14193.944	495.077	0.000***
Strategy: Boundary	-3192.678	582.384	0.000***
Strategy: Preferred	-4499.912	582.384	0.000***
Strategy: Preferred _{est}	-5812.469	582.384	0.000***
Study Site: Nebraska	-581.110	841.114	0.490
Study Site: Texas-	4998.208	498.924	0.000***
Marathon			
Group Var	288795.758	237.465	-

Table 2.5: Mixed linear regression results correlating Dynamic Time Warping (DTW) distances with the thermoregulation strategy as an explanatory variable and study site as a fixed effect. Model coefficients were evaluated using z-statistics derived from maximum likelihood estimation. Individual snakes were treated as a random effect. Based on this model, the simulated body temperatures with parameters estimated (Preferred_{est}) was the only thermoregulatory sub model that was significantly better at reducing DTW compared to the random thermoregulatory sub model, which is represented by the intercept group. Overall, study site differences were more significant than the specific thermoregulation strategy, which could indicate there may be significant differences at the population and individual level in thermoregulation patterns.

Study Site	Sub	Parameters	Sampling Granularity	ML	Window	Accuracy	Precision	Recall	F1	TP	FP	TN	FN	AUC
	Model	Estimated?	(Min)	Method	Size	Score								
Texas-	preference	Yes	70	rf	NaN	0.7167	0.5476	0.6053	0.5750	23	19	63	15	0.7234
Marathon														
Texas-	preference	No	70	rf	NaN	0.6917	0.5455	0.1579	0.2449	6	5	77	32	0.5485
Marathon														
Texas-	preference	No	15	rf	NaN	0.6902	0.4571	0.0952	0.1576	16	19	365	152	0.5227
Marathon														
Texas-	random	Yes	15	rnn	6.0	0.6886	0.0000	0.0000	0.0000	0	2	376	168	0.4320
Marathon														
Texas-	random	Yes	70	rnn	8.0	0.6875	0.5600	0.3684	0.4444	14	11	63	24	0.6924
Marathon														
Texas-	random	No	70	rnn	4.0	0.6724	0.0000	0.0000	0.0000	0	0	78	38	0.6884
Marathon														
Texas-	random	Yes	70	rnn	9.0	0.6667	0.5094	0.7105	0.5934	27	26	47	11	0.6975
Marathon														
Texas-	random	Yes	70	rnn	5.0	0.6609	0.4898	0.6316	0.5517	24	25	52	14	0.7321
Marathon														
Texas-	random	No	70	rnn	8.0	0.6607	0.5000	0.6579	0.5682	25	25	49	13	0.6696
Marathon														
Texas-	random	Yes	70	rnn	7.0	0.6549	0.4902	0.6579	0.5618	25	26	49	13	0.6523
Marathon														

Table 2.6: Results of the top 10 most accurate machine learning models predicting microhabitat occupancy of all models ran. Populations were subdivided by the study site and custom models were built from these sub populations marked by the column 'Study Site'. The first six columns are the model specifications, columns 7-10 showcase model performance, and c the results of our confusion matrix for each model and AUC which indicates model validity (11-15). Metrics such as accuracy, precision, recall, and F1 score are presented alongside additional performance metrics but accuracy is how we sorted the data set to evaluate our top models.

Sub-Model	Parameters Estimated?	Sampling Granularity (Min)	ML Method	Window Size	Accuracy	Precision	Recall	F1 Score	TP	FP	TN	FN	AUC
random	Yes	15	RF	NaN	0.6110	0.5415	0.8511	0.6619	463	392	280	81	0.6274
random	Yes	70	rnn	9.0	0.6102	0.5823	0.4107	0.4817	46	33	109	66	0.6109
preference	Yes	70	RF	NaN	0.6084	0.5600	0.4870	0.5209	56	44	104	59	0.5989
random	Yes	70	rnn	4.0	0.6062	0.5765	0.4261	0.4900	49	36	108	66	0.6277
preference	Yes	15	rnn	7.0	0.6055	0.5604	0.5717	0.5660	311	244	421	233	0.6173
random	No	70	rnn	8.0	0.6039	0.5882	0.3540	0.4420	40	28	114	73	0.6247
preference	Yes	15	rnn	5.0	0.6036	0.5537	0.6066	0.5789	330	266	401	214	0.6203
preference	Yes	15	rnn	6.0	0.6033	0.5550	0.5938	0.5737	323	259	407	221	0.6122
random	Yes	70	rnn	10.0	0.6008	0.5500	0.4955	0.5213	55	45	97	56	0.6538
random	No	70	rnn	6.0	0.5992	0.5568	0.4336	0.4876	49	39	105	64	0.6166

Table 2.7: The top 10 models from machine learning pipeline predicting microhabitat occupancy for all snakes sampled (study site = total population) under various model conditions. Filtering the data this way yields us models where we assume that intraspecific differences among populations can be generalized with a single model. The first five columns are the model specifications, columns 6-9 showcase model performance, and columns 10-14 are further details to how performance metrics were calculated. In our analysis we primarily focused on the accuracy of the model over metrics such as precision, recall, and F1 Score.

Figures

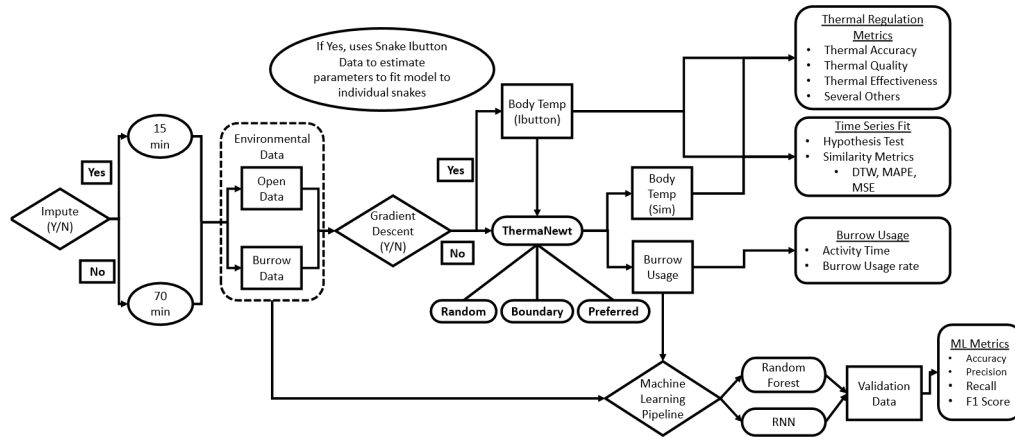


Figure 2.1: Workflow of the simulation analysis conducted. ThermaNewt, is the name for the simulation model based on Newton’s law of cooling. Random, Boundary, and Preferred to represent our three thermoregulation sub-models.

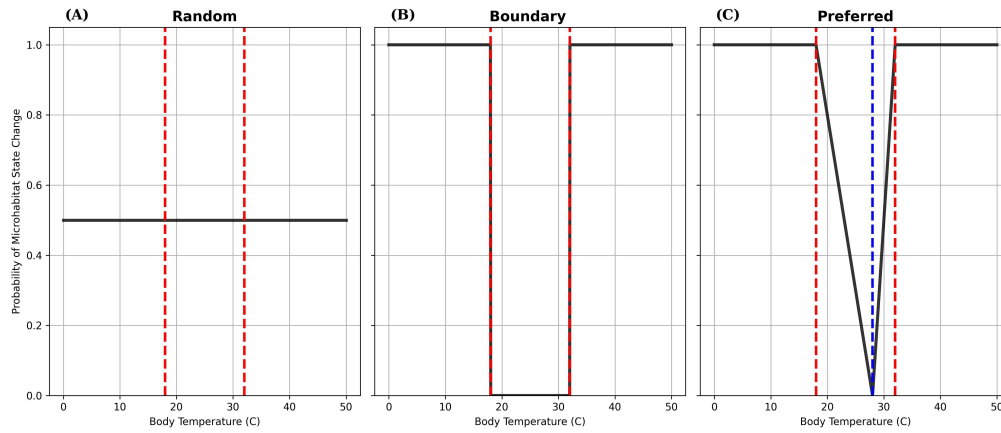


Figure 2.2: Behavioral response functions shown with black lines for our three thermoregulatory sub-models. The x axis is the organism's internal body temperature and the y axis is the probability of an agent switching to the optimal thermal refugia. Red lines represent the thermal preference range we set for the snakes. A) Represents the random model, where our modeled organism flips states at random regardless of internal body temperature. B) The boundary model where the organism changes state if it is no longer in the thermal preference range. C) The preferred model represents an organism trying to maintain its body temperature along a thermal optima (shown in blue).

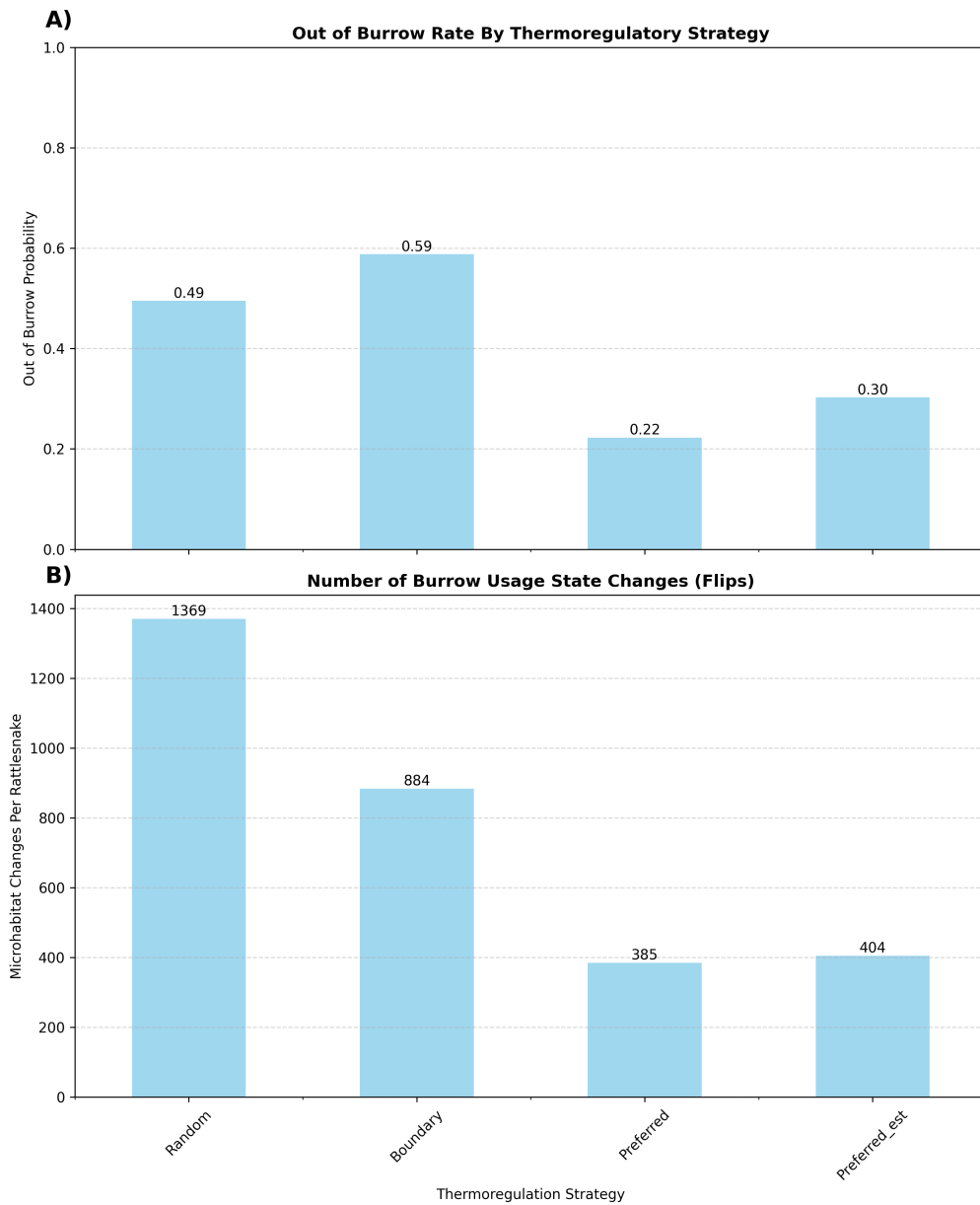


Figure 2.3: Both graphs showcase microhabitat usage metrics by thermoregulation strategy. Figure A, the y-axis represents the probability of being in the open, where 1 is 100% probability of being in the open and 0 is 100% probability of being in the burrow. Figure B is the average count of state flips from being in the open to back to the burrow or vice versa per snake.

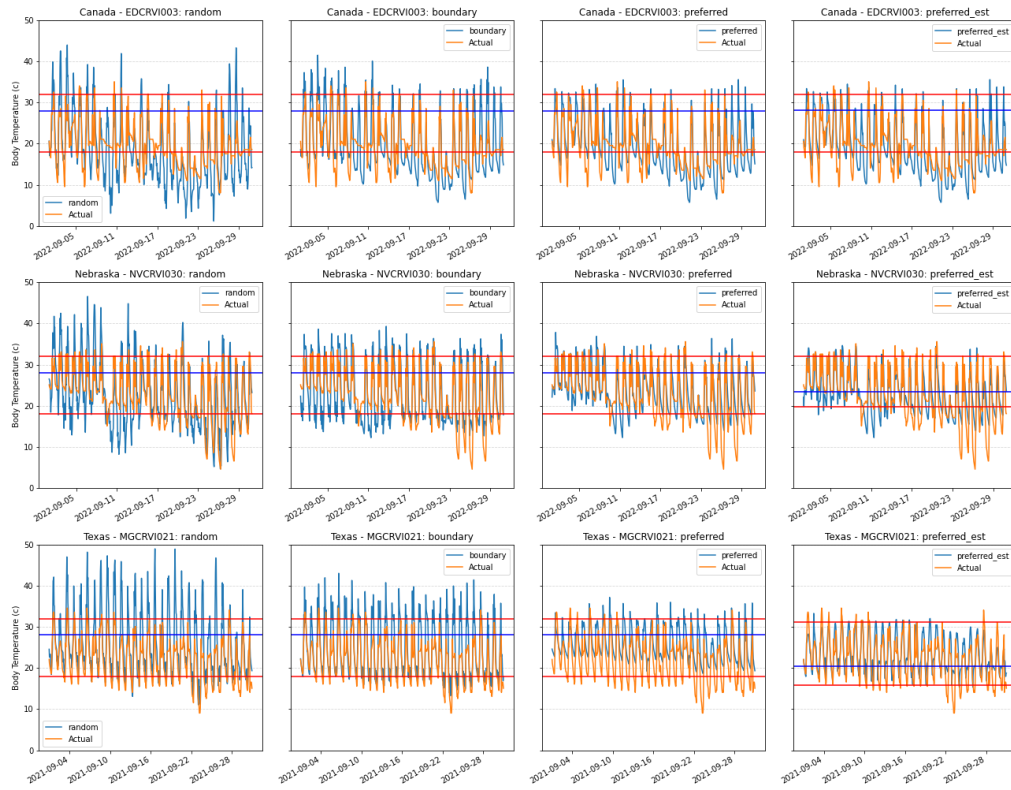


Figure 2.4: Plot matrix to showcase simulated body temperature of the various thermoregulation strategies (blue) plotted alongside empirical rattlesnake body temperature (orange) for the month of September. Thermal preference zone marked by red lines. The x axis is the date and the y axis is body temperature. The first row is a snake (EDCRVI003) collected in Canada, the second row is a Nebraska snake (NVCRI030), and the third is a snake collected in Texas (MGCRVI021). This was with non-imputed data which has a sampling frequency of 70 minutes.

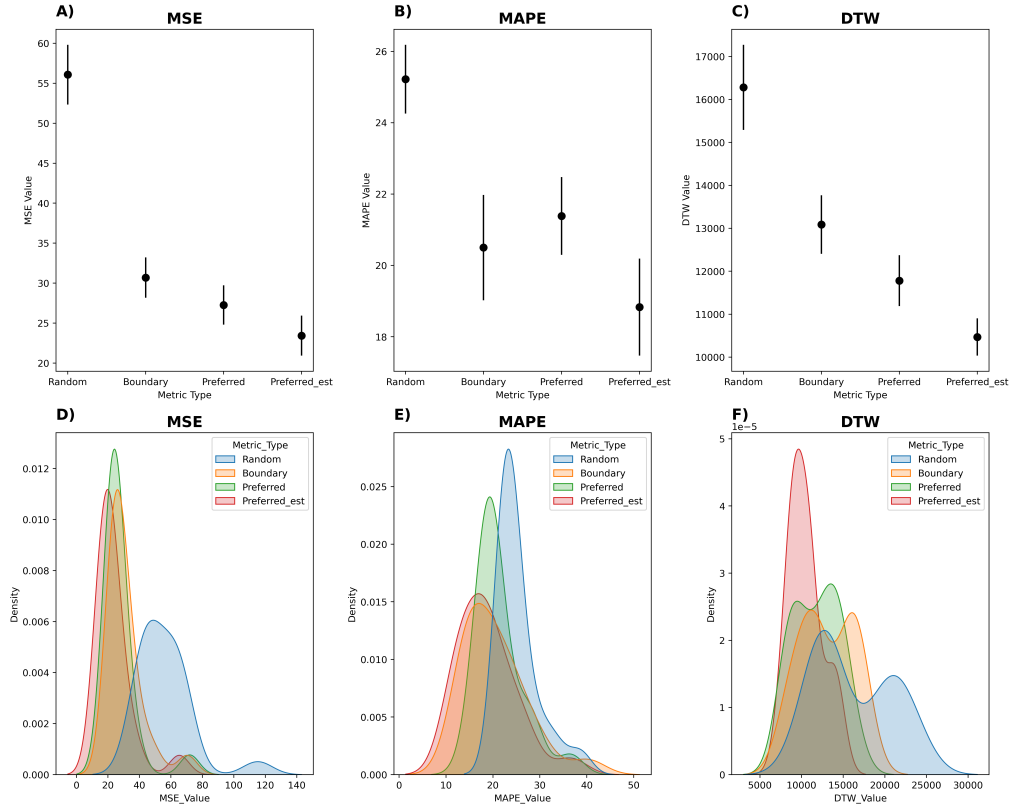


Figure 2.5: This figure presents a time series distance analysis using Mean Squared Error (MSE), Mean Absolute Percentage Error (MAPE), and Dynamic Time Warping (DTW) for each thermoregulatory strategy. The top row displays the mean and standard error of the time series distance metrics, illustrating the precision and variability of each metric across thermoregulatory sub-models. The bottom row features kernel density distribution plots of the distance values, providing a visual representation of the accuracy distribution for each thermoregulatory strategy. This analysis allows for a quantitative assessment of the effectiveness and consistency of different thermoregulatory sub-models in simulating real-world body temperature dynamics

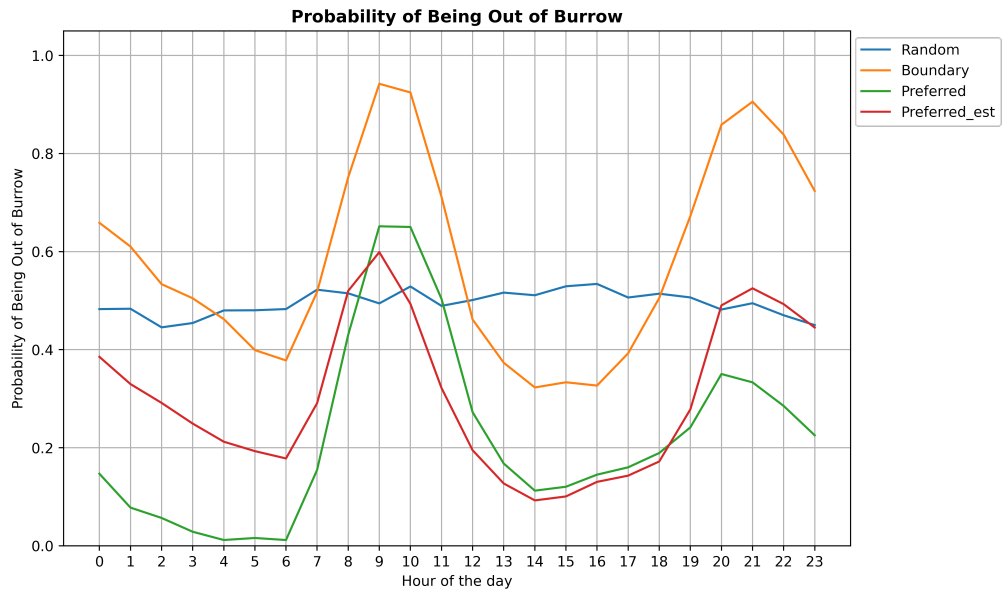


Figure 2.6: Probability of being in the open by hour. The y-axis represents the probability of being out of the burrow, where 1 is 100% probability of being in the open and 0 is 100% probability of being in the burrow.

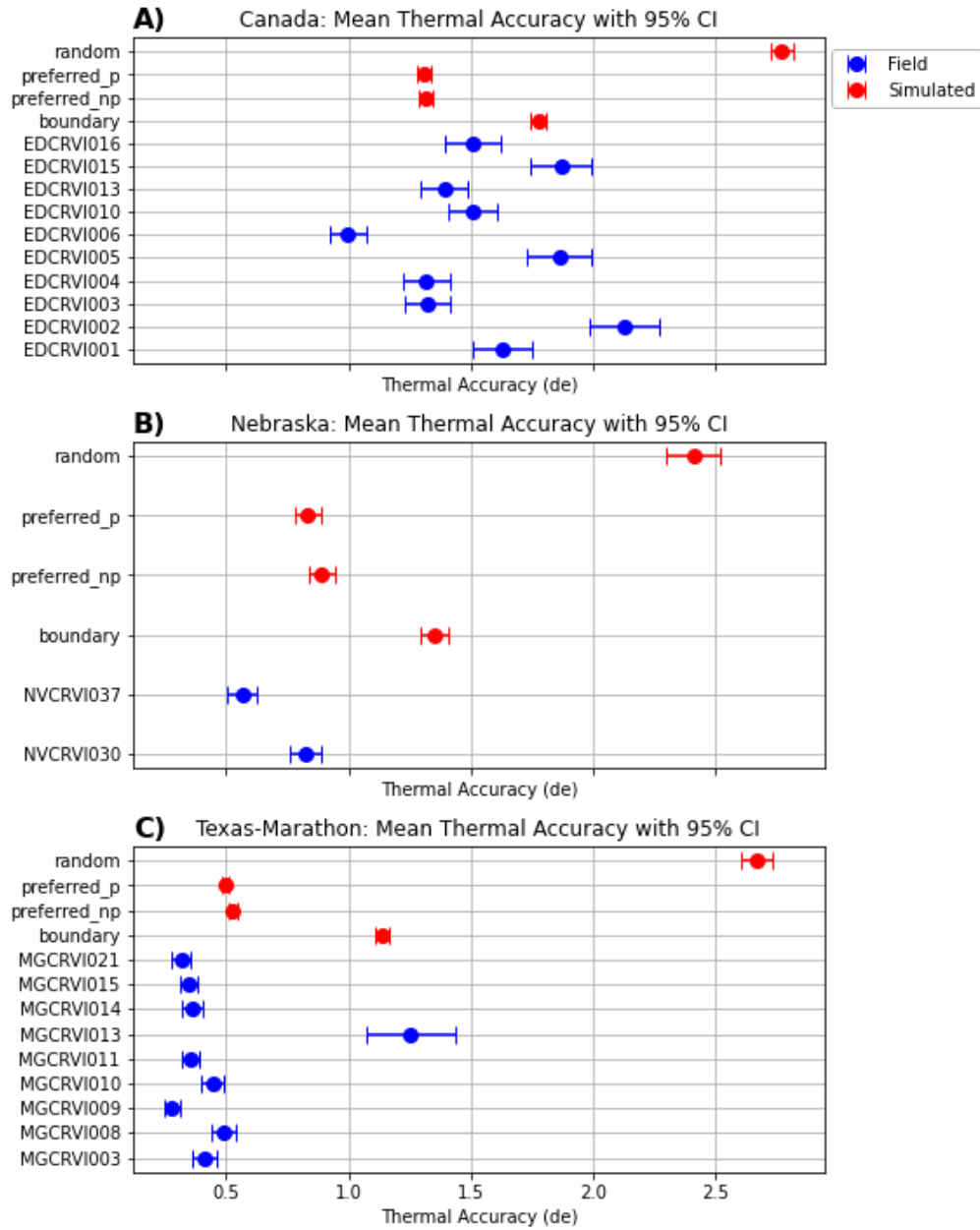


Figure 2.7: Thermal accuracy for snakes caught in the field, with simulated agents included. Thermal accuracy (db) is a metric that measures the difference between an organism's body temperature (T_b) from its thermal preference zone. High values of thermal accuracy indicate poor thermal accuracy [13, 21, 27].

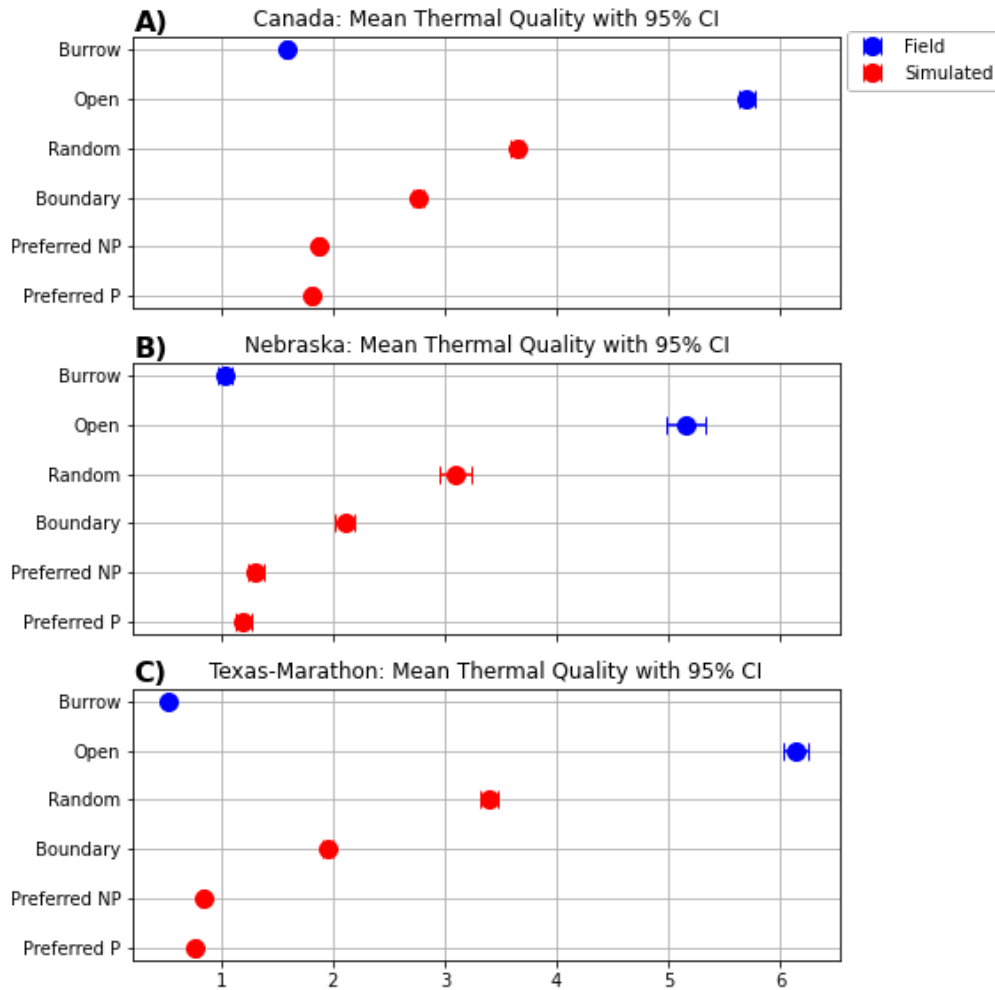


Figure 2.8: Thermal quality by microhabitat and for simulated snakes. Thermal quality (d_e) is a metric that measures the difference between environmental temperature (T_e) from the thermal preference zone [13, 21, 27]. Thermal quality traditionally cannot be estimated for snakes caught in the field due to not knowing what microhabitat (T_e) they may be sampling. However, we can assess this for simulated agents to gain a better understanding of the thermal conditions snakes may experience in field conditions.

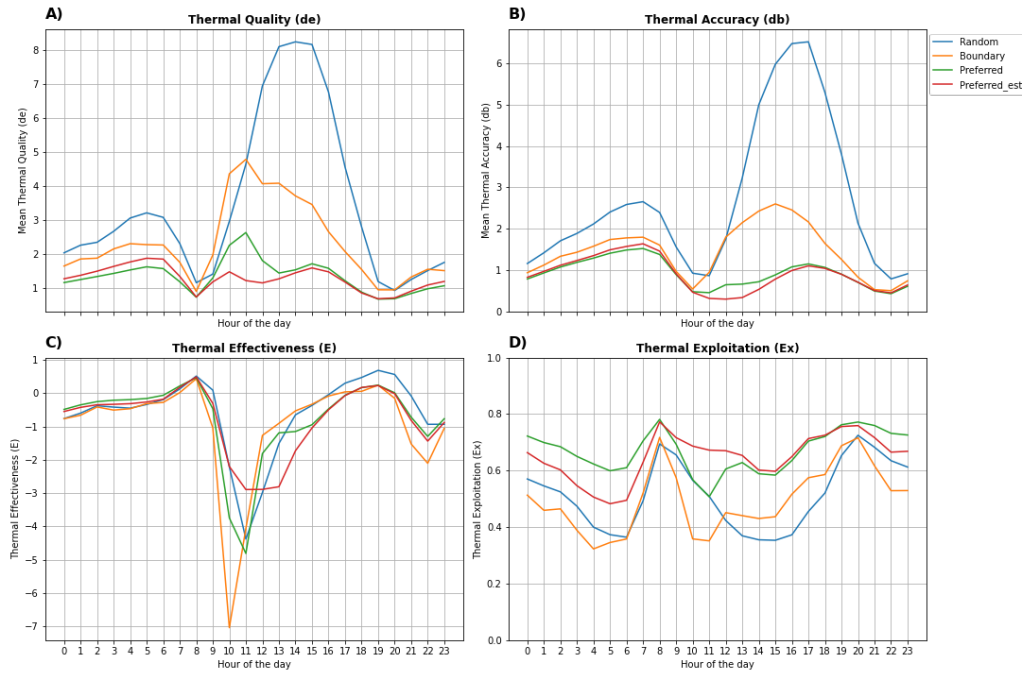


Figure 2.9: Plot grid of four thermal indices calculated by hour of the day. Figure A showcases thermal quality (de) is a metric that measures the difference of the thermal operative temperature (T_e) from the thermal preference zone. So high values of de indicate low quality thermal habitat. Thermal accuracy (db) which is a metric that measures the difference between an organism's body temperature (T_b) from its thermal preference zone. High values of db indicate poor thermal accuracy. Figure C showcases thermal effectiveness (E) which is one minus the ratio of mean db and mean de. Values of one indicate careful and precise thermoregulation; zero indicates the animal does not need to thermoregulate and is thermoconforming, while values approaching negative one indicates periods of where the organism is in poor habitat and are actively avoiding thermoregulation. Finally, Figure D is the thermal exploitation index (Ex) which is the percentage of time spent in the thermal preference zone. Higher values indicate more time spent in the thermal preference zone.

Machine Learning Model Pipeline Accuracy Distributions

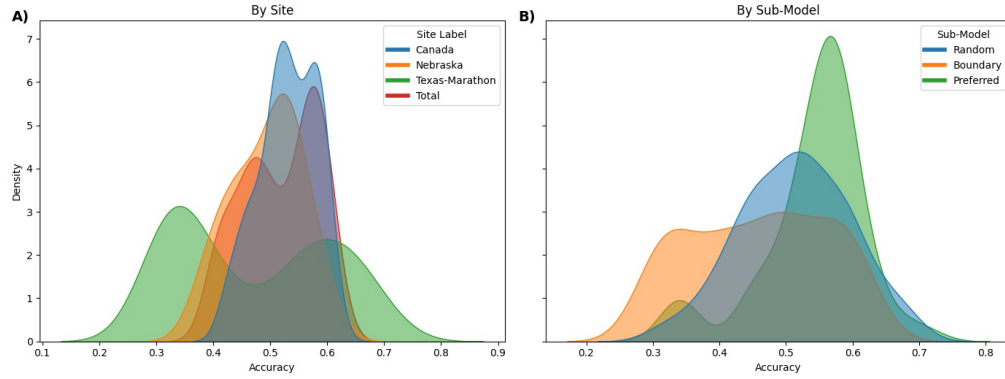


Figure 2.10: Kernel density plots of the accuracy results for all machine learning models built. Figure A is the results grouped by the sample population (Study Site) and Figure B is the results grouped by the thermoregulatory sub-model used to simulate training labels.

References

- [1] Karla Alujević, Leah Bakewell, Ian T. Clifton, Christian L. Cox, Luke O. Frishkoff, Eric J. Gangloff, Guillermo Garcia-Costoya, Matthew E. Gifford, Madison Glenwinkel, Samir A.K. Gulati, Alyssa Head, Monica Miles, Ciara Pettit, Charles M. Watson, Kelly L. Wuthrich, and Michael L. Logan. 3d printed models are an accurate, cost-effective, and reproducible tool for quantifying terrestrial thermal environments. *Journal of Thermal Biology*, 119:103762, 2024.
- [2] Matthew A. Barbour and Rulon W. Clark. Diel cycles in chemosensory behaviors of free-ranging rattlesnakes lying in wait for prey. *Ethology*, 118(5):480–488, 5 2012.
- [3] Albert F Bennett. Thermal dependence of muscle function. *American Journal of Physiology-Regulatory, Integrative and Comparative Physiology*, 247:R217–R229, 1984.
- [4] Donald J. Berndt and James Clifford. Using dynamic time warping to find patterns in time series. In *Proceedings of the 3rd International Conference on Knowledge Discovery and Data Mining*, AAAIWS’94, page 359–370. AAAI Press, 1994.
- [5] Leo Breiman. Random forests. *Machine Learning*, 45(1):5–32, Oct 2001.
- [6] Gregory P. Brown and Patrick J. Weatherhead. Thermal ecology and sexual size dimorphism in northern water snakes, *nerodia sipedon*. *Ecological Monographs*, 70(2):311–330, 2000.
- [7] Lauren B. Buckley, Joseph C. Ehrenberger, and Michael J. Angilletta. Thermoregulatory behaviour limits local adaptation of thermal niches and confers sensitivity to climate change. *Functional Ecology*, 29(8):1038–1047, 8 2015.
- [8] Hayley L. Crowell, Katherine C. King, James M. Whelan, Mallory V. Harmel, Gennese Garcia, Sebastian G. Gonzales, Paul H. Maier, Heather Neldner, Thomas Nhu, John T. Nolan, and Emily N. Taylor. Thermal ecology and baseline energetic requirements of a large-bodied ectotherm suggest resilience to climate change. *Ecology and Evolution*, 11(12):8170–8182, 6 2021.
- [9] Hans Dreisig. A time budget model of thermoregulation in shuttling ectotherms. *Journal of Arid Environments*, 8(3):191–205, 1985.

- [10] Edward M. Dzialowski. Use of operative temperature and standard operative temperature models in thermal biology. *Journal of Thermal Biology*, 30(4):317–334, 2005.
- [11] Jeffrey L. Elman. Finding structure in time. *Cognitive Science*, 14(2):179–211, 1990.
- [12] Jongsik Ha, Yong Seong Shin, and Ho Kim. Distributed lag effects in the relationship between temperature and mortality in three major cities in south korea. *Science of the Total Environment*, 409(18):3274–3280, 8 2011.
- [13] Paul E Hertz, Raymond B Huey, and R D Stevenson. Evaluating temperature regulation by field-active ectotherms: The fallacy of the inappropriate question. *Source: The American Naturalist*, 142(5):796–818, 1993.
- [14] Gergely Horváth, Tibor Sos, Gábor Bóné, Csanád Endre Lőrincz, Péter László Pap, and Gábor Herczeg. Integrating behavioural thermoregulatory strategy into the animal personality framework using the common lizard, *Zootoca vivipara* as a model. *Scientific Reports*, 14(1):14200, 2024.
- [15] Raymond B. Huey and Montgomery Slatkin. Cost and benefits of lizard thermoregulation. *The Quarterly Review of Biology*, 51(3):363–384, 1976. PMID: 981504.
- [16] Michael Kearney and Warren Porter. Mechanistic niche modelling: combining physiological and spatial data to predict species’ ranges. *Ecology Letters*, 12(4):334–350, 2009.
- [17] Pippa Kern, Rebecca L. Cramp, and Craig E. Franklin. Physiological responses of ectotherms to daily temperature variation. *Journal of Experimental Biology*, 218(19):3068–3076, 10 2015.
- [18] Al Kinlaw. A review of burrowing by semi-fossorial vertebrates in arid environments. *Journal of Arid Environments*, 41(2):127–145, 1999.

- [19] J.J.H. Nati, M. B.S. Svendsen, S. Marras, S. S. Killen, J. F. Steffensen, D. J. McKenzie, and P. Domenici. Intraspecific variation in thermal tolerance differs between tropical and temperate fishes. *Scientific Reports*, 11(1): :21272, 12 2021.
- [20] Fabian Pedregosa, Gaël Varoquaux, Alexandre Gramfort, Vincent Michel, Bertrand Thirion, Olivier Grisel, Mathieu Blondel, Peter Prettenhofer, Ron Weiss, Vincent Dubourg, Jake Vanderplas, Alexandre Passos, David Cournapeau, Matthieu Brucher, Matthieu Perrot, and Edouard Duchesnay. Scikit-learn: Machine learning in python. *Journal of Machine Learning Research*, 12:2825–2830, 2011.
- [21] Karin Piasečná, Alena Pončová, Miguel Tejedo, and Lumír Gvoždík. Thermoregulatory strategies in an aquatic ectotherm from thermally constrained habitats: An evaluation of current approaches. *Journal of Thermal Biology*, 52:97–107, 2015.
- [22] Alan J Redder. Daily and seasonal activity patterns of prairie rattlesnakes (*crotalus viridis viridis*) in wyoming. *ProQuest Dissertations and Theses*, page 115, 1994.
- [23] J. Marcus Rowcliffe, Juliet Field, Samuel T. Turvey, and Chris Carbone. Estimating animal density using camera traps without the need for individual recognition. *Journal of Applied Ecology*, 45(4):1228–1236, 8 2008.
- [24] P. F. Scholander, Raymond Hock, Vladimir Walters, and Laurence Irving. Adaptation to cold in arctic and tropical mammals and birds in relation to body temperature, insulation, and basal metabolic rate. *Biological Bulletin*, 99(2):259–271, 1950.
- [25] Michael W. Sears and Michael J. Angilletta. Costs and benefits of thermoregulation revisited: Both the heterogeneity and spatial structure of temperature drive energetic costs. *American Naturalist*, 185(4):E94–E102, 2015.
- [26] R. D. Stevenson. The relative importance of behavioral and physiological adjustments controlling body temperature in terrestrial ectotherms. *The American Naturalist*, 126(3):362–386, 1985.
- [27] Emily N. Taylor, Luisa M. Diele-Viegas, Eric J. Gangloff, Joshua M. Hall, Bálint Halpern, Melanie D. Massey, Dennis Rödder, Njal Rollinson, Sierra Spears, Baojun Sun, and Rory S. Telemeco. The thermal ecology and physiology of reptiles and amphibians: A user's guide. *Journal of*

Experimental Zoology Part A: Ecological and Integrative Physiology, 335(1):13–44, 2021.

- [28] The pandas development Team. pandas-dev/pandas: Pandas, April 2024.
- [29] Guido Van Rossum and Fred L. Drake. *Python 3 Reference Manual*. CreateSpace, Scotts Valley, CA, 2009.
- [30] Mathew Vickers, Carryn Manicom, and Lin Schwarzkopf. Extending the cost-benefit model of thermoregulation: High-temperature environments. *American Naturalist*, 177(4):452–461, 4 2011.
- [31] Stuart Young, Johanna Rode-Margono, and Rajan Amin. Software to facilitate and streamline camera trap data management: A review. *Ecology and Evolution*, 8(19):9947–9957, 10 2018.

Chapter 3 - Climate Warming Reshapes Ectotherm– Endotherm Predator–Prey Interactions Through Temperature-Dependent Behavior

Michael Remington^{1,2}, Ryan J. Hanscom^{1,2}, Timothy E. Higham², Jeet Sukumaran¹,
Xiaofeng Xu¹, Rulon W. Clark¹

1 Evolutionary Biology, San Diego State University, San Diego, California, USA **2**
Evolution Ecology and Organismal Biology (EEOB), University of California:
Riverside, Riverside, California, USA

* mremington@sdsu.edu

Abstract

Understanding animal behavioral responses to climate change and the associated cascading ecosystem shifts is a central goal for conservationists in the coming century. Although rising temperatures will affect physiology, behavior, species interactions, and population dynamics across the globe, ectothermic species are likely to respond more strongly to temperature shifts as their body temperature is directly related to environmental temperature. Thus, key species interactions between ectotherms and endotherms may be particularly prone to disruption. Here we present an ensemble modeling framework for an endotherm-ectotherm predator-prey system (a rodent/rattlesnake species pair) distributed across a latitudinal gradient. Our approach links an empirically driven agent-based simulation to the Rosenzweig-MacArthur model in order to tie the effects of temperature-dependent predator behaviors at fine temporal scales to long-term population dynamics. The results of our model suggest that climate change may lead to lower densities of prey communities due to more days of favorable foraging temperatures for rattlesnakes. Rattlesnake prey consumption is projected to increase on average by approximately 20% annually under +3°C of warming. Across all sites, increased prey consumption emerged primarily from phenological expansion of the active season rather than increases in daily metabolic demand, highlighting the length of the summer active season as the dominant mechanism linking warming to trophic pressure. A stability analysis showed that the system tended to display oscillatory dynamics regardless of warming across all populations we assessed.

Introduction

Projected global temperature increases due to anthropogenic warming are expected to have cascading effects on the stability of ecosystems as warmer temperatures impact metabolism, behavior, and species interactions [1,2]. Predator-prey relationships have long been known to stabilize ecological communities, as predators regulate prey populations, shaping community structure [3]. Thus, developing process-based models to understand and potentially predict effects of warming on predator-prey relationships is essential for understanding and mitigating the effects of climate change in the coming century.

Ectothermic predators are expected to be particularly susceptible to warming temperatures as their body temperature, physiology, and muscle performance are directly influenced by ambient temperature [4,5]. As ectotherms compose 99% of all animal species, understanding how they will respond to novel climate conditions is a central goal of modeling efforts [6]. Ectotherms may adapt to warmer climates through a combination of behavioral thermoregulation and physiological adaptations that alter the breadth of their original thermal niche [7,8]. To maintain body temperatures within a tolerable range, ectotherms may seek thermal refugia by altering spatial behavior, such as altering microhabitat preferences or moving to higher elevations [9,10]. Ectotherms can also achieve thermal refuge by altering temporal patterns including activity times [11,12] or yearly phenology [13]. Due to the rapid pace of climate change [14], behavioral adaptations may be more likely, as behavior is labile. In contrast, most physiological adaptations can act only on standing genetic variation within the population [7,15].

Physiological thermal traits such as preferred body temperature and critical thermal limits are often characterized within a thermal performance curve framework [16,17]. Physiological ecologists then use thermal indices such as thermal accuracy and thermal quality to understand thermoregulatory performance (the ability to maintain a body temperature within a preferred thermal range) [18]. Ectotherms tend to avoid body temperatures close to their thermal critical limits, resulting in a preferred temperature range that is usually slightly lower than their thermal optima [19]. Thus, warmer conditions are not certain to be deleterious and may even increase performance in certain traits [20]. This means the effects of warmer temperatures will not only be species-specific, but population-specific, as ectotherms of the same species can vary across populations with respect to body size, current thermal quality of microhabitats, and biotic interactions [4].

Although these studies demonstrate that abiotic conditions strongly influence ectotherm physiology and behavior, translating these effects to higher levels of biological organization remains challenging. In particular, it is unclear whether thermally driven shifts in behavior and phenology meaningfully alter predator–prey interaction strength and population stability under climate warming. Addressing this scaling problem requires modeling frameworks that can link individual-level behavioral decisions to long-term population dynamics while remaining mechanistically interpretable.

One classical way to quantify foraging rates in predator-prey systems is using the Holling foraging function. This is a classical mathematical model for predicting density dependent prey consumption rates. This approach has recently been leveraged in a study

of endotherm-ectotherm predator-prey interactions that found warmer temperatures increased the prey encounter rate and overall prey consumption of a sit-and-wait predator [21]. Furthermore, the Holling function readily scales to population-level predator-prey modeling, as it can be coupled with the Rosenzweig-MacArthur model. This model is leveraged to understand population dynamics of predator-prey systems and accounts for non-linear foraging rates of predators, making it a useful method to map how varying consumption rates impact population dynamics and system stability [22].

Here, we extend this approach by embedding the Holling type II function at two levels of biological organization: within an agent-based model that uses a novel ectotherm utility-based behavioral algorithm to link temperature, physiology, and ecology to hourly behavioral decisions, as well as a Rosenzweig–MacArthur model to evaluate annual predator and prey population densities and stability. Our study showcases a pipeline that links an empirical agent-based simulation model to the Rosenzweig-MacArthur model to assess whether changing ectotherm behavior under warming environmental temperatures will impact predator-prey interactions between an endothermic species (in our case study, kangaroo rats) and their ectothermic predator (rattlesnakes). Using field data to parameterize the model, we examine the impact of warming on several simulated populations in arid grassland habitats distributed across a latitudinal gradient. This framework allows us to link dynamic behavioral strategies of ectothermic rattlesnakes, balancing foraging and thermoregulatory needs, to emergent population level dynamics. Specifically, this work addresses two central questions: (1) how will key traits linked to ectothermy shift under warming conditions, and (2) will

those changes materially alter the relationship between rattlesnakes and their small mammal prey?

Materials and Methods

Purpose

To model population stability under various climate scenarios, we developed an empirically driven agent-based model to simulate annual predator-prey interactions and coupled it to a modified Rosenzweig-MacArthur mathematical predator-prey model to assess long-term population stability [23]. The primary purpose of our model is to simulate temperature-dependent behavior and foraging processes of rattlesnake agents at

the annual scale and then approximate consumption rates to understand population stability at the multi-generational scale. Our models are informed both by published literature and by our empirical studies of Prairie rattlesnakes (*Crotalus viridis*), a wide-ranging and abundant species that opportunistically consume nocturnal small mammals as their main prey, including Ord's kangaroo rats [24]. We do not explicitly model a kangaroo rat population; rather we model a nocturnal small mammal population as a prey density parameter and assume the kangaroo rats are a subset of this. Our approach is not intended to simulate interacting predator-prey agents, but rather to generate individual-level performance distributions for predators that can be mapped to population dynamics.

We leverage the Python package Mesa [25] as the programming framework for our agent-based model (ABM), named Suffugium (a Latin term meaning a place of refuge). This model is designed to simulate thermally dependent predator-prey dynamics between rattlesnakes and a small mammal prey population in a spatially implicit landscape with thermal heterogeneity based on microhabitat. We treat the individual rattlesnakes as isolated consumers, meaning the behavior of one does not impact any of the others; thus, the population size is akin to replicate agents rather than an ecological population.

The model aims to capture how ectotherms adjust their behavioral patterns in response to simulated environmental temperature increases and the resulting effects on overall annual consumption rates and prey population density. Snake agents that cannot consume prey faster than the rate of metabolic caloric usage die and are dropped from the simulation. This is the only source of mortality, so survivorship estimates are only in

reference to the ability to keep up with metabolic demand and do not consider other selection pressures real populations may face (i.e., predation, disease, etc - although such pressures could be layered into future iterations of the model).

The model is modular, meaning we simulate individuals at particular sites parameterized by field data, and we assume there is no migration or immigration between sites. Suffugium is at the hourly scale, so we leverage it in the first part of our analysis to understand changing behavioral and environmental dynamics. The Rosenzweig-MacArthur (RM) model is then used for the population stability analysis. A stepwise modeling framework for the cross site and scenario analysis is as follows:

- (1) Suffugium simulates rattlesnake behavior under nominal parameter settings to compare annual foraging and thermoregulation patterns.
- (2) Suffugium simulates a year of hourly scale rattlesnake agent behavior across a map of plausible prey densities and calculates individual prey consumption rates. The prey density to prey consumption map is then fit to the Holling type 2 foraging function in order to determine annual population scale attack rates and handling time parameters.
- (3) The RM Model simulates predator-prey dynamics under a nominal set of parameters to understand how population density changes under different thermal conditions.
- (4) Stability analysis of the RM model identifies critical tipping points of attack rate, handling time, prey, and carrying capacities of prey and predator populations.

Ecological Data and Analysis

Ecological data for our models is derived from field studies conducted at three locations spanning the latitudinal range of *Crotalus viridis*: southeastern Alberta, Canada; northern Nebraska; and south-central Texas (see [24] for details on field research). Individual snakes at these sites were surgically implanted with radio transmitters (Wildlife Materials, SOPI-2380-MVS) and temperature loggers (Thermochrom iButtons DS1922L- F5, accuracy = $\pm 0.5^{\circ}\text{C}$), which recorded field-active body temperatures (T_b) every 70 minutes. At each site we also placed three replicate physical operative thermal models (OTMs) in each of three different microhabitats typically used by this species: underground (inside small mammal burrows), shaded (under thickly vegetated shrubs), and exposed (laid out on open ground without cover). OTMs consisted of hollow copper tubes that replicate thermal qualities of snake bodies [26].

We then summarized the array of microhabitats temperatures by aggregating across devices to remove spatial complexity to form one hourly value for each microhabitat-specific temperature vector. For this simulation study, we only use open and burrow temperature profiles since we are modeling snake foraging and movement behavior when interacting with nocturnal small mammals.

Several key parameters used to model rattlesnake behavior were estimated using data from the field study including population specific body sizes, body temperature statistics, and brumation periods. For body sizes, we analyzed descriptive statistics

(mean, standard deviation) and body mass of agents are sampled from a normal distribution with parameters from the field data (Supplementary Figure 3.9).

For the thermal biology of snakes, we assessed statistical quartiles and mean hourly temperatures per season from implanted temperature loggers in order to understand how body temperature varies by site. Typically, these values are determined in laboratory settings in reference to specific performance traits [18]. For this study however, since we were assessing field conditions, we roughly estimate *Crotalus viridis* voluntary thermal tolerances by statistical analysis of mean hourly body temperatures. We assumed equal thermal performance traits for all three populations and future climate scenarios.

We assumed a common thermal preference range of 19–32°C, with a thermal optimum of 29°C. In the summer months when snakes are in the peak active season, the 75th percent quartile of body temperatures for all three sites ranged from 28–30°C which is why we chose a thermal optima of 29°C. The 90th percentile of body temperatures at the Nebraska and Texas sites reached approximately 29 to 32°C, which guided our selection of the upper bound of thermal preference. The 10th percentile body temperatures in summer months range from 15–20°C (Supplementary Table 3.5). Additionally, our estimated thermal preference values closely corresponded with thermal experimentally measured preference ranges of a closely related rattlesnake species, *Crotalus oreganus* [27,28].

For critical thermal limits we assessed maximum and minimum values across all seasons shown in Table 3.4. The maximum observed body temperatures ranged from 37

to 42°C; assuming these are voluntary maximal temperatures and to remain conservative, we set the upper critical limit at 45°C. Minimum observed body temperatures varied widely across sites and seasons from 3°C to about 5°C, so we assumed a generalized lower critical limit of 5°C.

During cold times of the year when environmental temperatures are low, rattlesnakes enter underground overwintering dens to maintain body temperatures above 0°C (brumation). Although the exact criteria for brumation is understudied, it is likely to primarily be temperature dependent [29,30]. To classify brumation times for each site and climate scenario, we used environmental field data to develop a general rule for brumation. More specifically, any day with burrow temperature below 5°C and with the mean of open and burrow temperatures also below 5°C constituted a brumation day. This rule yielded a brumation calendar for current conditions and that closely aligns with the observed brumation period and could be applied to future warming scenarios in our model (Figure 3.2).

Experimental Design

For our experimental design, we simulated predator–prey interactions at three locations (Canada, Nebraska, and Texas) under current climate conditions using empirical environmental temperature profiles. To simulate warming effects, we perturbed empirical temperatures using a uniform additive offset model of mean hourly temperature, adding +1 °C, +2 °C, and +3 °C [27,31]. Although this is a simplification of warming compared to IPCC climate projections, additive perturbations better enable the

experimental isolation of the effects warmer temperatures may have on behavior, serving as the independent variable in the experimental design [31]. Body size ranges were parameterized at the site level and held constant in all warming scenarios as shown in Figure 3.9. Each simulation spanned a single year time period, and brumation periods were set accordingly.

The Suffugium model outputs behavioral rates of rattlesnake agents, thermal summary statistics, small mammal consumption rates, and rattlesnake agent survivorship. We ran Suffugium under two experimental conditions. The first consisted of a nominal baseline scenario, where prey density was fixed at a value of 7 individuals per hectare to compare annual behavioral and thermal ecology patterns across study sites and climate scenarios. Reported densities of *Dipodomys ordii* vary substantially across the species' range; one survey in Alberta, Canada documented densities ranging from 4 to 16 individuals per hectare [32]. In contrast, populations have been reported as low as 2.2 individuals per hectare in Saskatchewan [33] and as high as 15.6 individuals per hectare in west Texas [34]. Each experiment was replicated eight times, resulting in a total of 96 simulations.

The goal of the second half of the analysis was to link our simulation results to a predator-prey population model in order to assess the system stability. To accomplish this, we ran simulations with Suffugium across a range of prey densities to approximate consumption rates for all experimental groups. We then used the model outputs to approximate the annual attack rate and handling time parameters in the Rosenzweig-

MacArthur predator prey model, which allowed us to simulate population sizes and run comparative stability analyses.

Suffugium Simulation Overview, Entities, and State Variables

The base model primarily governs initializing individuals and the landscape, collecting data, and running agent step functions. The only dynamic agent in our model is the rattlesnake, as we treat the small mammal population as a fixed landscape parameter that is only active during nighttime hours.

The landscape module queries a thermal database of environmental temperatures that are microhabitat specific, while also logging time variables at each time step (hour, day, month, and year). The landscape class is spatially implicit, meaning we do not initialize a grid from the mesa package. During each time step the landscape module queries microhabitat temperatures to be sampled by agents.

We explicitly model rattlesnakes as dynamic agents that are encoded with a utility-based behavioral algorithm for activity and switching behavioral state, as well as metabolism, thermal condition, and brumation sub-models. At each hourly timestep, rattlesnake agents update body temperature, metabolic state, and behavior in response to environmental temperatures and internal energetic constraints. The kangaroo rat population is treated as a subset of a general prey population with a limited activity budget where the population is assigned a certain number of hours during active times.

The primary goal of our model is to link environmental temperature to individual behavioral decisions. This is accomplished through a utility-based algorithm embedded in the rattlesnake agents which is a feedback process linking environmental temperature,

body temperature, behavior and microhabitat choice (illustrated in Figure 3.1).

Rattlesnake agents exhibit five possible behaviors: foraging, thermoregulating, resting, searching, and brumating. Search and brumate are deterministic behaviors triggered by specific conditions, whereas forage, thermoregulate, and rest are probabilistically selected based on utility values.

The behavioral algorithm governs two critical state variables for each agent: its current microhabitat and current behavior. Microhabitats correspond with behavioral selections and dictate environmental temperature (Table 3.1). The internal body temperature state variable and the microhabitat temperature are passed into a function based on Newton's law of cooling to calculate the body temperature of the agent for the next hour. See the behavior sub-model section for more details regarding how utility values are calculated and behaviors are sampled.

This feedback process allows us to model metabolic rates for rattlesnakes, which drive starvation, the only source of mortality for rattlesnake agents in our model. The model treats metabolic state as a caloric energy bank. To determine hourly energy expenditure, we leveraged a regression based standard metabolic rate equation and parameters from the literature [35]. Output from this equation is dependent on body size, and body temperature, and is converted from VO_2 ($mlO_2/hour$) to calories per hour. When rattlesnake agent behavioral states are active (Foraging, Searching, and Thermoregulating), SMR is increased by 50% to simulate active metabolic rate. Each hour, snake agents burn calories from their energy bank and can only gain calories by successfully catching prey. When their energy bank drops below zero, the snake agent

dies of starvation. See the metabolism sub-model section in the supplementary material for more details on equations and conversion factors.

Suffugium Sub-Models

See supplementary materials for details on the Metabolism, Behavioral Utility Algorithm, Foraging, Thermoregulation, Resting, and Brumation sub-models of the agent-based model.

Rosenzweig-MacArthur Mathematical Model

The Lotka-Volterra Model is one of the most widely used classical models of predator-prey systems. The Rosenzweig-MacArthur Model is an extension of this framework that leverages a more realistic assumption of foraging dynamics by integrating the Holling type II foraging model for nonlinear foraging dynamics where the predator consumption rate plateaus after a set number of meals, as well as modeling logistic prey growth [36].

We leverage a variant of the Rosenzweig-MacArthur where we set a carrying capacity for predators to model logistic growth as well. This modification reflects the hectare-scale context of our simulations: rattlesnakes have large home ranges, and individuals are likely to relocate rather than reach artificially high local densities. By incorporating a predator carrying capacity, we capture the spatial limitation of predator populations alongside the resource limitation from prey availability. This also allowed us to vary the predator carrying capacity to identify tipping points of predator densities that lead to unstable local population dynamics.

$$\begin{cases} \frac{dx}{dt} = rx \left(1 - \frac{x}{K_{\text{prey}}}\right) - \frac{axy}{1 + ahx} \\ \frac{dy}{dt} = e \frac{axy}{1 + ahx} \left(1 - \frac{y}{K_{\text{pred}}}\right) - my \end{cases} \quad (3.1)$$

Equation 3.1 showcases the full model where x represents the small mammal prey population density and y represents the rattlesnake population density. In the prey equation ($\frac{dx}{dt}$) the parameter r is the annual prey reproduction rate and K_{prey} is the prey carrying capacity. In the predator equation ($\frac{dy}{dt}$), e is the conversion rate of prey consumed to offspring, K_{pred} is the predator carrying capacity per hectare, and the parameter m is the annual mortality rate of the population, which is calculated as the negative natural log of annual survivorship. Two key parameters which we leverage to link the simulation framework to the model are the attack rate parameter (a) and the handling time (h). The attack rate represents the rate of prey consumption in units of prey encountered over time per predator, while the handling time represents the amount of time between meals. The max amount of meals a predator consumes in the model can be calculated as $1/h$.

To estimate generalized small mammal population reproduction rates, we took the average intrinsic growth rate between the two most common small mammal species at our field sites: a Kangaroo Rat species (*Dipodomys ordii*) and Deer Mice (*Peromyscus maniculatus*). We formulated a two age class Leslie matrix (Adult, and Juvenile) and calculated survivorship and fecundity from values found in Table 3.2 to calculate the intrinsic growth rate of both species. Fecundity is calculated for the adult age class as the product of litters per year, litter size, and female population proportion ($lpyr * L * F$).

From the Leslie matrix, we take the natural log of the dominant eigen value to calculate the species-specific r value [37].

Estimating Annual Attack Rate and Handling time

In order to link the simulation outputs of each site and scenario to the Rosenzweig-MacArthur model; we estimated the annual attack rate (a) and handling time (h) parameters in the Holling type II foraging function as follows:

$$C = \frac{aN}{1 + ahN} \quad (2)$$

- C : Annual Prey Consumption from Suffugium simulations.
- a : The predator encounter rate per annually.
- N : The mean number of prey per hectare set by the prey density map.
- h : The handling time for prey caught annually.

The attack rate determines the rate at which predators catch prey and the handling time acts as the saturation point where $(1/h)$ is the max meals. To estimate these parameters, we used a nonlinear least squares curve fitting method from observed consumption rates from Suffugium to expected using the Scipy Package in Python [38]. These estimated values are then substituted into the RM Model (1) to simulate population dynamics.

Stability Analysis and Root Finding

In order to better understand the tipping points and patterns of system stability of the predator prey dynamics, we sought to determine when both the predator function and prey function are equal to zero such that $f(x,y) = 0$ (also known as the steady state of the system). To do this we leverage a 2D Newton root finder function with the method set to 'hybrid' from the Scipy package in Python [38]. We also passed in the analytical form of the Jacobian into this function.

The Jacobian is a matrix of the partial derivatives of the RM model. This is essential for stability analysis as the Jacobian is necessary for finding parts of parameter space where $\frac{dx}{dt}, \frac{dy}{dt} = 0$. We analytically derived the Jacobian as:

$$J(x, y) = \begin{bmatrix} \frac{\partial f}{\partial x} & \frac{\partial f}{\partial y} \\ \frac{\partial g}{\partial x} & \frac{\partial g}{\partial y} \end{bmatrix} = \begin{bmatrix} r \left(1 - \frac{2x}{K_{\text{prey}}}\right) - \frac{ay}{(1 + ahx)^2} & -\frac{ax}{1 + ahx} \\ \frac{eay}{(1 + ahx)^2} \left(1 - \frac{y}{K_{\text{pred}}}\right) & \frac{eax}{1 + ahx} \left(1 - \frac{2y}{K_{\text{pred}}}\right) - m \end{bmatrix} \quad (3)$$

We leverage this analysis to find threshold values of predator and prey carrying capacities in respect to attack rate and handling time and assess the stability of each site and scenario.

Population Density Simulation

To assess population stability across sites and climate scenarios, we simulated predator–prey dynamics under the Rosenzweig–MacArthur model over a 300-year period with $\Delta t = 0.01$. Population trajectories were obtained using a fourth-order Runge–Kutta numerical integration scheme. Mean population densities were also assessed across this simulation in order to summarize overall changes in population density.

Attack rates and handling times for each simulation vary and were calculated from simulations using Suffugium (see section *Estimating Annual Attack Rate and Handling time*). Variables r , e , m , K_{pred} , and K_{prey} were held constant across simulations and all were initiated with a small mammal population prey density of 7 individuals/hectare, and a predator population density of 1 individual per hectare. See Table 3.2 for parameter values.

Sensitivity Analysis and Model Validation

Sensitivity analysis and model validation methods and results are presented in the supplementary material.

Results

Behavior and Thermoregulatory Patterns

Under the nominal set of simulations, during the active season, we found that thermal trends differed among sites: Texas snake agents maintained the highest mean body temperatures and the lowest proportion of time thermoregulating. Nebraska snakes consistently exhibited intermediate patterns, while Canada snakes had the lowest body temperatures and spent the most time thermoregulating (Figure 3.3A, B).

Across warming scenarios, thermal conditions linearly improve for rattlesnakes as both thermal accuracy and quality decrease (Figure 3.3A, C, E). Because thermal accuracy represents the deviation between T_b and the thermal optimum, lower values indicate that snakes are operating closer to their physiological preference. Accordingly,

snakes spent less time thermoregulating under warming (Figure 3.3B). Warming disproportionately affected Canada and Nebraska as thermal accuracy dropped by 2°C but only by approximately 1°C from base conditions in Texas (Figure 3.3B).

Our results show that these thermal improvements are primarily from more favorable environmental conditions rather than enhanced thermoregulatory performance. Thermal quality (the difference between environmental temperature and thermal optima) also decreases by a similar magnitude to thermal accuracy, which indicates environmental conditions are matching T_{opt} (Figure 3.3C). Because nightly minimum temperatures increase under warming scenarios, snakes reach their preferred body temperature through passive thermoconformation rather than active behavioral thermoregulation, leading to both lower thermal accuracy and thermal quality values.

Despite warmer temperatures leading to higher metabolic rates (Equation 3.4), our model found minimal to no increase in foraging rates, while there was an increase in time spent resting (Figure 3.3D, F). This indicates that across all sites under warming scenarios, rattlesnakes will be less thermally constrained by cold nighttime temperatures, with minimal costs associated with foraging for longer hours leading to fewer constraints on non-foraging behavioral activities.

Predator-Prey Interactions

To assess how individual traits and climate conditions influence emergent outcomes, we modeled the effects of body mass, brumation length, and warming on prey consumption and survivorship while accounting for differences among study sites (Table 3.3). We fit an ordinary least squares (OLS) model for the nominal set simulations on

total prey consumed ($R^2 = 0.383$) with site fixed effects. Survivorship was modeled using mixed-effects logistic regression with a random intercept for site was also developed.

In the OLS model, larger snakes consumed more prey ($\beta = 0.0056, p < 0.001$), and warming increased consumption ($\beta = 0.0707, p < 0.001$). The interaction between warming and mass further showcased the trend of larger snakes eating more during warming scenarios ($Mass \times Warming : \beta = 0.0002, p < 0.001$). Reductions in brumation periods increased consumption ($\beta = -0.0008, p < 0.001$), consistent with the longer active season available to forage for snakes.

In the survivorship model, warming increased survival odds ($\beta = 0.458, p < 0.001$) and larger snakes benefited more under warming ($Mass \times Warming : \beta = 0.001, p < 0.001$), while mass showed a small negative baseline association indicating smaller snakes had better survivorship ($\beta = -0.001, p < 0.001$). Survivorship also increased with longer brumation ($\beta = 0.001, p < 0.001$) and with higher thermal accuracy values ($\beta = 0.616, p < 0.001$).

Further analysis on nominal set simulations found that the nocturnal foraging rate of snake agents does not substantially increase with warming, but overall prey consumption increases when prey density exceeds 3 individuals per hectare (Figure 3.4A). Snake survivorship is also impacted to a minimal degree across warming scenarios, with the greatest differences seen between sites, as Texas has the highest survivorship among sites when prey densities were less than about 8 individuals per hectare (Figure 3.4B).

When analyzing the distribution of annual prey consumed by snakes over the year (Figure 3.12), across all 3 sites, we see a similar trend: the max, min, and mean number

of prey consumed increases across warming scenarios. When we fit the Holling type II model back to the data, the model corresponds with the mean prey consumption per prey density closely while also yielding estimates for attack rate and handling time.

The saturation constant ($1/\text{handling time}$) of the Holling type II model represents the asymptotic prey consumption per year that best fits the simulated data. From a plot of attack rates over the saturation constant (Figure 3.5), the saturation constant increases at a significantly greater magnitude than the attack rate. All three sites show that under 3 degrees of warming, individual rattlesnake agents will consume at least one additional prey item annually, with the greatest increase at the Texas site. The saturation constant increases at a larger proportional rate than the attack rate at all three sites, indicating that the longer active season rather than the increased metabolic demand is the primary cause of increased prey consumption.

Population Dynamics and Stability

To evaluate how changes in individual behavior and thermal performance scale up to influence broader ecological outcomes, we examined the population dynamics and stability across sites and warming scenarios. We simulated densities of predator and prey populations by passing estimated attack rates and handling times into the Rosenzweig-MacArthur model. All sites exhibit oscillatory population dynamics with the Canada site having lower but more frequent oscillations of prey densities, the Texas site exhibiting high densities but less frequent oscillations, and Nebraska being intermediate. Warming scenarios tended to dampen the amplitude of oscillations at all sites (Figure 3.6). Canada, in particular, exhibits a shift in the timing of oscillations. As the climate warms, prey

populations take longer to reestablish to a max density. Overall, rattlesnake densities had low variance across sites and warming scenarios, but we did see a reduction in average small mammal prey density with warming at all sites (Figure 3.7).

Our previous simulation assumed a carrying capacity of 50 individuals per hectare for the prey population density and 3 individuals per hectare for the predator. In order to assess if this assumption affected whether we would observe stable populations densities, we performed a stability analysis varying predator and prey carrying capacities with respect to attack rate and handling time. Across all warming scenarios, the system remained within the oscillatory region of parameter space, never converging to constant population densities but also not entering predator extinction regions. Overall, there are narrow regions of parameter space where the system is not oscillatory, regardless of warming scenario or site differences (Figure 3.8), so this assumption likely does not impact our previous analysis simulating population dynamics (Figure 3.6).

The stability map suggests the predator–prey system is expected to exhibit oscillatory or weakly dampened cycles rather than undergoing an abrupt transition to alternative stable states under warming scenarios. Consequently, warming scenarios may shift overall densities but are unlikely to induce catastrophic tipping points in population dynamics stemming from changes in the behavior or metabolism of ectothermic predators.

Discussion

Behavioral and Physiological Responses to Warming

The asymmetrical effects of warming on ectotherms versus endotherms has the potential to disrupt key species interactions [39,40]. Here, our goal was to establish a modeling pipeline to quantify these effects by linking empirical data on temperature, physiology, and population demographics to community-scale stability in an ectotherm–endotherm predator–prey system under warming scenarios. Using an agent-based model, we were able to link temperature to behavior in order to quantify annual prey consumption patterns. By leveraging these outputs in the Rosenzweig-MacArthur model, we assessed emergent population dynamics.

A key and counterintuitive result from our model was warming scenarios actually reduced the need for thermoregulation but did not necessarily increase daily foraging rates (Figure 3.3B, D). This is largely because snake agents are nocturnal hunters of small mammals, a foraging strategy that naturally buffers them from unfavorably warm daytime surface temperatures as well as warmer nights providing more favorable conditions for ectotherms. These results suggest that increased annual prey consumption under warming is driven primarily by phenological shifts rather than changes in daily behavior or metabolism. In other words, although snakes may consume more prey annually, their hourly and daily behavioral routines remain largely conserved.

Warmer conditions in our agent-based model also altered aspects of rattlesnake behavior by improving thermal accuracy, lengthening the summer active season, and increasing time spent in the “rest” state (i.e., not foraging or thermoregulating). Because

our model includes only four behavioral states: brumation, resting, thermoregulating, and feeding-the. The rest state likely encompasses additional behaviors we did not explicitly model, such as mate searching or gestation of young. Thus, an increase in resting behavior may reflect greater behavioral flexibility under warming. This flexibility could influence other fitness-related processes, particularly reproduction. For example, male rattlesnake reproductive success is closely tied to movement patterns and the ability to locate females during the spring mating season [41,42]. A longer active season and reduced need for thermoregulation could therefore allow males more time for mate searching or intensify male–male competition for access to females.

Consequences for Predator-Prey Interactions Across a Latitudinal Gradient

Our model indicated that warmer temperatures may offer only short-term ecological benefits for rattlesnakes. More favorable nighttime temperatures increased behavioral flexibility, and longer summer activity periods are benefits at the individual scale but become detriments at the community scale, as both predator and prey densities declined under warming scenarios (Figure 3.7). This decline arose from a positive feedback loop in which rattlesnake agents increased prey consumption during longer activity windows, which reduced prey abundance over time, ultimately leading to population decreases for both species.

These projected population declines raise the question of whether certain phenotypic traits, such as body size, might be under differential selection in warming environments. It is speculated climate change will cause negative selection for larger body sizes but whether this is true for ectotherms is contentious [43]. At the community

level, possible reductions in body size may act as a stabilizing mechanism of the system across generations as smaller snakes will require less prey per season [44]. Counter to this however, our analysis shows that Texas snake agents have the smallest body sizes (Supplementary Material Figure 3.9), but the lowest population density (Figure 3.7). There was also only a weak correlation between the interaction between mass and survivorship so warming may not cause significant selection against large body rattlesnakes (Table 3.3).

However, our simulations only included relatively small-bodied mammalian prey. Previous analyses of snake body sizes have indicated that prey size may be one of the primary drivers of body size in snakes, as they are gape-limited predators that can only incorporate large bodied prey into their diet if they themselves are large [45]. Thus, our simulated snakes may not be able to realize the primary benefit of larger body size and only pay the cost. Future iterations of this modeling framework could include more variation in prey size, providing a benefit snake agents could realize if they attained a sufficient body size.

Because demographic constraints can dominate trait-mediated effects at broad spatial scales, it is also important to consider latitudinal differences in mortality. A critical selection pressure on wild rattlesnakes is high juvenile mortality during overwintering periods [46]. Not only do our simulations suggest that adult rattlesnake mortality should decrease with shorter brumation periods as Texas snake agents tended to have the highest rate of survivorship (Figure 3.4B), but shorter brumation from warming would also be expected to increase juvenile survivorship leading to increases in intrinsic

growth rate, a factor not captured in our analysis of the Rosenzweig-MacArthur model. Changes in phenology caused by anthropogenic warming leading to increases in the active season has been observed in other vipers [30]; thus, smaller neonatal rattlesnakes in our system may see increases in survivorship especially in Canada and Nebraska.

Integrating ABM and Population Models: Implications, Limitations, and Future Directions

One factor that may cause our model to underestimate predation rates is that we only model metabolic demand in reference to the minimum demand needed for survivorship. Other frameworks such as dynamic energy budget theory incorporate metabolic demand with respect to body size growth, reproduction, as well as assimilation and allocation rules [47]. Future iterations could integrate more complex energy budgets to accurately simulate the full suite of metabolic costs, thereby providing a more realistic estimate of lifetime prey consumption and its consequences for predator–prey stability. These refinements at the individual level would in turn improve the accuracy of the attack-rate and handling-time parameters passed to the RM model.

From the prey perspective, our framework assumed small mammal behavior to be constant due to their nocturnal foraging patterns and physiological adaptations to arid environments. However, this assumption may not hold under extreme warming scenarios as a mortality analysis of Banner-tailed Kangaroo Rats (*Dipodomys spectabilis*) found that high diurnal land surface temperatures were strong predictors of population declines [48]. Contrary to this, meta-analyses have found that nocturnal small mammals may be largely insulated from the impacts of global warming, even in extreme desert

environments [49]. Furthermore, prey refuge availability represents a key stabilizing mechanism for prey populations in arid systems as microhabitat usage or dispersal allows small mammals to avoid predators [50]. Inclusion of local spatial dynamics into our modeling framework could enhance the realism as small mammals could shift microhabitat usage to buffer the potential warming induced prolonged activity periods of rattlesnakes.

Our agent-based simulation framework, Suffugium, was built with adaptability and modification in mind. Future iterations of this simulation framework could layer in dynamics such as reductions in seed nutritional quality in the context of water loss, changes in annual dynamics where temperatures may constrain activity times, losses in high quality habitat, and other ecological factors to better encapsulate the effects of climate change on populations. More broadly, by linking individual-level thermoregulatory and foraging decisions to population-level stability, this modeling approach offers a tractable framework for predicting how physiological and behavioral processes mediate ecosystem responses to climate change.

Conclusion and Future Work

There has been a general call for ecological modeling frameworks to be process driven and to incorporate multiple scales of biological organization in order to expand the predictive power and reliability of models for environmental management decisions [51,52]. No model can encapsulate all aspects of an organism's ecology and biology, but formulating a parsimonious model of key processes and state variables coupled with testable assumptions is a useful approach for formulating a predictive modeling framework. By linking ecological data to population process through a dynamic ABM and the Rosenzweig-MacArthur model we showcased one application of a general framework for predicting warming effects on predator behavior and the implications of these shifts on predator-prey population dynamics. This modeling framework is not intended to directly predict population sizes, but rather to identify which behavioral and physiological processes are most likely to drive population-level responses to warming. In this system, reductions in brumation length emerged as a key mediator of predator-prey dynamics, suggesting that phenological shifts of ectothermic predators in northern climates may represent a critical axis along which climate change influences trophic interactions. By explicitly linking individual behavior to population stability, this approach provides a generalizable tool for generating testable hypotheses and guiding future empirical and modeling efforts in other ectotherm-endotherm systems.

Figures

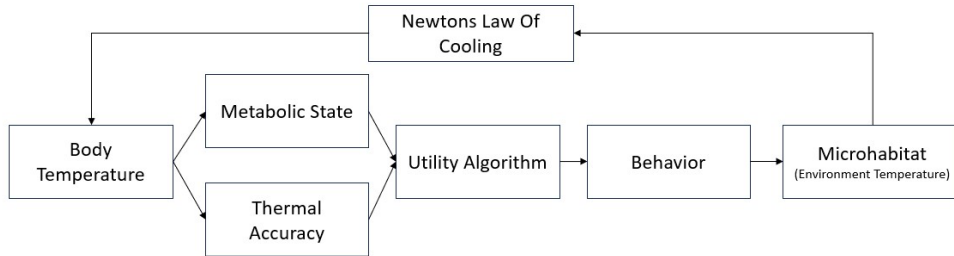


Figure 3.1: Rattlesnake sub-model conceptual diagram.

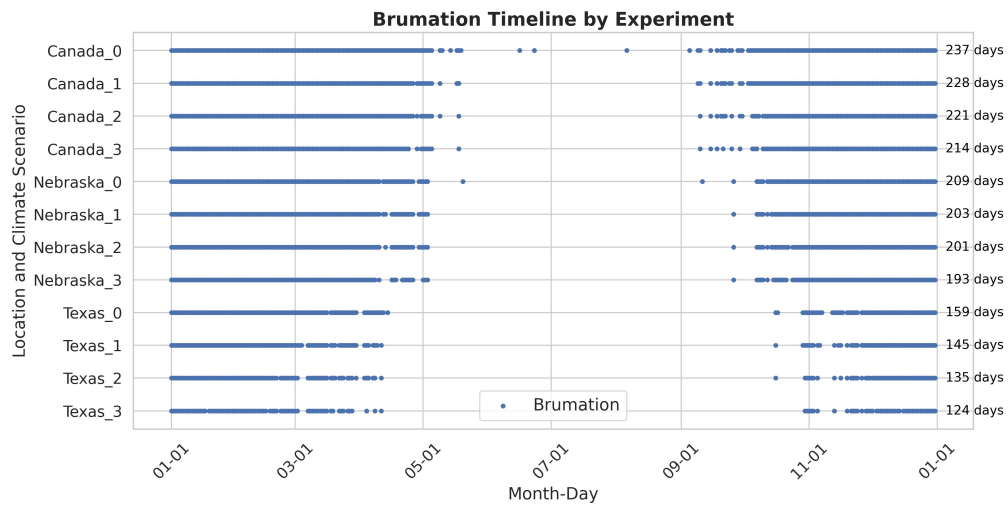


Figure 3.2: Brumation periods for each site and climate condition showcasing the schedule of brumation days. We used data from free ranging snakes to derive a brumation rule for simulated agents. Brumation is initiated when, on any given day, at least one hourly burrow temperature falls below 5°C and the mean of burrow and open microhabitat temperatures is also below 5°C.

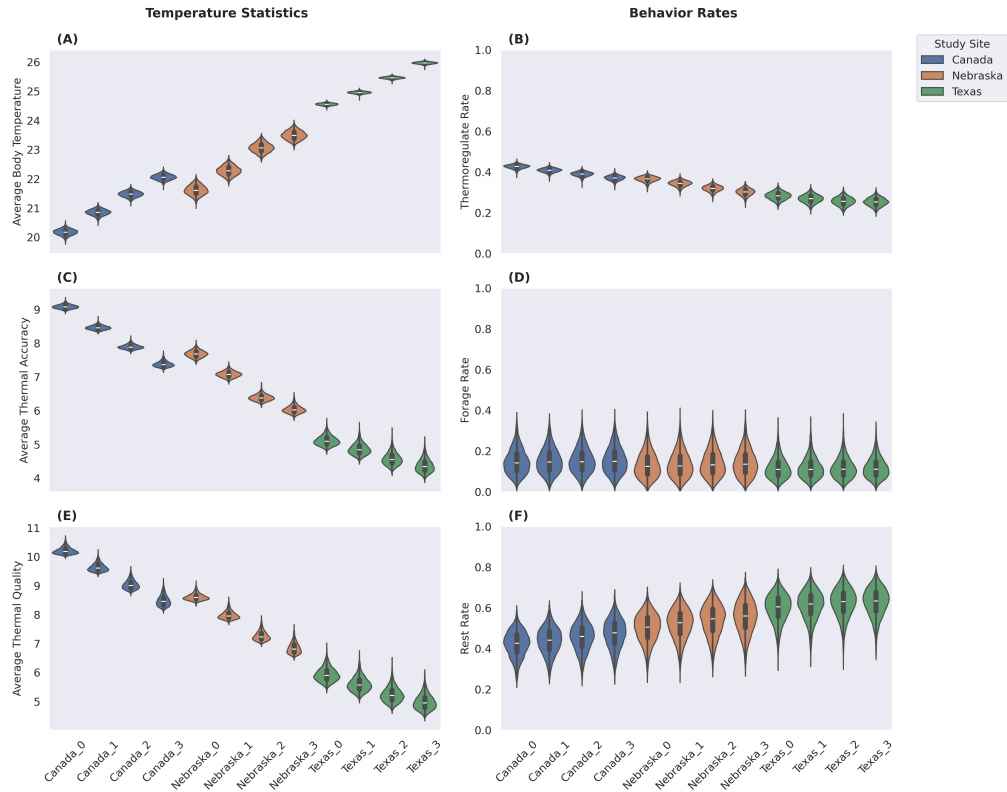


Figure 3.3: Descriptive statistics for thermal ecology metrics of the nominal set of the 1-year Suffugium simulation during the active season. The nominal is initiated at a prey density of 7 small mammals per hectare. Average body temperature (A) of snake agents increases with warming at all sites. Thermal Accuracy (C) is the difference between thermal optima (29°C) and body temperature. Thermal quality (E) is the absolute difference between environmental temperature and thermal optima. Right panels display behavioral profiles for the snakes adjusted by the length of the brumation period to make them directly comparable. Warming temperatures at all three sites decreases the need to thermoregulate (B) but only minimally increase the need to forage (D), resulting in more time spent in non-foraging (“rest”) states (F).

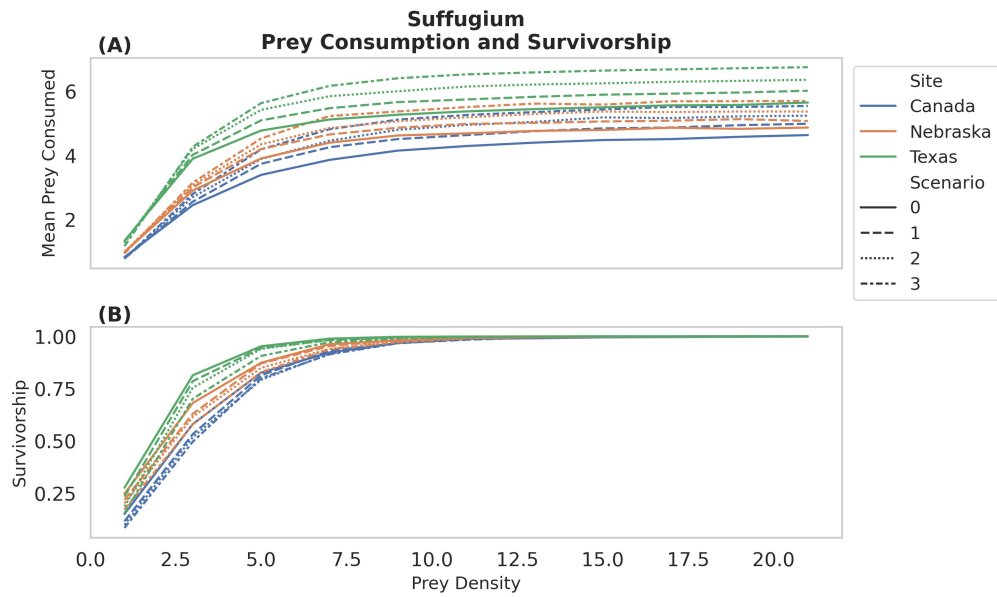


Figure 3.4: Results of prey density map simulations measuring mean prey consumed (A) and snake survivorship (B) with respect to the prey density parameter. Under warming conditions prey consumption increases at all sites, but snake agent survivorship remains similar.

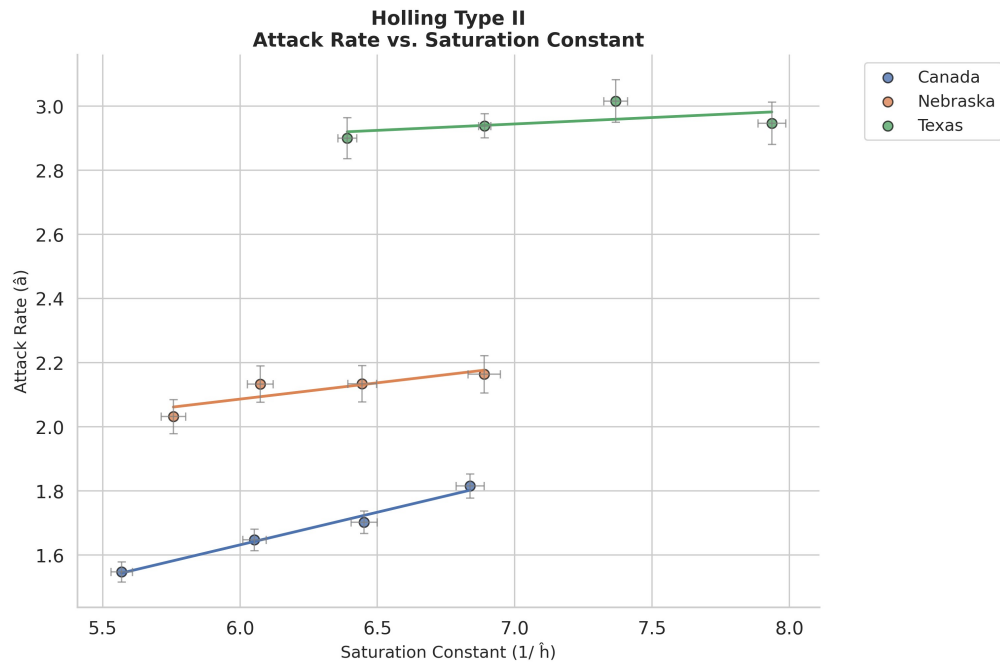


Figure 3.5: Fitting prey consumption rates to the Holling type II model shows that the saturation point (the maximum number of meals) is expected to grow at a larger magnitude than the attack rate, indicating that predators are not necessarily getting more efficient at prey capture but will have more time in the year to consume prey.

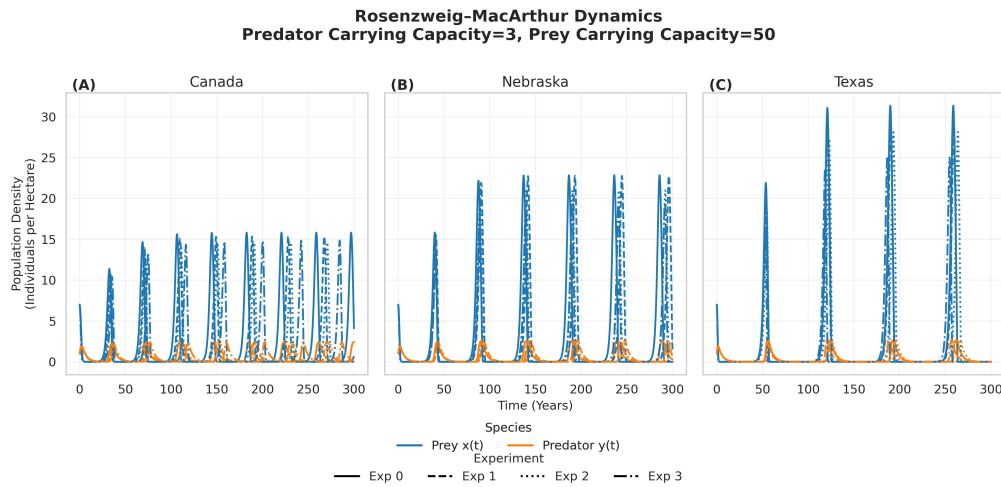


Figure 3.6: Population density simulations using the Rosenzweig-MacArthur Model show some variation across sites. Canada (A) populations tend to have lower prey densities but more rapid oscillations, while Texas (C) exhibits less frequent oscillations but higher prey densities. Nebraska (B) is intermediate between the two.

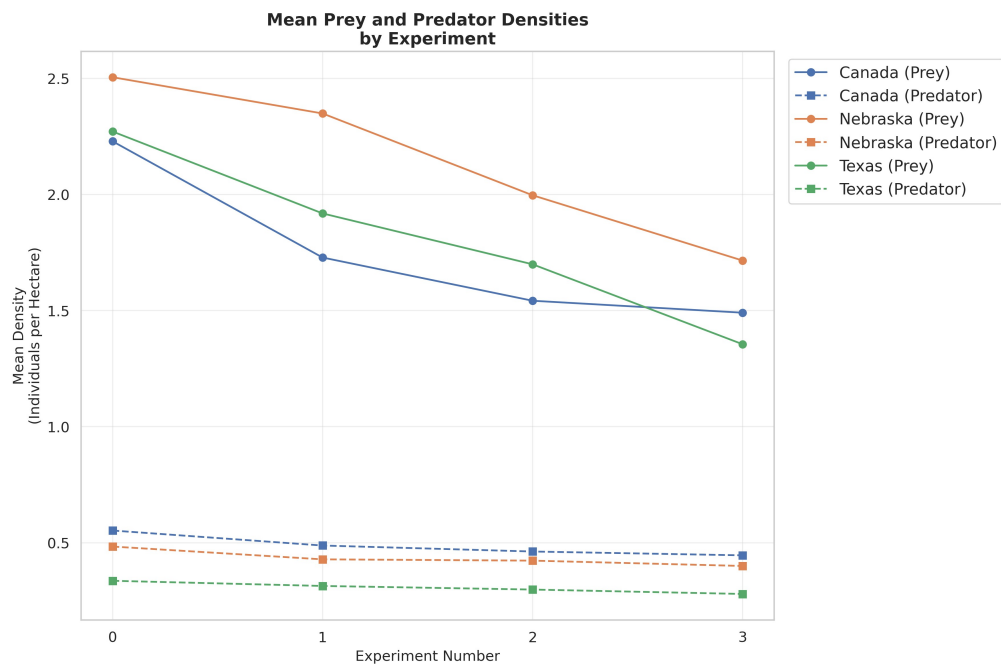


Figure 3.7: Estimated prey and predator densities across sites and climate scenarios. Our model indicates that warming temperatures lead to reductions in overall prey density at all 3 of the sites and across all climate scenarios.

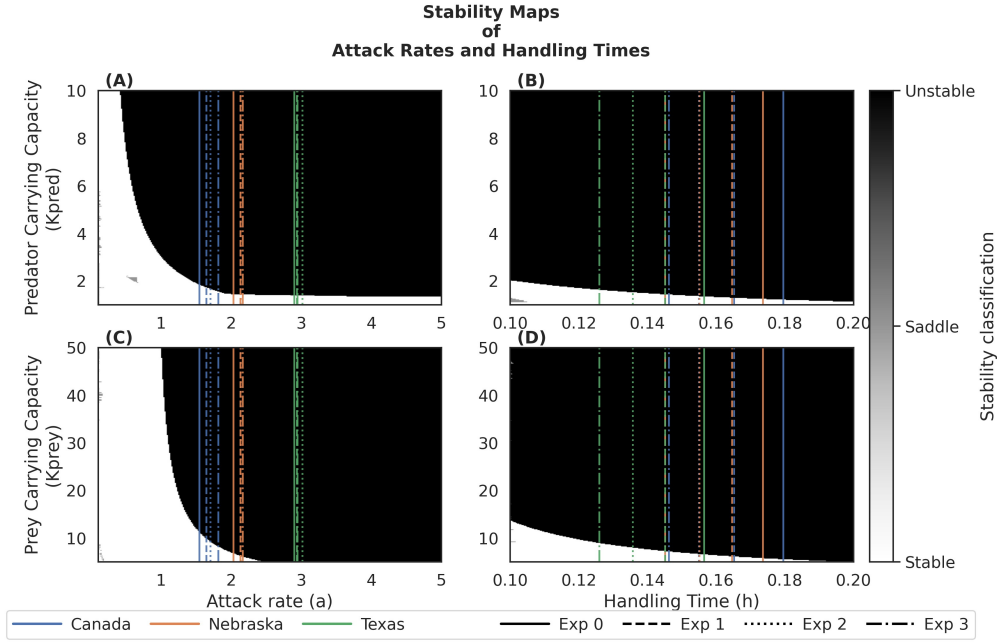


Figure 3.8: Stability maps of estimated attack rates ($\hat{a}$) and handling times ($\hat{h}$) by predator and prey carrying capacities. In figures (A) and (C), we hold handling time constant at 0.15 to see how variation in attack rate ($\hat{a}$) interacts with predator (K_{pred}) and prey (K_{prey}) carrying capacities, respectively. Figures (B) and (D) show the corresponding relationships for handling time ($\hat{h}$) while holding attack rate constant at 2. Black regions indicate parameter combinations leading to unstable oscillations, gray regions represent saddle equilibria, and white regions denote stable coexistence equilibria. Colored vertical lines mark site-specific parameter estimates, while line styles denote experimental warming scenarios. Overall, stability regions are narrow, suggesting that predator–prey coexistence at local spatial scales may be sensitive to small changes in $\hat{a}$, $\hat{h}$, and carrying capacities.

Tables

Behavior	Microhabitat	SMR/AMR	Utility	Description
Function				
Rest	Burrow	SMR	Metabolic State	Return to the burrow to minimize energy expenditure.
Forage	Open	AMR	Metabolic State	Actively hunting for prey agents to increase metabolic state.
Thermoregulate	Either	AMR	Thermal Accuracy	Probabilistically choose the best microhabitat to maintain body temperature as close to thermal optima as possible.
Brumation	Wintering Den	SMR	NA	Enter dormancy during cold periods to a wintering den which has a set constant temperature calculated from empirical data.
Search	Open	AMR	NA	Search processed a successful forage event to model snakes finding prey after a successful strike.

Table 3.1: Summary of predator behavioral states with corresponding microhabitat, metabolic state (Standard Metabolic Rate SMR/Active Metabolic Rate AMR), and active foraging status.

Parameter	Model	Class	Value	Notes
Individual Replicates per Site $\times$ Scenario	Simulation	—	3000	—
Active Hours	Suffugium	Rattlesnake	17:00– 11:00	Crepuscular and nocturnal hours.
Initial Body Temperature	Suffugium	Rattlesnake	25°C	—
Initial Calories	Suffugium	Rattlesnake	70cal	—
Max Meals	Suffugium	Rattlesnake	3 prey	—
k	Suffugium	Rattlesnake	0.01	Cooling rate (Newton’s law of cooling).
Thermal Preference Min	Suffugium	Rattlesnake	19°C	See methods.
Thermal Preference Max	Suffugium	Rattlesnake	32°C	See methods.
Thermal Preference Optimum	Suffugium	Rattlesnake	29 C	See methods.
Critical Thermal Limit Min	Suffugium	Rattlesnake	5°C	See methods.
Critical Thermal Limit Max	Suffugium	Rattlesnake	45°C	See methods.
Critical Thermal Limit Max Steps	Suffugium	Rattlesnake	2 hours	Number of steps before death.
Strike Success Probability	Suffugium	Rattlesnake	0.22	From [53].
$\lambda_{1\text{mass}}$	Suffugium	Rattlesnake Metabolism	0.93	From [35].
$\lambda_{2\text{temp}}$	Suffugium	Rattlesnake Metabolism	0.044	From [35].
$\lambda_{3\text{constant}}$	Suffugium	Rattlesnake Metabolism	−2.58	From [35].
Prey Body Size	Suffugium	—	50g	—
Prey Density	Suffugium	Interaction	7	Used in the nominal set. Varies with the prey density map.

Small Mammal Active Hours	Suffugium	Interaction	20:00–06:00	Nocturnal.
Calories per Gram	Suffugium	Interaction	1.38	From [27].
Digestion Efficiency	Suffugium	Interaction	0.8	From [27].
Prey Handling Time	Suffugium	Interaction	2 hours	From [54].
Attack Rate	Suffugium	Interaction	0.01 encounters per hour	Assuming 1 encounter per every 100 hours spent foraging.
Brumation Body Temperature	Suffugium	Brumation	10°C	Mean body temperature during winter periods (Figure 3.11).
Snake Annual Mortality Rate (m)	Rosenzweig–MacArthur	Rattlesnake	0.223	Assuming 80% annual survivorship.
Prey Intrinsic Growth Rate (r)	Rosenzweig–MacArthur	Small Mammal	0.588	Annual intrinsic growth rate. Calculated as average r value between Kangaroo Rats and Deer mice.
Rattlesnake Mean Litter Size	Rosenzweig–MacArthur	Rattlesnake	4.6	From [55].
Predator Conversion Efficiency (e)	Rosenzweig–MacArthur	Rattlesnake	(4.6/14)	Fraction predator offspring per prey consumed. Assuming 14 meals every 2 years needed to produce viable clutch as rattlesnakes reproduce either biennially or triennially [55].
Attack Rate (a)	Rosenzweig–MacArthur	Rattlesnake	2 yr ⁻¹	Only used in nominal simulations to represent baseline consumption efficiency.
Handling Time (h)	Rosenzweig–MacArthur	Rattlesnake	0.15 yr	Only used in nominal simulations to represent baseline prey processing time.
Prey carrying capacity (K_{prey})	Rosenzweig–MacArthur	Small Mammal	50	We assume this value for max small mammal density a hectare could hold.
Predator carrying capacity (K_{pred})	Rosenzweig–MacArthur	Rattlesnake	3	0-2.5 individuals per hectare <i>Crotalus viridis</i> in Idaho [56].

Deer Mouse Litters per Year (dmlpyr)	Rosenzweig-MacArthur	Deer Mouse (<i>Peromyscus maniculatus</i>)	3	3–4 litters per year [57].
Deer Mouse Offspring per Litter (dmL)	Rosenzweig-MacArthur	Deer Mouse (<i>Peromyscus maniculatus</i>)	4	3-5 offspring per litter [57].
Deer Mouse Adult Survivorship (dmSa)	Rosenzweig-MacArthur	Deer Mouse (<i>Peromyscus maniculatus</i>)	0.55	Deer Mice have low annual survivorship [57].
Deer Mouse Juvenile Survivorship (dmSj)	Rosenzweig-MacArthur	Deer Mouse (<i>Peromyscus maniculatus</i>)	0.45	Deer Mice have low annual survivorship [57].
Deer Mouse Female Proportion (dmF)	Rosenzweig-MacArthur	Deer Mouse (<i>Peromyscus maniculatus</i>)	0.5	–
Kangaroo Rat Litters per Year (kratpyr)	Rosenzweig-MacArthur	Kangaroo Rat (<i>Dipodomys ordii</i>)	1.5	1-2 peak breeding seasons per year [58].
Kangaroo Rat Offspring per Litter (kratL)	Rosenzweig-MacArthur	Kangaroo Rat (<i>Dipodomys ordii</i>)	4	3-5 offspring per litter [58].
Kangaroo Rat Adult Survivorship (kratSa)	Rosenzweig-MacArthur	Kangaroo rat (<i>Dipodomys ordii</i>)	0.65	Annual death rate of 0.35 for all age classes [58].
Kangaroo Rat Juvenile Survivorship (kratSj)	Rosenzweig-MacArthur	Kangaroo rat (<i>Dipodomys ordii</i>)	0.65	[58].
Kangaroo Rat Female Proportion (kratF)	Rosenzweig-MacArthur	Kangaroo rat (<i>Dipodomys ordii</i>)	0.5	–

Table 3.2: Key parameters used in the simulation and analytical models.

Predictor	Estimate (β)	SE	z / t	p	95% CI	Interpretation/Effect
(A) OLS model: Total prey consumed						
Intercept (Canada)	5.512	0.357	15.44	< 0.001	[4.81, 6.21]	Baseline prey consumed
Nebraska	0.433	0.039	11.02	< 0.001	[0.36, 0.51]	+0.43 meals vs. Canada
Texas	0.983	0.125	7.89	< 0.001	[0.74, 1.23]	+0.98 meals vs. Canada
Mass	0.0056	0.00007	75.50	< 0.001	[0.005, 0.006]	Larger snakes eat more
Warming	0.0707	0.020	3.60	< 0.001	[0.03, 0.11]	Warmer conditions increase feeding
Mass $\times$ Warming	0.0002	0.00004	5.24	< 0.001	[0.000, 0.000]	Warming amplifies mass effect
Brumation length	-0.0008	0.00006	-12.22	< 0.001	[-0.001, -0.001]	Shorter brumation $\rightarrow$ more prey consumption
Model fit	R ² = 0.383; Adj. R ² = 0.383; AIC = 194,800; N = 60,000.					
(B) Mixed model: Survivorship (logistic, Study site random intercept)						
Intercept	-8.765	0.757	-11.58	< 0.001	[-10.25, -7.28]	Baseline log-odds of survival
Mass	-0.001	0.000	-58.33	< 0.001	[-0.001, -0.000]	Slight negative at baseline
Warming	0.458	0.004	121.59	< 0.001	[0.45, 0.47]	Warming increases survival odds
Mass $\times$ Warming	0.000	0.000	23.10	< 0.001	[0.000, 0.000]	Larger snakes benefit more under warming
Brumation length	0.001	0.000	101.91	< 0.001	[0.001, 0.001]	Longer brumation $\rightarrow$ higher survival
Thermal accuracy	0.616	0.003	195.87	< 0.001	[0.61, 0.62]	Imprecise thermoregulation improves survival
Study-site Var.	1.705	4.596	-	-	-	Random site variance
Model fit	Log-Likelihood = 21,741.97; REML; N = 60,000; Groups = 3.					

Table 3.3: Results of regression models showing the effects of body mass, warming level, and brumation length on (A) total prey consumption and (B) survivorship. Study site is included as a control or random effect as indicated. Robust (HC3) standard errors are reported for OLS model.

Supplementary Material

Suffugium Sub-Models

This section provides technical details of the Suffugium sub-models used in agent-based simulations.

Metabolism

Ectotherms regulate their body temperature behaviorally to avoid heat stress and regulate metabolism. We simulated energy dynamics via an “EctothermMetabolism” component based on mass, temperature, and activity level. This module tracks the metabolic state of individuals over time and integrates Standard Metabolic Rate (SMR) scaling with mass and temperature to calculate energy expenditure while resting. Standard Metabolic Rate (SMR), used as a proxy for $\dot{V} O_2$ is calculated as a log-linear function of body mass and temperature:

$$\log_{10}(\text{SMR}) = X_1 \cdot \log_{10}(\text{Mass}) + X_2 \cdot T + X_3 \quad (3.4)$$

- Mass is body mass of the rattlesnake agent(g),
- T is body temperature (°C),
- X_1, X_2, X_3 are empirically derived coefficients.

This equation was adapted from [35], and the coefficients were chosen based on estimates reported in that study. To obtain the SMR in non logarithmic units, we exponentiation the result:

$$\text{SMR} = 10^{\log_{10}(\text{SMR})} \quad (3.5)$$

When snakes partake in behaviors that make them active, we calculate their Active Metabolic Rate (AMR) by scaling SMR with the activity coefficient. Hourly energy expenditure is scaled by the activity coefficient** (1 for resting, 1.5 for active behaviors) and then is converted from $V O_2$ to calories show here:

$$\delta_{cal} = SMR \times \alpha \times \text{conversion constants} \quad (3.6)$$

- α : activity coefficient
- Conversion factors:
 - 1 mL O_2 = 19.874 J
 - 1 J = 2.39×10^{-4} Calories

We leveraged digestion data from a study on *Crotalus oreganus* consuming small mammals [27] in order to estimate conversion factors of grams of prey to calories (1.38) and digestion efficiency of (80% which represents 20% loss in calories from digestion). Caloric gain from consuming prey is:

$$E_{\text{gain}} = Mass_{\text{prey}} \times C_g \times \eta \quad (3.7)$$

- $Mass_{\text{prey}}$ the mass of a nocturnal small mammal prey
- C_g : calories per gram of prey
- η : digestion efficiency

Each rattlesnake agent is initialized with a metabolic state of 70 calories (equal to the caloric value of 1 prey). We use a 'max meal' input parameter of 3 prey to model a state of digestion/satiation (snakes typically retreat to thermal refugia to digest large meals). This value is then converted to a max metabolic state computed as:

$$M_{max} = m_{max} \times C_g \times Mass_{prey} \quad (3.8)$$

- m_{max} : maximum meals an agent can process.
- C_g : calories per gram of prey
- M_{prey} : expected prey mass. This is the mean between max prey mass and min prey mass which is set as an input parameter.

This value is used in the utility algorithm to calculate the utility for behaviors rest and forage (see below).

Behavior and the Utility Algorithm

Rattlesnakes are the only agent with a dynamic behavioral profile. Small mammals can only be active or inactive at certain times of the day but are not dynamics entities of the model. Rattlesnake agent's decisions are memory-less and there are no mechanisms for explicitly learning. Rattlesnake agents have 5 possible behaviors to employ at a given time step (outlined in Table 3.1). Certain behaviors are activated conditionally such as brumation, prey searching, resting, and thermoregulation; however,

during active hours, snakes may choose their behavioral state for one time step via a utility algorithm from these 3 behaviors: Rest, Thermoregulate, or Forage. The behavior chosen during active hours at a given time step is based on a stochastic expected utility behavioral decision algorithm.

Utility is a term classically used in economics referring to the subjective satisfaction derived from a choice or outcome. Expected Utility Theory is often used when agents choose between risky or uncertain outcomes by comparing their utility values [59]. Although typically used to understand human behavior, the utility concept has been leveraged for ecological systems to formulate discrete choice models for ectotherms [60].

We developed a system of utility functions in order to compare the utility of behaviors snakes can employ based on their internal states:

$$\begin{aligned}
 U_{\text{rest}} &= \frac{M}{M_{\text{max}}} \\
 U_{\text{forage}} &= 1 - \frac{M}{M_{\text{max}}} \\
 U_{\text{thermoregulate}} &= \left| \frac{T_b - T_{\text{opt}}}{T_{\text{max}}} \right|
 \end{aligned} \tag{3.9}$$

- M : Current Metabolic state
- M_{max} : maximum metabolic state
- T_b : Current body temperature

- T_{opt} : The preferred optimal temperature.
- T_{max} : A normalizing constant that represents the max amount of deviation from T_{opt} .

Once computed, a utility vector is formed and passed through a sparsemax function. Sparsemax is a variant of the softmax activation function which is typically used in the context of neural networks, to determine the probability distribution of possible states a node can sample from [61]. In our case we leverage this function to produce a sparse probability distribution over behaviors from which the agent samples to determine its behavior for the current timestep. This algorithm allows agents to respond to poor thermal conditions and hunger dynamically, but they are imperfect decision makers, meaning there is a probability they do not make the optimal decision at any given timestep. Once a behavior is chosen by an agent, the corresponding protocol for behavior is activated.

Foraging and Searching behavior

For the foraging protocol, an individual becomes active, uses the open microhabitat, and then consumes prey according to a variant of the Holling type 2 foraging function shown here:

$$\lambda = \frac{saN}{1 + sahN} \quad (3.10)$$

- λ : prey consumed per hour
- s : the probability of strike success per encounter

- a : the predator encounter rate per hour.
- N : The mean number of prey per hectare.
- h : the handling time, in hours, for prey struck.

Since the calculated prey encounter rate represents the expected number of prey consumed per hour, it is typically a very small and continuous value. To model whether a successful encounter actually occurs in a given hour, we treat it as a Poisson process and use a Poisson draw to convert the continuous rate into a probabilistic binary outcome—determining whether an individual successfully consumes a prey item during that time step. If a prey is not consumed, the forage protocol ends completing behavior for this step. If a prey is consumed, a random, active prey is selected to be consumed by the snake agent and the calories gained is calculated through Equation 3.7, completing the forage protocol.

Prey searching is a post-strike foraging behavior to model the active search rattlesnakes typically conduct to find small mammal prey after a strike [62]. This is driven by a search counter. The time spent searching is determined by the 'handling time' parameter which is a part of the Holling type 2 foraging function (see below). We approximate a handling time of 2 hours based off literature values [54,62,63].

Thermoregulation

The thermoregulation sub-model enables rattlesnake agents to dynamically adjust their microhabitat in response to deviations from their preferred body temperature. This decision is based on a probabilistic mechanism that quantifies the mismatch between the agent's current body temperature and its preferred thermal range. Once this protocol is activated, the snake agent is set to active and then it decides whether to maintain its current microhabitat state or switch microhabitats by calculating a 'probability of switching states' is calculated by:

$$U(T_{\text{body}}) = \begin{cases} \frac{T_{\text{body}} - T_{\text{opt}}}{T_{\text{max}} - T_{\text{opt}}} & \text{if } T_{\text{body}} \geq T_{\text{opt}} \\ \frac{T_{\text{opt}} - T_{\text{body}}}{T_{\text{opt}} - T_{\text{min}}} & \text{if } T_{\text{body}} < T_{\text{opt}} \end{cases} \quad (3.11)$$

- $U(T_{\text{body}})$: The utility of switching microhabitat states dependent on the body temperature in respect to its thermal preferences.
- T_{body} : rattlesnake body temperature.
- T_{opt} : the optimal preferred temperature for performance.
- T_{max} : The maximum value of the thermal preference zone.
- T_{min} : The minimum value of the thermal preference zone.

This function can also be visualized in Figure 3.11. On a successful probability check, the agent is assigned the microhabitat that best fits its thermoregulatory needs. The protocol is used primarily in the utility algorithm, but is also called when the individual's body temperature is outside of its critical thermal limits. Once an individual's body temperature falls outside this range, it has a set number of steps until it dies from either freezing or overheating. The counter is reset once the individual's body temperature returns into the thermal critical bounds.

Resting

Resting is the simplest of our protocols, as when it is called, the agent returns to the burrow microhabitat and is set to inactive. This is called either during inactive hours, or when it is sampled in our utility algorithm. Biologically, we are assuming that when an agent has a comfortable body temperature and is satiated it will try to minimize energy and exposure by entering a resting state within a refuge microhabitat.

Brumation

Snake agents are inactive on brumation days. During brumation, rattlesnake agent body temperature was set to 10°C. Our field data indicated snakes at all sites tended toward this value (this is higher than burrow microhabitat winter temperatures because winter hibernacula are deeper underground than burrows used as refugia during the summer) (Figure 3.11).

Deriving the Jacobian Matrix

In order to conduct a stability analysis of our variant of the RM model that includes a predator carrying capacity shown in Equation 3.1. From this, we formulated the Jacobian Matrix which is a 2x2 matrix of partial derivatives shown in equation 3. In this section; we will showcase how this was derived analytically.

To derive $\frac{\partial f}{\partial x}$, we take the derivative of the prey equation $\frac{dx}{dt}$ in respect to x. First, we split the equation into two parts such that:

$$\frac{\partial f}{\partial x} = \partial f_1(x) - \partial f_2(xy)$$

where

$$f_1(x) = rx(1 - \frac{x}{K_{prey}})$$

$$f_2(x, y) = \frac{axy}{1 + ahx}$$

For $f_1(x)$, we factor the term rx such that

$$f_1(x) = rx - \frac{rx^2}{K_{prey}}$$

then take the derivative in respect to x to get

$$r - \frac{2rx}{K_{prey}}$$

then factoring out r returning

$$\partial f_1(x) = r(1 - \frac{2x}{K_{prey}})$$

Next, taking the derivative of $f_2(x,y)$ in respect to x involves using the quotient rule such that $u = axy$ $v = 1 + ahx$ then passing this into the quotient rule

$$\frac{u'v - uv'}{v^2} = \frac{(ay)(1 + ahx) - (axy)(ah)}{(1 + ahx)^2}$$

this simplifies to

$$\partial f_2(x, y) = \frac{ay}{(1 + ahx)^2}$$

With this the final form of this equation we arrive at is

$$\frac{\partial f}{\partial x} = r(1 - \frac{2x}{K_{prey}}) - \frac{ay}{(1 + ahx)^2}$$

The next term to solve for in the Jacobian is $\frac{\partial f}{\partial y}$ which involves taking the derivative of $\frac{dx}{dt}$ in respect to y . Since y is only in the term $f_2(x,y)$, we can treat $f_1(x)$ as a constant and it is dropped when we take the derivative. This leads to a simple derivative of $f_2(x,y)$ and results in the final solution of

$$\frac{\partial f}{\partial y} = -\frac{ax}{1 + ahx}$$

.

For the predator equation, we derive the partial derivative in respect to x . Since the right-side term $(-my)$ does not contain x , this term is treated as a constant and drops out.

For the right-side term, we leverage the product rule such that

$$(e)g_1(x, y) = \frac{axy}{1 + ahx}$$

and

$$g_2(y) = 1 - \frac{y}{K_{pred}}$$

To take the derivative of $g_1(x,y)$; we use the quotient rule where

$$u(x) = axy$$

$$v(x) = 1 + ahx$$

$$\frac{u'v - uv'}{v^2} = \frac{(ay)(1 + ahx) - (axy)(ah)}{(1 + ahx)^2}$$

which simplifies to

$$\frac{\partial g_2}{\partial x} = \frac{ay}{(1 + ahx)^2}$$

Since $g_2(y)$ does not contain x, the derivative of a constant results in Equation 3.12.

Plugging our terms back into the product rule results in

$$\frac{\partial g}{\partial x} = e \frac{\partial g_1}{\partial y} g_2 + g_1 \frac{\partial g_2}{\partial y} = e \frac{ay}{(1 + ahx)^2 (1 - \frac{y}{K_{pred}})} + \frac{axy}{1 + ahx} \quad (3.12)$$

which simplifies to

$$\frac{\partial g}{\partial x} = \frac{eay}{(1 + ahx)^2} (1 - \frac{y}{K_{pred}})$$

The final partial derivative needed is taking the derivative of $\frac{dy}{dx}$ in respect to y. The derivative of the right side of the equation $-my$ is $-m$, and for the left side, we leverage the product rule again

And

$$(e)g_1(x, y) = \frac{axy}{1 + ahx}$$

$$g_2(y) = 1 - \frac{y}{K_{pred}}$$

where

$$\frac{\partial g_1}{\partial y} = \frac{ax}{1 + ahx}$$

$$\frac{\partial g_2}{\partial y} = -\frac{1}{K_{pred}}$$

plugging these terms into the product rule results in

$$\frac{\partial g_1}{\partial y} g_2 + g_1 \frac{\partial g_2}{\partial y} = \left(\frac{ax}{1 + ahx}\right)\left(1 - \frac{y}{K_{pred}}\right) + \left(\frac{axy}{1 + ahx}\right)\left(\frac{-1}{K_{pred}}\right)$$

To simplify this term, we factor out $\frac{ax}{1+ahx}$ then combine like terms. This is then substituted back into the partial derivative of g in respect to y such that we get the final partial derivative of $\frac{dy}{dx}$ in respect to y in the form of

$$\frac{\partial g}{\partial y} = e \frac{ax}{1 + ahx} \left(1 - \frac{2y}{K_{pred}}\right) - m$$

Model Validation

To assess how well the agent-based model does at reproducing rattlesnake biological dynamics we assessed emergent thermal patterns and feeding rates compared to data from snakes in the field and literature values.

Body Temperature

Understanding how accurately simulated snakes replicate body temperature profiles provides confidence in thermal metrics and behavioral profiles predicted under warming scenarios. To quantify this, we aligned simulated snake body temperature profiles to hourly temperatures of field active snakes and also compared monthly averages.

Comparing distributions of mean hourly body temperatures between simulated and empirical snakes using a Kolmogorov–Smirnov (KS) test, we found that the two temperature profiles were significantly different at each site, indicating there is a discrepancy between these two groups. Overall, we find that simulated snakes tend to run slightly cooler than field active snakes as bias at all sites is approximately -1.2°C (Table 3.6).

When comparing an individual temperature profiles, we see the timing of temperature oscillations broadly correspond between simulated and empirical temperature, but simulated snakes tend to have colder daily minimum temperatures on certain nights (Figure 3.13A, D, G). The timing of brumation periods where body temperatures have less variance align more closely (Figure 3.13B, E, H), but our assumption of holding simulated snake body temperatures at 10°C tend to be warmer than empirical snake body temperatures in Jan-Apr, but colder across the other months (Figure 3.13C, F, I). During the active season, the overall distributions and tails align but body temperatures of field active snakes tend to be left skewed with the peak around 29

- 30C, while simulated temperatures follow a normal distribution with a peak at about 23
- 24C (Figure 3.14).

One explanation is the maximum thermal preference of 32C in our model may be an underestimate. From a behavioral perspective, field snakes have access to a wider range of microhabitat and behavioral strategies than exist in our model—for example, snakes can thermoregulate by having part of their body outside the burrow as an intermediate between burrow and open temperatures, or retreating to a shaded area rather than the burrow when they are too warm. Another biological explanation is that larger snakes may be able to retain heat better due to having a larger body size which would explain why the algorithm performed the best at replicating temperature dynamics at the Texas site (Table 3.6). Other dynamics that elevate snake body temperatures in field settings not incorporated in our model are digestion, gestation, and ecdysis [64–66].

Feeding Rates

Due to rattlesnakes being metabolically efficient sit-and-wait predators, they can go weeks to months without consuming prey [67,68]. Bioenergetic estimates suggest that meeting basic annual maintenance costs may require consuming prey mass totaling approximately 70 – 93% of their body weight in prey mass annually [69,70]. The mean body mass of the rattlesnake populations in this study ranged from 258 – 472g (Figure 3.9) and since we assumed a prey mass of 50g, we should expect our simulated snakes on average to consume 4 – 9 prey items annually to reflect feeding patterns of free ranging rattlesnakes. Corroborating this, a study on the diet of Western rattlesnakes in Idaho

found that individuals consumed on average 6 prey items per year, with a diet consisting of almost exclusively small mammals [56].

Overall, our simulated snakes did tend to match empirical trends. The saturation point, calculated by fitting the Holling type II foraging function to our simulated consumptions rates, ranged from 5.5 – 8.0 prey items annually depending on site and climate scenario (Figure 3.5). The simulated snakes tended to have a median number of days between meals to be about 3 weeks, but with a high standard error indicating this ranged from a week and half to a full month (Figure 3.15). There was a slight decrease in this value under warming scenarios but only by a few days.

Sensitivity Analysis

Since we ran two separate models, we conducted two separate sensitivity analysis, one for the agent-based simulation model Suffugium analyzing the variable mean prey consumed, and one for the Rosenzweig-MacArthur model analyzing mean prey and predator density over a 300-time step simulation similar to the analysis done in Figure 3.6.

A One Factor at a Time (OFAT) sensitivity analysis was conducted for both the agent-based model Suffugium and the Rosenzweig-MacArthur model separately. This involves running the model under a nominal set then varying each independent variable to assess how much this changes outcomes. For Suffugium, this is the “Prey Consumed” variable and for the RM model, we analyzed average prey and predator densities over a 300-year simulation.

To quantify the change in output, we calculated influence as:

$$I^* = \frac{\left| \frac{Y_{\text{new}} - Y_{\text{nominal}}}{Y_{\text{nominal}}} \right|}{\left| \frac{X_{\text{new}} - X_{\text{nominal}}}{X_{\text{nominal}}} \right|} \quad (3.12)$$

Influence values less than 1 indicate low sensitivity and a linear relationship between the input variable and output while an influence greater than 1 indicates a nonlinear relationship.

Suffugium Sensitivity Analysis

From the Suffugium sensitivity analysis (Figure 3.16), we see overall the system is relatively insensitive to input parameter variation as the range of results between all

sensitivity groups only ranges from 4 – 6 meals and no dimensionless influence metric exceed 1. The parameter the system is most sensitive to is the “max meals” parameter which is the max number of calories an agent can hold at any one time acting as a storage tank for the snake agents. This sensitivity reflects the model’s behavioral logic, where snakes initiate foraging based on their remaining energetic reserves; a smaller ‘max meals’ threshold limits their ability to store energy and increases starvation risk.

The two other parameters associated with foraging, attack rate, and strike success performance appear to only be sensitive to decreases in the parameter value indicating the nominal parameters may be at a threshold value where agents are able to stay satiated purely by adjusting foraging rates rather than being constrained by success in foraging outcomes. Conversely, changes in parameters associated with thermoregulation (k, thermal preference min, max, and optimum had little to no impact on prey consumed which is surprising because changes in these values should lead to shifts in thermoregulation rates which would impact the foraging rate. However, this also might be explained by foraging parameters being set at a value where there isn’t much constraint on the snake agents ability to catch prey.

Rosenzweig-MacArthur Sensitivity Analysis

For the Rosenzweig-MacArthur model, prey population density is extremely sensitive to the prey to offspring parameter (e) and the handling time parameter (h) (Figure 3.17A). Both the prey and predator population being sensitive to the handling time parameter (h) makes sense ecologically as this parameter dictates the number of

prey consumed by a predator at a given timestep (Figure 3.17A, B). However, the system being sensitive to lower ranges in the (e) parameter is interesting because this indicates that slower reproduction rates for the predator not only increases prey density but predator density as well.

This could indicate a population stabilizing feedback between snake reproduction frequency and prey abundance. This could explain why rattlesnakes have slower reproduction cycles of either occurring biennially or triennially, as higher reproduction rate leads to over exploitation of prey populations and constrain the ability of female snakes to gain enough weight for gestation and reproduction [55]. Our estimate of 4.6 offspring per 14 meals may be too high which could explain why our small mammal population densities were relatively low (Figure 3.7). From the perspective of prey reproduction rate the system is relatively insensitive to changes to the intrinsic growth rate of either the small mammals (Figure 3.17B, D). This suggests that predator constraints exert a stronger regulatory influence on population dynamics than prey reproductive potential under our parameter space.

Supplementary Figures

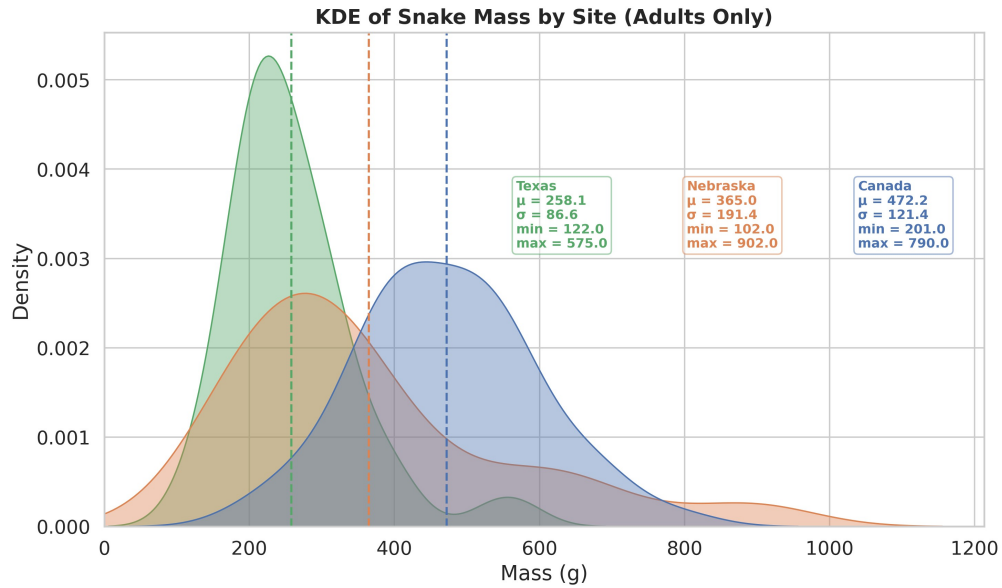


Figure 3.9: Distributions of body size for our three study sites. We found that body masses tend to be greater in northern populations.

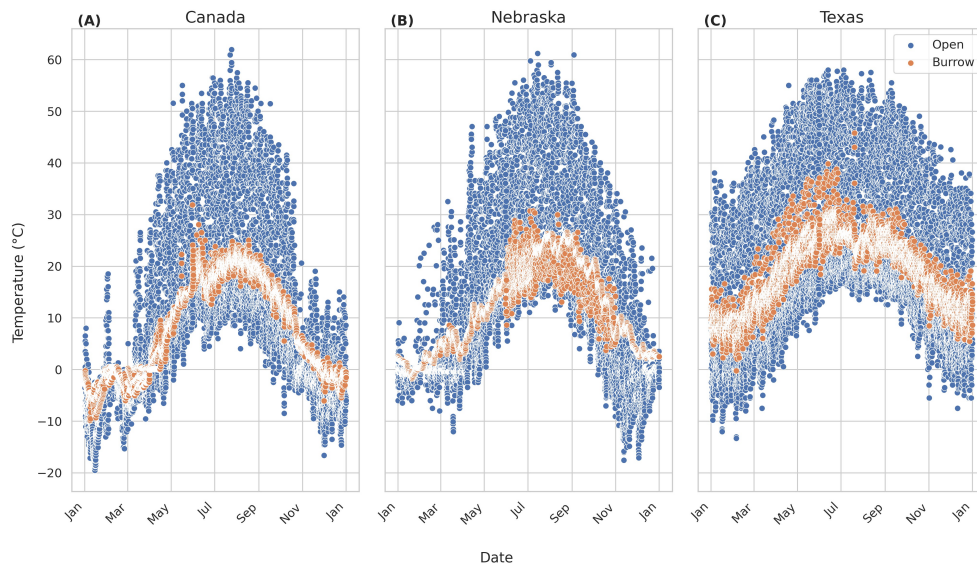


Figure 3.10: Scatter plots of open and burrow temperatures aggregated from an array of operative temperature models deployed at each study site. This is the base environmental data used for Experiment 0. This data was experimentally increased by 1, 2, and 3°C to simulate the experimental groups.

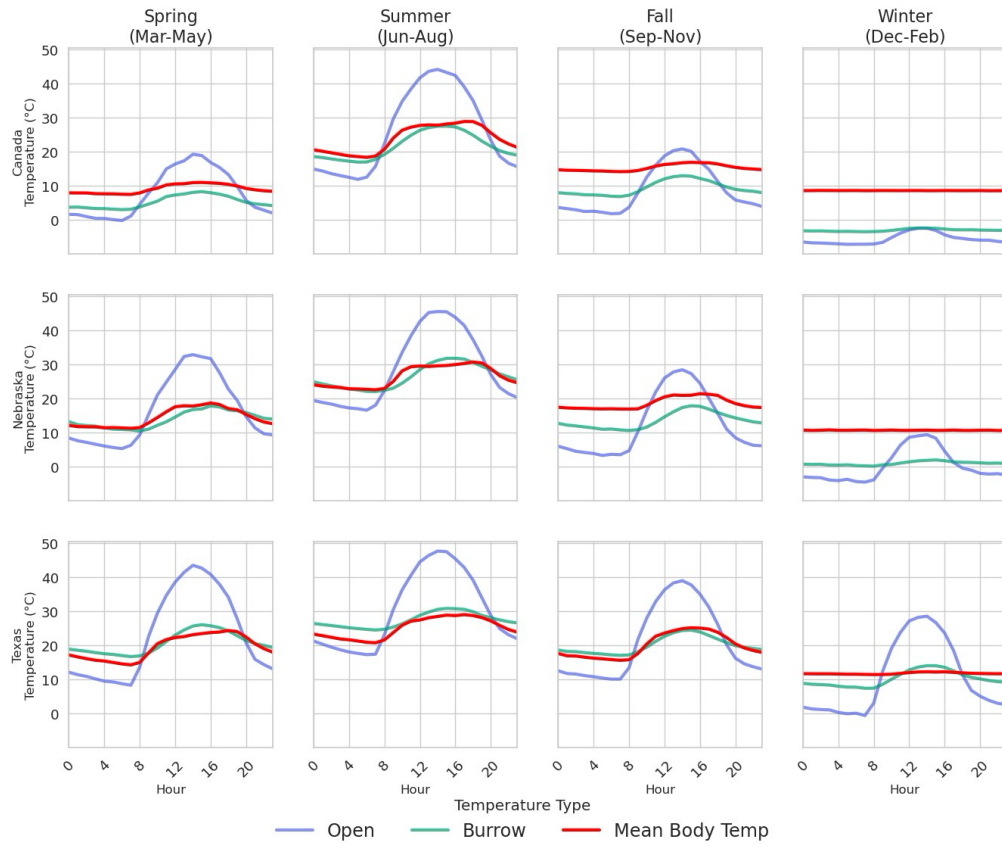


Figure 3.11: Mean hourly temperatures for burrow, open, and rattlesnakes for each site and season. During the brumation behavioral state, we set the snake agents body temperature to 10°C based on live snake body temperatures in the winter months.

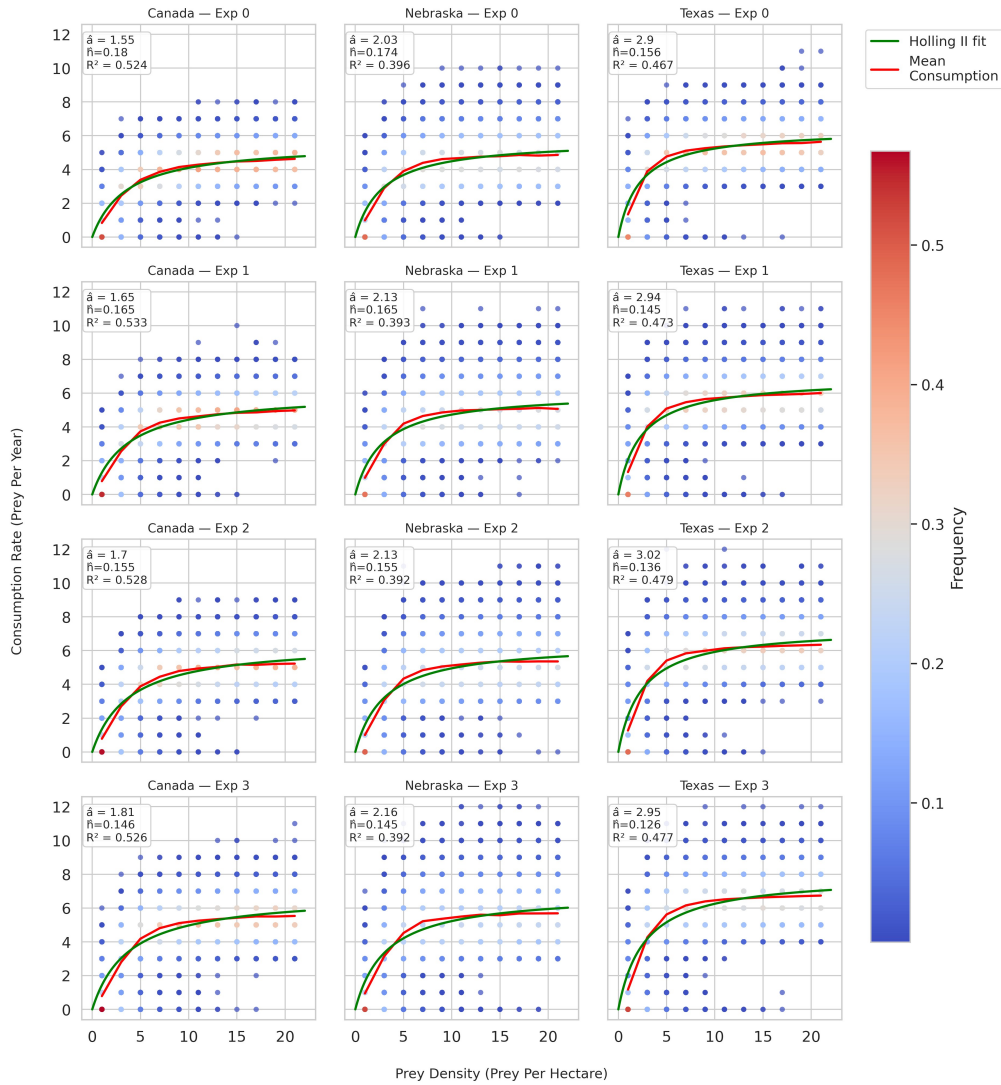


Figure 3.12: The rate of prey consumption as a function of prey density across simulations. Fitting this data to the Holling type II foraging model (Green) closely matching with average prey consumption rates (Red). The parameter $\hat{a}$ is the estimated attack rate, $\hat{h}$ is the estimated handling time, and R^2 is how well the model fits the data. Across all three sites, we see similar trends of warming temperatures leading to increased attack rates and decreased handling times.

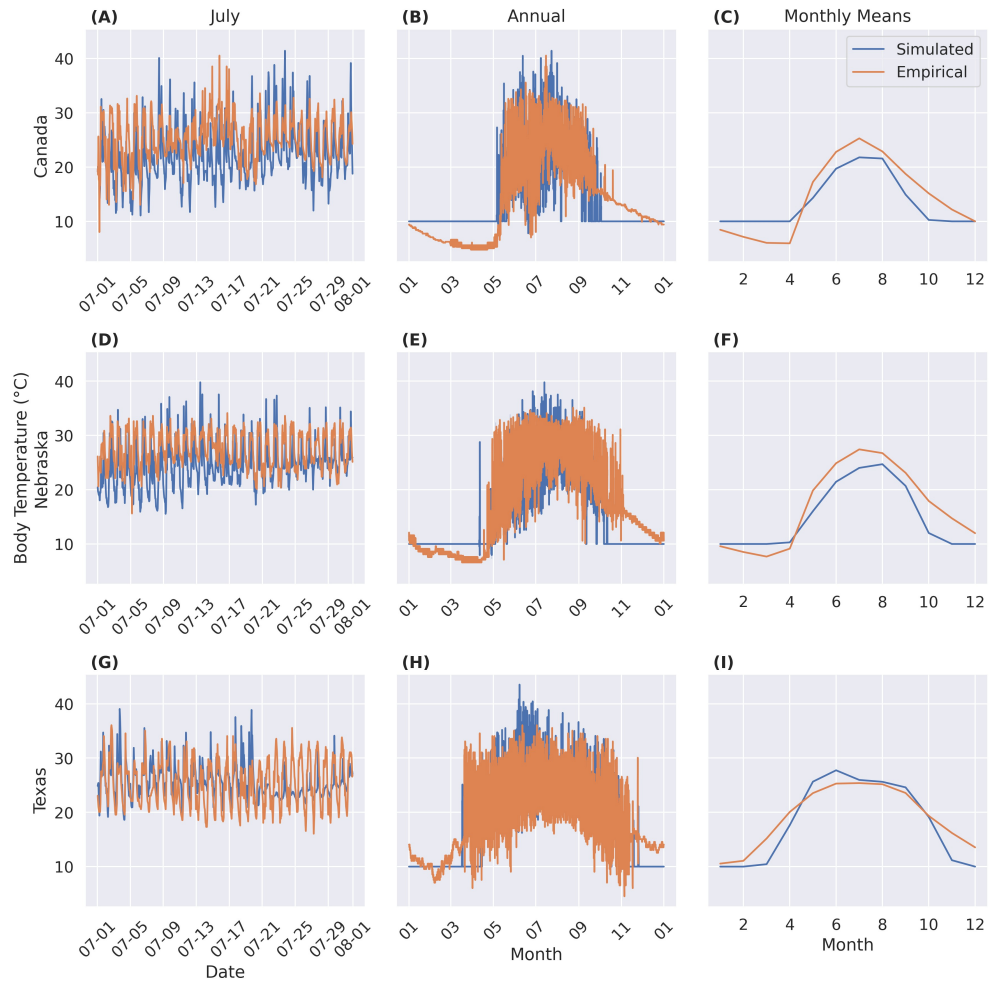


Figure 3.13: A qualitative comparison between simulated snake body temperatures and field active snake body temperatures. Column 1 (Figure A, D, and G) showcases body temperatures of a single snake versus a simulated snake at that site for the month of July. Column 2 (Figure B, E, H) is the same data as column 1 but over the course of a full year. Column 3 (Figure C, F, I) is a comparison of the average body temperature each month of the populations of simulated versus field snakes.

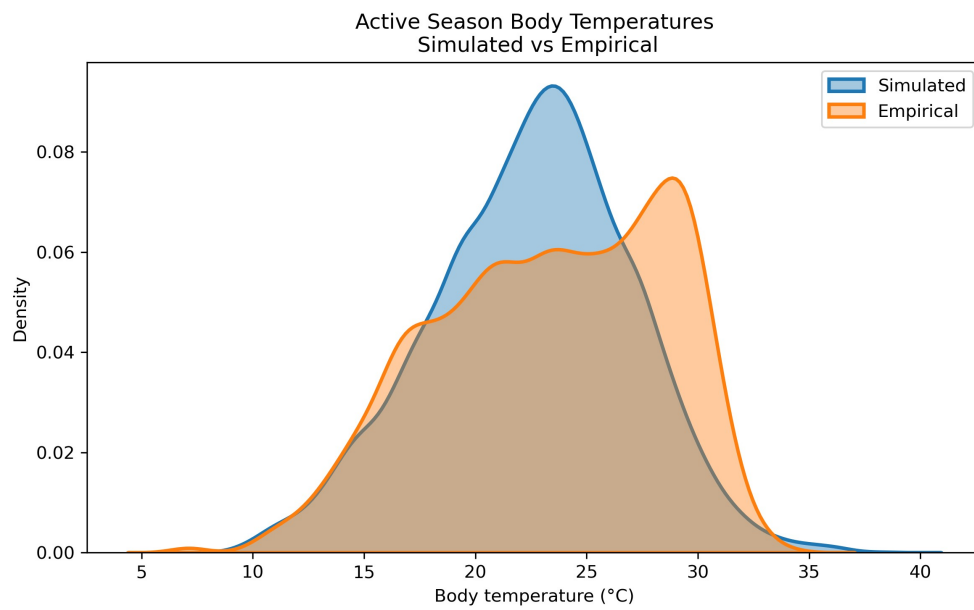


Figure 3.14: The distribution of body temperatures of simulated versus field snakes body temperatures during the active season.

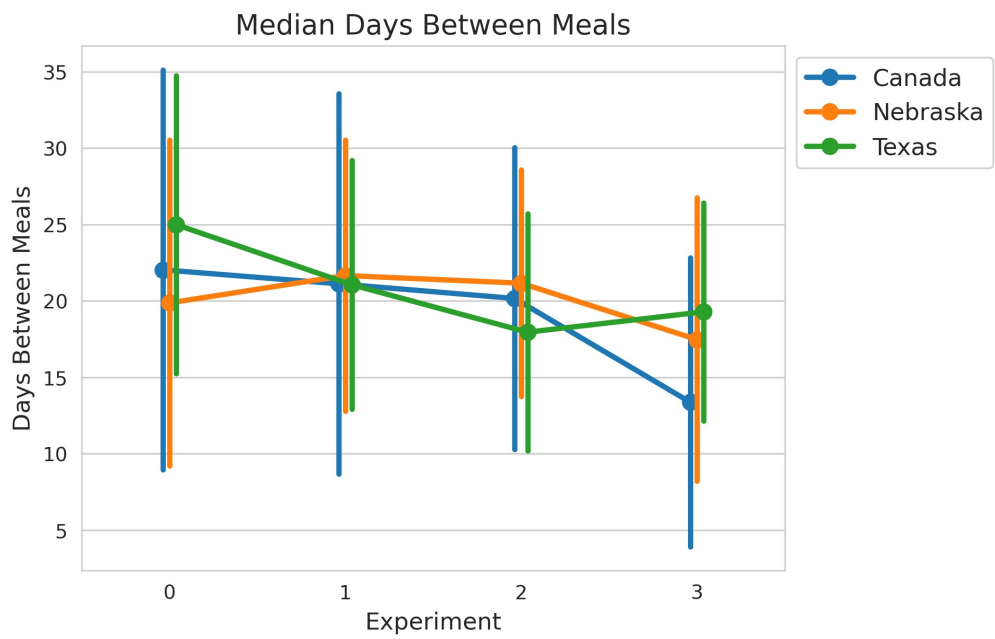


Figure 3.15: Median days between a successful prey capture for simulated snakes across each climate scenario.

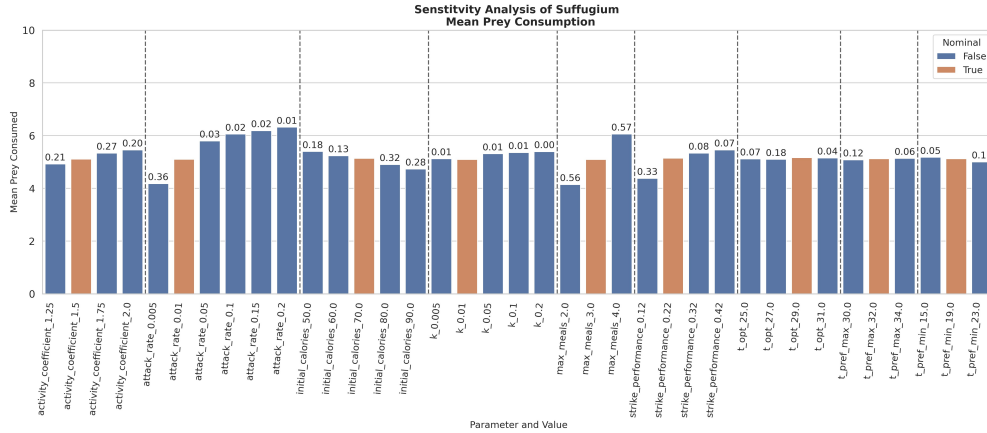


Figure 3.16: One factor at a time (OFAT) sensitivity analysis of simulations from the Suffugium agent-based model. We summarized the output by taking the mean of the prey consumption rates. For this analysis, we leveraged Texas site data at baseline experimental temperatures (Exp 0). The x-axis shows the manipulated variable and values input into simulations. The nominal set (orange) is baseline parameters we leveraged in the nominal set simulation analysis (see results section). Blue bars are deviations in the parameter of interest. Numbers on top of bars denote the measured influence metric which is the ratio of the percent change in prey consumed over the percent change in the parameter value with respect to the nominal (See Table 3.2 for nominal set variables). Overall, simulations had little parameter sensitivity as no influence value exceeds 1 and prey consumption rates tend to vary between 4 – 6.

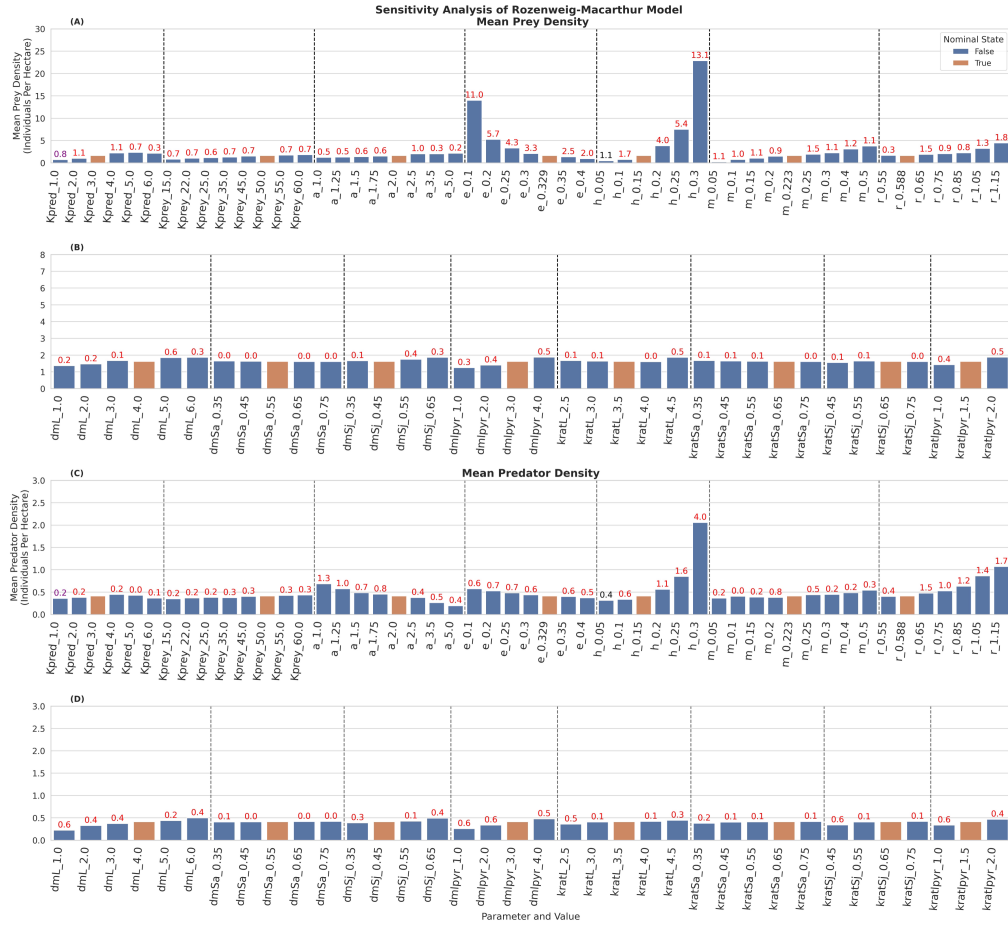


Figure 3.17: Sensitivity analysis (OFAT) of mean prey density and predator density simulated in the Rosenzweig-MacArthur Model. For the nominal set (orange), we set an attack rate of 2 and a handling time of 0.15. Figures (A, C) are direct parameters in the Rosenzweig-MacArthur Model. Figures (B, D) are parameters used to calculate the intrinsic growth rate of the prey population (See Table 3.2). Numbers above bars indicate the influence. The color of the influence value represents if the simulation was stable equilibrium (black), a saddle point equilibrium (purple), or unstable equilibria (red).

Supplementary Tables

Study Site	Mean $\pm$ SE	Std	Min	10%	25%	Median	75%	90%	Max	Observations (N)
Canada	14.12 $\pm$ 0.0195	7.80	3.52	6.02	7.61	11.62	19.07	26.63	41.58	159,213
Nebraska	17.92 $\pm$ 0.0513	8.28	4.58	8.09	10.09	16.12	25.13	30.12	37.59	26,011
Texas	21.08 $\pm$ 0.0139	6.73	3.05	11.61	15.11	21.66	26.14	29.62	42.64	234,941

Table 3.4: Descriptive statistics for empirical rattlesnake body temperatures from telemetry data grouped by study site, with mean reported with standard error.

Season	Study Site	Mean $\pm$ SE	Std	Min	10%	25%	Median	75%	90%	Max	N
Fall	Canada	15.27 $\pm$ 0.0218	4.13	3.55	11.12	12.15	14.16	17.12	20.07	37.56	35,912
Fall	Nebraska	18.57 $\pm$ 0.0692	5.04	4.58	14.09	15.11	16.61	21.60	26.63	35.60	5,312
Fall	Texas	19.95 $\pm$ 0.0321	6.24	3.05	12.62	15.12	18.61	25.12	29.08	37.62	37,813
Spring	Canada	9.07 $\pm$ 0.0374	6.77	3.52	4.59	5.59	6.52	8.09	19.62	37.04	32,796
Spring	Nebraska	14.37 $\pm$ 0.1235	7.62	5.58	7.59	8.59	11.11	17.60	28.62	37.12	3,803
Spring	Texas	19.49 $\pm$ 0.0332	6.48	3.09	12.16	14.10	18.08	24.63	29.12	38.60	38,147
Summer	Canada	23.71 $\pm$ 0.0312	5.81	4.08	15.66	19.62	23.64	28.13	31.55	41.08	34,737
Summer	Nebraska	26.46 $\pm$ 0.0504	4.55	8.09	20.62	23.62	26.63	30.10	32.12	37.59	8,153
Summer	Texas	24.95 $\pm$ 0.0121	4.14	11.60	19.58	21.66	24.62	28.04	30.62	42.64	116,889
Winter	Canada	8.58 $\pm$ 0.0083	1.56	4.02	6.53	7.57	8.61	9.61	10.60	12.10	35,706
Winter	Nebraska	10.70 $\pm$ 0.0439	1.99	7.59	8.09	8.59	11.10	12.60	13.12	14.09	2,054
Winter	Texas	11.90 $\pm$ 0.0141	2.73	4.51	9.09	10.09	11.66	13.10	14.60	35.61	37,596

Table 3.5: Descriptive statistics for empirical rattlesnake body temperatures from telemetry data grouped by meteorological season and study site. Mean values are reported with standard error.

Site	Bias (°C)	RMSE (°C)	KS Stat.	KS p
Total	−1.2106	4.1334	0.3229	0
Canada	−0.8417	4.2441	0.3800	0
Nebraska	−1.9030	4.1545	0.2964	0
Texas	−0.9085	3.9992	0.3992	0

Table 3.6: Validation statistics comparing hourly simulated and empirical body temperatures across study sites. Bias is defined as $\text{mean}(T_{\text{sim}} - T_{\text{emp}})$. RMSE stands for Root mean squared error which measures the average magnitude of error. Kolmogorov–Smirnov (KS) statistic quantifies the maximum discrepancy between the cumulative distributions of simulated and empirical body temperatures, with values near 0 indicating close agreement and values approaching 1 indicating strong divergence. KS p is the p -value determined from the Kolmogorov–Smirnov test.

References

1. IPCC. Impacts of 1.5°C Global Warming on Natural and Human Systems. Cambridge University Press; 2022.
2. Abram PK, Boivin G, Moiroux J, Brodeur J. Behavioural effects of temperature on ectothermic animals: unifying thermal physiology and behavioural plasticity. *Biological Reviews*. 2017;92:1859–1876. doi:10.1111/brv.12312.
3. Paine RT. The Pisaster-Tegula Interaction: Prey Patches, Predator Food Preference, and Intertidal Community Structure. *Ecology*. 1969;50:950–961.
4. Brown JH, Gillooly JF, Allen AP, Savage VM, West GB. Toward a metabolic theory of ecology. vol. 85. *Ecology*; 2004. p. 1771–1789.
5. Bofill SIH, Blom MPK. Climate change from an ectotherm perspective: evolutionary consequences and demographic change in amphibian and reptilian populations; 2024.
6. Atkinson D, Sibly RM. Why are organisms usually bigger in colder environments? Making sense of a life history puzzle. *Trends in Ecology & Evolution*. 1997;12:235–239. doi:10.1016/S0169-5347(97)01058-6.
7. Buckley LB, Ehrenberger JC, Angilletta MJ. Thermoregulatory behaviour limits local adaptation of thermal niches and confers sensitivity to climate change. *Functional Ecology*. 2015;29:1038–1047. doi:10.1111/1365-2435.12406.
8. Logan ML, Cox RM, Calsbeek R. Natural selection on thermal performance in a novel thermal environment. *Proceedings of the National Academy of Sciences of the United States of America*. 2014;111:14165–14169. doi:10.1073/pnas.1404885111.
9. Villén-PérezS, Carrascal LM, Seoane J. Foraging Patch Selection in Winter: A Balance between Predation Risk and Thermoregulation Benefit. *PLoS ONE*. 2013; 8(7):e68448. doi:10.1371/journal.pone.0068448.

10. Wasserman TN, Cushman SA, Shirk AS, Landguth EL, Littell JS. Simulating the effects of climate change on population connectivity of American marten (*Martes americana*) in the northern Rocky Mountains, USA. *Landscape Ecology*. 2012;27:211–225. doi:10.1007/s10980-011-9653-8.
11. Ito K, Higginson AD, Ruxton GD, Papastamatiou YP. Incorporating thermodynamics in predator–prey games predicts the diel foraging patterns of poikilothermic predators. *Journal of Animal Ecology*. 2021;doi:10.1111/1365-2656.13608.
12. Levy O, Dayan T, Porter WP, Kronfeld-Schor N. Time and ecological resilience: can diurnal animals compensate for climate change by shifting to nocturnal activity? *Ecological Monographs*. 2019;89. doi:10.1002/ecm.1334.
13. Stenkovski M, Bell JR, Ellwood ER, Inouye BD, Kobori H, Lee SD, et al. Disorder or a new order: How climate change affects phenological variability. *Ecology*. 2022;doi:10.1002/ecy.3846.
14. IPCC. Climate Change 2022: Impacts, Adaptation and Vulnerability. Summary for Policymakers. Cambridge, UK and New York, USA: Cambridge University Press; 2022.
15. Tinbergen N. On aims and methods of Ethology. *Zeitschrift für Tierpsychologie*. 1963;20:410–433(4). doi:10.1111/J.1439-0310.1963.TB01161.X.
16. Schulte PM, Healy TM, Fanguie NA. Thermal performance curves, phenotypic plasticity, and the time scales of temperature exposure. *Integrative and Comparative Biology*. 2011;51:691–702. doi:10.1093/icb/icr097.
17. Sinclair BJ, Marshall KE, Sewell MA, Levesque DL, Willett CS, Slotsbo S, et al.. Can we predict ectotherm responses to climate change using thermal performance curves and body temperatures?; 2016.
18. Taylor EN, Diele-Viegas LM, Gangloff EJ, Hall JM, Halpern B, Massey MD, et al. The thermal ecology and physiology of reptiles and amphibians: A user’s guide. *Journal of Experimental Zoology Part A: Ecological and Integrative Physiology*. 2021;335:13–44. doi:10.1002/jez.2396.
19. Huey RB, Kingsolver JG. Evolution of thermal sensitivity of ectotherm performance. *Trends in ecology & evolution*. 1989;4(5):131–135.
20. Stone GN, Willmer PG. Warm-Up Rates and Body Temperatures in Bees: The Importance of Body Size, Thermal Regime and Phylogeny. *Journal of Experimental Biology*. 1989;147(1):303–328. doi:10.1242/jeb.147.1.303.

21. Twardochleb LA, Treake TC, Zarnetske PL. Foraging strategy mediates ectotherm predator–prey responses to climate warming. *Ecology*. 2020;101. doi:10.1002/ecy.3146.
22. Banerjee M, Zhang L. Time delay can enhance spatio-temporal chaos in a prey–predator model. *Ecological Complexity*. 2016;27:17–28. doi:10.1016/j.ecocom.2015.12.001.
23. Fryxell JM, Packer C, McCann K, Selberg EJ, Saether BE. Resource Management Cycles and the Sustainability of Harvested Wildlife Populations. *Science*. 2010;328:899–903. doi:10.1126/science.1186440.
24. Hanscom R. From Ambush to Activity: Using Accelerometry to Reveal Cryptic Behaviors of Rattlesnakes and Kangaroo Rats. University of California, Riverside; 2025. Available from: <https://escholarship.org/uc/item/4ft2985w>.
25. Kazil J, Masad D, Crooks A. Utilizing Python for Agent-Based Modeling: The Mesa Framework. 2020; p. 308–317.
26. Alujević K, Bakewell L, Clifton IT, Cox CL, Frishkoff LO, Gangloff EJ, et al. 3D printed models are an accurate, cost-effective, and reproducible tool for quantifying terrestrial thermal environments. *Journal of Thermal Biology*. 2024;119:103762. doi.org/10.1016/j.jtherbio.2023.103762.
27. Crowell HL, King KC, Whelan JM, Harmel MV, Garcia G, Gonzales SG, et al. Thermal ecology and baseline energetic requirements of a large-bodied ectotherm suggest resilience to climate change. *Ecology and Evolution*. 2021;11:8170–8182. doi:10.1002/ece3.7649.
28. Loughran CL, Scoville AG, Beck DD. Body Size Effects on Thermoregulation and Consequences for Activity in Northern Pacific Rattlesnakes (*Crotalus oreganus*). *Herpetologica*. 2025;81(4):371 – 380. doi:10.1655/Herpetologica-D-25-00014.
29. Sexton OJ, Marion KR. Experimental Analysis of Movements by Prairie Rattlesnakes, *Crotalus viridis*, During Hibernation. *Oecologia*. 1981; p. 37–41.
30. Rugiero L, Milana G, Petrozzi F, Capula M, Luiselli L. Climate-change-related shifts in annual phenology of a temperate snake during the last 20 years. *Acta Oecologica*. 2013;51:42–48. doi:<https://doi.org/10.1016/j.actao.2013.05.005>.
31. Buckley LB. Linking traits to energetics and population dynamics to predict lizard ranges in changing environments. *American Naturalist*. 2008;171. doi:10.1086/523949.

32. Gummer DL. Status of the Ord's Kangaroo Rat in Alberta. Edmonton, Alberta: Alberta Environmental Protection, Wildlife Management Division; 1997. Available from: <https://open.alberta.ca/publications/1997-sar-statusordskangarooalberta-1997>.
33. Kenny RJ. Population, distribution, habitat use and natural history of Ord's kangaroo rat (*Dipodomys ordi*) in the sand hill areas of south-western Saskatchewan and south-eastern Alberta. 1989.
34. Garner HW. Population dynamics, reproduction, and activities of the kangaroo rat, *Dipodomys ordii*, in western Texas. 1970;.
35. Dorcas ME, Hopkins WA, Roe JH. Effects of Body Mass and Temperature on Standard Metabolic Rate in the Eastern Diamondback Rattlesnake (*Crotalus adamanteus*). Source: *Copeia*. 2004;2004:145–151.
36. Feng W, Rocco N, Freeze M, Lu X. Mathematical analysis on an extended Rosenzweig-MacArthur model of tri-trophic food chain. *Discrete and Continuous Dynamical Systems - S*. 2014;7(6):1215–1230. doi:10.3934/dcdss.2014.7.1215.
37. Leslie PH. On the Use of Matrices in Certain Population Mathematics. *Biometrika*. 1945;33(3):183–212.
38. Virtanen P, Gommers R, Oliphant TE, Haberland M, Reddy T, Cournapeau D, et al. SciPy 1.0: Fundamental Algorithms for Scientific Computing in Python. *Nature Methods*. 2020;17:261–272. doi:10.1038/s41592-019-0686-2.
39. Aragón P, Rodríguez MA, Olalla-Tárraga MA, Lobo JM. Predicted impact of climate change on threatened terrestrial vertebrates in central Spain highlights differences between endotherms and ectotherms. *Animal Conservation*. 2010;13:363–373. doi:10.1111/j.1469-1795.2009.00343.x.
40. Buckley LB, Hurlbert AH, Jetz W. Broad-scale ecological implications of ectothermy and endothermy in changing environments. *Global Ecology and Biogeography*. 2012;21:873–885. doi:10.1111/j.1466-8238.2011.00737.x
41. Glaudus X, Rodríguez-Robles JA. Vagabond males and sedentary females: spatial ecology and mating system of the speckled rattlesnake (*Crotalus mitchellii*). *Biological Journal of the Linnean Society*. 2011;103(3):681–695. doi:10.1111/j.1095-8312.2011.01677.x.
42. Clark RW, Schuett GW, Repp RA, Amarello M, Smith CF, Herrmann HW. Mating Systems, Reproductive Success, and Sexual Selection in Secretive Species: A Case Study of the Western Diamond-Backed Rattlesnake, *Crotalus atrox*. *PLOS ONE*. 2014;9(3):1–12. doi:10.1371/journal.pone.0090616.

43. Ohlberger J. Climate warming and ectotherm body size - from individual physiology to community ecology. *Functional Ecology*. 2013;27:991–1001. doi:10.1111/1365-2435.12098.
44. Jonsson T, Ebenman B. Effects of Predator-prey Body Size Ratios on the Stability of Food Chains. *J theor Biol*. 1998;193:407–417.
45. Hampton PM, Moon BR. Gape size, its morphological basis, and the validity of gape indices in western diamond-backed rattlesnakes (*Crotalus atrox*). *Journal of Morphology*. 2013;274(2):194–202. doi:https://doi.org/10.1002/jmor.20087.
46. Charland MB. Size and winter survivorship in neonatal western rattlesnakes (*Crotalus viridis*). *Canadian Journal of Zoology*. 1989;67(7):1620–1625. doi:10.1139/z89-231.
47. Nisbet RM, Muller EB, Lika K, Kooijman SALM. From Molecules to Ecosystems through Dynamic Energy Budget Models. Source: *Journal of Animal Ecology*. 2000;69:913–926.
48. Moses MR, Frey JK, Roemer GW. Elevated surface temperature depresses survival of banner-tailed kangaroo rats: Will climate change cook a desert icon? *Oecologia*. 2012;168:257–268. doi:10.1007/s00442-011-2073-2.
49. Riddell EA, Iknayan KJ, Hargrove L, Tremor S, Patton JL, Ramirez R, et al. Exposure to climate change drives stability or collapse of desert mammal and bird communities; 2021. Available from: <https://www.science.org>.
50. Chivers WJ, Gladstone W, Herbert RD, Fuller MM. Predator-prey systems depend on a prey refuge. *Journal of Theoretical Biology*. 2014;360:271–278. doi:10.1016/j.jtbi.2014.07.016.
51. Urban DL. Modeling ecological processes across scales; 2005.
52. Getz WM, Marshall CR, Carlson CJ, Giuggioli L, Ryan SJ, Romanach SS, et al. Making ecological models adequate. *Ecology Letters*. 2018;21:153–166. doi:10.1111/ele.12893.
53. Whitford MD, Freymiller GA, Higham TE, Clark RW. The Effects of Temperature on the Kinematics of Rattlesnake Predatory Strikes in Both Captive and Field Environments. *Integrative Organismal Biology*. 2020;2. doi:10.1093/iob/obaa025.
54. Chiszar D, O’Connell B, Greenlee R, Demeter B, Walsh T, Chiszar J, et al. Duration of strike-induced chemosensory searching in long-term captive rattlesnakes at national zoo, audubon zoo, and San Diego Zoo. *Zoo Biology*. 1985;4:291–294. doi:10.1002/zoo.1430040310.

55. Macartney JM, Gregory PT. Reproductive Biology of Female Rattlesnakes (*Crotalus viridis*) in British Columbia. *Copeia*. 1988;1988(1):47–57.
56. Diller LV, Johnson DR. Food Habits, Consumption Rates, and Predation Rates of Western Rattlesnakes and Gopher Snakes in Southwestern Idaho. *Herpetologica*. 1988;44:228–233.
57. Sullivan J. *Peromyscus maniculatus*; 1995. In: Fire Effects Information System, [Online]. U.S. Department of Agriculture, Forest Service, Rocky Mountain Research Station, Fire Sciences Laboratory (Producer). Available from: <https://www.fs.usda.gov/database/feis/animals/mammal/pema/all.html>.
58. Sullivan J. *Dipodomys ordii*; 1995. In: Fire Effects Information System [Online]. Available from: <https://www.fs.usda.gov/database/feis/mammal/dior/all.html>.
59. Davis JB, Hands DW, Mäki U. The Handbook of Economic Methodology. Cheltenham, UK: Edward Elgar Publishing; 1998. Available from: <https://www.elgaronline.com/view/9781852787950.xml>.
60. George AD, Connette GM, Thompson FR, Faaborg J. Resource selection by an ectothermic predator in a dynamic thermal landscape. *Ecology and Evolution*. 2017;7:9557–9566. doi:10.1002/ece3.3440.
61. Martins AFT, Fern'andez Astudillo R. From Softmax to Sparsemax: A Sparse Model of Attention and Multi-Label Classification. arXiv preprint arXiv:160202068. 2016;doi:10.48550/arXiv.1602.02068.
62. Teshera MS, Clark RW. Strike-Induced Chemosensory Searching in Reptiles: A Review. *Herpetological Monographs*. 2021;35(1):28 – 52. doi:10.1655/0733-1347-35.1.28.
63. Clark RW. Post-Strike Behavior of Timber Rattlesnakes (*Crotalus horridus*) During Natural Predation Events. *Ethology*. 2006;112(11):1089–1094. doi:<https://doi.org/10.1111/j.1439-0310.2006.01271.x>.
64. Beck DD. Effects of Feeding on Body Temperatures of Rattlesnakes: A Field Experiment. *Physiological Zoology*. 1996;69(6):1442–1455. doi:10.1086/physzool.69.6.30164268.
65. Gier PJ, Wallace RL, Ingermann RL. Influence of Pregnancy on Behavioral Thermoregulation in the Northern Pacific Rattlesnake *Crotalus Viridis Oreganus*. *Journal of Experimental Biology*. 1989;145(1):465–469. doi:10.1242/jeb.145.1.465.

66. Gibson AR, Smucny DA, Kollar J. The effects of feeding and ecdysis on temperature selection by young garter snakes in a simple thermal mosaic. *Canadian Journal of Zoology*. 1989;67(1):19–23. doi:10.1139/z89-004.
67. Maag DW, Francioli YZ, Shaw N, Soni AY, Castoe TA, Schuett GW, et al. Hunting behavior and feeding ecology of Mojave rattlesnakes (*Crotalus scutulatus*), prairie rattlesnakes (*Crotalus viridis*), and their hybrids in southwestern New Mexico. *Ecology and Evolution*. 2023;13. doi:10.1002/ece3.10683.
68. Nowak EM, Theimer TC, Schuett GW. Functional and Numerical Responses of Predators: Where Do Vipers Fit in the Traditional Paradigms? *Biological Reviews*. 2008;83(4):601–620. doi:<https://doi.org/10.1111/j.1469-185X.2008.00056.x>.
69. Beck DD. Ecology and Energetics of Three Sympatric Rattlesnake Species in the Sonoran Desert. Source: *Journal of Herpetology*. 1995;29:211–223.
70. Beaupre S, Agugliaro J, Van Dyke JU, Zaidan III F. Annual energy budgets of the timber rattlesnake: advancements, refinements, and open questions. In: Dreslik MJ, Hayes WK, Beaupre SJ, Mackessy SP, editors. 1st ed. *ECO Herpetological Publishing and Distribution*, Rodeo, NM; 2017.96