Uumarrty: Agent Based Simulation Model of Predator Prey Interactions with a Game Theoretical Framework

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ABSTRACT

Evolutionary game theory boasts a rich history of application in the study of phenotypic evolution and behavioral strategies. Complementing this, agent-based modeling offers a powerful simulation framework that allows for explicit modeling and parameterization of individual agents within a virtual environment. The agent-based modelling approach empowers ecologists and evolutionary biologists to accurately model highly complex and dynamic systems. Leveraging these methodologies, we developed the agent-based model Uumarrty, which integrates concepts from game theory to investigate the evolution of behavioral phenotypes. Our model embraces essential game theoretical principles, including pay-offs, mixed versus pure strategies, and optimal behavioral strategies, seamlessly within the agent-based framework. Furthermore, we introduced a novel metric called the Nash score, which serves as an analog of the evolutionarily stable strategy within our agent-based environment. With this innovative approach, researchers gain a versatile tool to comprehensively explore optimal behavioral strategies and assess their evolutionary stability. To demonstrate the efficacy of our model, we applied it to a predator-prey system involving kangaroo rats and rattlesnakes. By examining various factors such as differing foraging gains by kangaroo rats, varying strike success of rattlesnakes by microhabitat, and the influence of introducing a second predator, we gained valuable insights into the evolution of microhabitat preferences within this predator-prey system.

Keywords: Agent-Based Models, Game Theory, Predator-Prey, Behavior, Simulation

1 INTRODUCTION

Mathematical models are one of the most powerful mechanisms for understanding the evolution of organisms, and have been fundamental in uncovering precisely how the process of natural selection leads to adaptation and evolution Hamilton (1964), Wright (1932). One of the most powerful and flexible modeling approaches for understanding behavioral evolution is game theory, which has a rich history of being used to understand optimal behavioral strategies and their evolutionary stability Smith (1982). Historically, games modeling animal behavior have been constructed in a deterministic, top-down, framework using a

set of differential equations parameterized by a payoff matrix. These models are used to determine what phenotype relative or mix of phenotypes in a population which maximizes Darwinian fitness Smith (1982). However, games can also be implemented in a bottom-up framework by using modern computational tools to implement agent-based models that simulate individuals with encoded phenotypes Adami et al. (2016). These populations of individuals evolve over time through a genetic algorithm, which builds simulations that reveal which phenotypes are optimal relative to others Adami et al. (2016), Kaviari et al. (2019).

Both mathematical game theory and agent-based models achieve similar ends through very different methodologies. One advantage of mathematical evolutionary game theory models over agent-based models is they give a deeper understanding of the stability of a given strategy in a standardized way Hamblin (2013), and do not have uncertainty in their conclusions DeAngelis and Diaz (2019). The core concept of an equilibrium in the game is the evolutionarily stable strategy (ESS). The ESS is a concept adapted from the Nash equilibrium in a general game theory context and the explicit definition is a strategy or phenotype such that, if all the members of a population adopt it, then no mutant strategy could invade the population under the influence of natural selection Smith (1982). The ESS provides researchers a standardized method for understanding if the circumstances under which a behavioral strategy is expected to be favored and becomes fixed in the population over alternative behaviors or strategies.

However, mathematical game theory has been criticized for the relatively simplistic set of assumptions that are incorporated into the framework McNamara (2013). For example, traditional game theory models assume an idealized population where there is an infinite population size, and all individuals of two competing populations have access to interact with one another meaning the populations are well mixed. These assumptions could be altered to match real world conditions by incorporating more parameters, but this reduces certainty and can be difficult in a mathematical framework. Agent-based modeling is effective at modelling complex, non-linear systems with fewer assumptions since it is implemented through dynamic computational algorithms that allows for parameterization at the individual level, population level, and of the landscape in which agents interact; details that can be difficult to encode into a mathematical framework. Conversely, agent-based models have more uncertainty associated with their outcomes, and the methodology of implementing and summarising agent-based models is less consistent compared to a mathematical framework DeAngelis and Mooij (2005), DeAngelis and Diaz (2019), Grimm et al. (2006). This showcases a trade off in using one methodology over the other as mathematical game theory reduces complexity and gives clearer insights, but agent-based models are better at modelling complex systems at multiple scales and providing more detailed understanding of a specific system system. Introducing new methods of agent-based models that are standardized but still flexible will capture the best of both approaches.

Our model, Uumarrty, is a new approach that incorporates many game theory principles into an agent-based framework. This includes modelling competing behavioral traits to assess optimal strategies, the integration of payoff scores to function as a fitness proxy, and the ability to model pure or mixed strategies. We also introduce a new metric for assessing the evolutionary stability of traits that we term *Nash score*. The Nash score is analogous to the ESS in that it captures the temporal dynamics of the system under particular combinations of strategies and quantifies the degree of divergence of a combination of strategies from the evolutionary stable strategy. The algorithm that determines the Nash score also provides several novel metrics to ascertain the stability of a given behavioral strategy to provide a nuanced look at how certain selection pressures influence the evolutionary stability of traits. These methods will help make additional agent-based models that adopt this framework more directly comparable to one another as it will standardize the inputs and outputs of the models. This gives researchers a tool to compose in silico

experimental designs to understand optimal behavioral phenotypes and their stability under a given set of ecological conditions.

To demonstrate how our methods can contribute to a better understanding of the evolution of optimal behavioral strategies, we apply our approach to a predator-prey system based on the microhabitat usage of kangaroo rats and rattlesnakes under various ecological conditions. The dynamics of microhabitat usage in rattlesnakes and kangaroo rat systems have been studied in both empirical Bouskila (1995), Embar et al. (2014), Brown (1988), Kotler (1984), Schroder (1987) as well as theoretical contexts, including a game theory model Bouskila (2001), an agent-based model Scharf (2021), and other mathematical frameworks Brown et al. (1999). This makes this system suitable for comparing our novel insights to a rich body of previous research. Microhabitat selection for foraging can be conceptualized as a direct fitness seeking trait McLane et al. (2011) which makes it an ideal behavioral trait to model through payoff scores as each successful foraging decision contributes to increased fitness. In a predator-prey system, there is an inherent conflict in microhabitat usage as prey face a trade off between predation and collecting enough food and resources to survive. Predators in these games seek microhabitats which will yield the best chance to catch prey. To mitigate this predation risk, organisms may develop dynamic foraging patterns of that use microhabitats in the landscape at rates that balance the food/safety tradeoff Bouskila (1995), Embar et al. (2014), Brown (1988). Modelling both predator and prey simultaneously is important, as behaviors of prey and predators may fluctuate in response to the decisions made by the other Lima (2002). Predators and prey may cause each other's behavioral strategy to fluctuate dynamically in a cyclical manner, or, depending on the conditions, either party can adopt an invariant stable strategy.

For this case study, we analyze a set of general ecological conditions to see what factors most influence the evolution of predator-prey microhabitat preferences. We incorporate both top-down effects, such as predator strike success and the presence of specialist predators (owls), and bottom-up effects, such as different energy gain by kangaroo rats when foraging in different in microhabitats. Our modeling exercises not only serve as an exemplar for combining traditional game theory metrics with computational tools, and also provides quantitative insights into the relative impact of top-down and bottom-up factors driving the microhabitat usage pattern, allowing us to evaluate general hypotheses concerning the impacts of the behavioral patterns of key predators on prey community and community composition.

2 METHODS

2.1 Construction of the Model

2.1.1 Agent Based Modelling and the Genetic Algorithm

Our model, which we termed "Uumarrty", is an agent based, stochastic predator prey model written in Python 3.8 Van Rossum and Drake (2009). The basic model has two main populations of agents: the kangaroo rat agent (prey) and the rattlesnake agent (predator). For the populations of agents, 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). 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 particular type of 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. Individuals that accrue a higher pay-off compared to others in the population are able to leave more offspring with the same microhabitat preference unless a random mutation occurs. At the end of each generation time, the pay-off scores from the set of agents who survived are aggregated by their microhabitat preference type. The proportion of the sum of pay-off scores of the individuals with a given microhabitat preference trait over the total sum of pay-off 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).

The pay-off score is a proxy for fitness that is parameterized by the user of the software. In our model, the only populations that are capable of reproducing are the kangaroo rats and the rattlesnakes. However, when the trait is actually 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 2).

2.1.2 Landscape

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 microhabitats; the bush and the open. The bush microhabitat represents any habitat that gives an aerial cover such as creosote (*Larrea tridentata*) or mesquite (*Prospis spp.*). The open microhabitat represents areas with sparse vegetation such as grasses and with no aerial cover. Agents operate and interact in these cells. The interactions vary based on the classification of the cell and the input parameters of the model. Pay-offs for foraging in these microhabitats are then accrued by the individual based on the microhabitat they occupy during a feeding event. Experimental parameters such as the number of owls (specialized aerial predators that only forage in the open), energy gain from prey foraging in a given microhabitat, and the probability of a predator's strike being successful in a microhabitat are set as initial conditions of the model. The specific parameters we use in our model can be seen in Table 1.

2.1.3 Classes of Agents

There are two classes of agents for our model, the predator class and the prey class. For both classes, the goal of the agent is to maximize their pay-off score and avoid dying. The pay-off score for each class of agent is a running score that accrues through out it's life time per cycle. Equation 1 represents how the energy score is calculated each cycle for each individual. In Equation 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.

$$p_{n+1} = p_n + \omega - \alpha \tag{1}$$

For predators, ω is dependent on an interaction with a prey agent and a strike success probability that can differ based on microhabitat. If a strike is successful, the prey agent is removed from the landscape and a energy amount α accrues to the predator agent's pay-off score. For prey agents, α 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, pay-off values for snake energy gain, snake energy cost, kangaroo rat energy gain (bush/open), and kangaroo rat energy cost were based on a previous game theory model analyzing the same system Bouskila (2001).

2.1.4 Pure and Mixed Strategies

Uumarrty is capable of modelling the microhabitat preference of an individual as a pure strategy or a mixed strategy Smith (1982). A pure strategy is where an individual exclusively prefers one microhabitat over another, while a mixed strategy is where individuals have a weighted preference for one microhabitat over another, but can still utilize both microhabitats for foraging over the course of their lifetime.

Equation 2 represent the probability of an individual moving into a given cell in a landscape. Microhabitat preference (mp) is the individual's weighted preference of a given microhabitat, bc is the total number of bush microhabitats in the landscape, oc is the number of open cells in the landscape, i is an individual bush cell in the landscape, and j is an individual open microhabitat cell. 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. 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.

$$
\begin{aligned}
Pr_i(bush) &= mp(\frac{1}{bc}) \\
Pr_j(open) &= (1 - mp)(\frac{1}{oc}) \\
\sum_{i=1}^{bc} Pr_i(bush) + \sum_{j=1}^{oc} Pr_j(open) &= 1
\end{aligned}
\tag{2}
$$

2.2 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 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 Tuckey 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 Seabold and Perktold (2010).

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 manor (Figure 3A), or may become constant (Figure 3B). We developed a novel method to classify the inflection points of the per generation microhabitat preference strategies in order to obtain metrics for stability analysis.

Our inflection 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 Savitzky and Marcel (1951) with a window size of three. We used two methods to classify inflection 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 oscilate between positive and negative values. If the first method does not classify an inflection 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, then this point would be classified as a minimum inflection point and the opposite 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 in order to only classify one local maxima point per strategy flip as rapid small changes of the data could produce a false local optima. From a biological context, inflection points would represent populations undergoing a shift toward a different microhabitat preference strategy, likely as a result of interspecific competition or predation.

From the inflection 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 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 inflection points and being a constant trend. However, general stochasticity from the model can lead to occasional false positive inflection points. To account for this, the algorithm has sensitivity conditions. If there are less than five inflection 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 1 or unstable 0.

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 as a whole 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 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 generally stable under a given set of experimental conditions.

2.3 Kangaroo Rats vs. Rattlesnakes

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 then introducing more complexity into the system in subsequent

experimental groups that follow. Each set of experiments is also ran 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 it may diverged 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 the reproduction frequency of kangaroo rats 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 in Whitford et al. (2019). Energy gain parameters are from a game theory model Bouskila (2001) that was in turn based on empirical field observations and experiments Bouskila (1995). Parameters used in case studies are listed in Table 1.

2.3.1 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 it's predator, we increase the energy gain for the kangaroo rats in one microhabitat over the other (Table 2). This experimental design should help researchers ascertain how the ecological impact of a bottom up regulation of energy gain from prey foraging influences the microhabitat preference of both the predator and prey.

2.3.2 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%, while decreasing the strike success in the open by 1% , thereby holding total selection pressure constant, but varying risk across microhabitats (Table 3).

2.3.3 Case Study 3: Introducing Owls

There have been several studies on the effects of owls on kangaroo rat and small mammal foraging (Bouskila (1995),Bouskila (2001), Embar et al. (2014)) that generally show owl predation results in kangaroo rats decreasing foraging time in open habitats, where they are susceptible to aerial attacks. 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 specialist predators in the context of microhabitat usage due to the canopy cover provided by bush microhabitats. The genetic algorithm applied to the kangaroo rats and rattlesnakes is not applied to the owl population. We hold the total number of predators constant but manipulate the ratio of snakes to owls in a landscape to see how this will influence the kangaroo rat and rattlesnake microhabitat preference (Table 4).

3 RESULTS

For each experimental group, we obtain results from an ANOVA test and a Tukey-post hoc test (Fig. 4) for both the rattlesnake and kangaroo rat population and; for pure and mixed microhabitat preference. The model output also summarizes mean microhabitat preference (Figure 5-6), the total amount of microhabitat usage strategy changes (Figure 7-8A,D,G), mean generations before a strategy flip (Figure 7-8B,E,H), and

the mean magnitude of how severe the strategy change is (Figure 7-8C,F,I). Finally, we visualize Nash score results as a heat map in Figure 9. For all the case studies, kangaroo rat and rattlesnake populations, the ANOVA results showcased a significant p-value showcasing 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 indicates that some experimental groups were more similar than others (Figure 4).

3.1 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 2), while keeping the effects of predation constant. When modeling microhabitat preference as a pure trait, in lower ordered experimental groups where the benefit of foraging in a particular microhabitat is greater than the cost of foraging (experimental groups 1, 2 and 3. respectively) the kangaroo rat population is distributed evenly in both microhabitat types (Figure 5A), with no statistical difference between these three experimental groups (Figure 4A). After experimental group 4, the kangaroo rat population adopts a dominant preference of the open occurs (Figure 5A) and there is no statistical difference in preference between experimental groups 4,5, and 6 (Figure 4A). The rattlesnakes, however, showed a more gradual transition to preferring the open in experimental groups 1,2, and 3. In experimental group 4 the population completely adopts a microhabitat preference for the open (Figure 5B).

The rattlesnake population microhabitat preference for the pure experiment showed high levels of evolutionary stability, as interpreted by our Nash score. Experimental group 4 and 5 have a Nash score greater than 0.5 (Figure 9B) meaning that over half of the simulations run with these specific experimental parameters reached an equilibrium state. In contrast, the kangaroo rat populations in this set of simulation has a Nash score of 0 (Figure 9A), with a large number of strategy flips and high variance for experimental groups 3-6 (Figure 7G). The kangaroo rat mean number of generations before a strategy flip and the mean magnitude of the strategy flip (Figure 7B, C) are relatively low in experimental groups 3,4,5, and 6 compared to experimental groups 1 and 2 further demonstrating they are switching strategies often.

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 maintain a limited preference for bush microhabitat persisted for all experimental groups (Figure 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 4C). The Nash score analysis shows that neither population is close to reaching an evolutionary stable strategy in this case study as all experimental groups have a Nash score of 0 (Figure 9A, B).

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

To explore the impact of varying rattlesnake strike success, each subsequent experimental group gradually increased the probability of rattlesnakes successfully striking prey in bush microhabitats while decreasing strike success in the open (Table 3). When microhabitat preference is modelled as a pure trait, kangaroo rats gradually shifts preferences toward the open across experimental groups, with the mean difference between experimental group 1 to experimental group 6 is -0.188 (Figure 4E). The magnitude of microhabitat preference shifts for the rattlesnake population by comparison is much smaller, as the largest difference between experimental groups is from group 1 to 5 with about a 0.05 preference shift for bush microhabitats. Neither the kangaroo rat population or the rattlesnake population microhabitat usage strategy

are evolutionary stable as the Nash score of all experimental groups is 0 (Figure 9). Both populations also have a high mean magnitude of strategy flips (Figure 7F) and the mean generations before a strategy flip is 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 5D), the mixed trait rattlesnake population tends to prefer the open (Figure 6D), with a mean difference of -0.138 between experimental groups group 1 and 6 (Figure 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 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 (Figure 6C). For both populations, these strategies are not evolutionary stable (Figure 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 8F). Experimental group 5 and 6 have an increased mean generations before a strategy flip (Figure 8E), meaning populations are not switching strategies as often compared to the control group (experimental group 1).

3.3 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 5E, F). Experimental group 1 and 2 show a gradual shift in microhabitat preference toward the bush with a mean microhabitat usage difference of 0.07 for the kangaroo rat population (Figure 4I) and 0.05 for the rattlesnakes (Figure 4J). Once the proportion of owls is equal to rattlesnakes (experimental group 4), an increased preference toward the bush is seen in both populations. Experimental group 3 to 4 has a mean difference of microhabitat preference of 0.327 for kangaroo rats (Figure 4 I) and 0.322 for rattlesnakes (Figure 4 J).

When modeling preference as a pure trait, kangaroo rats preference toward the bush 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 9A). The rattlesnake population does not reach equilibrium in any of the experimental groups for this case study. Experimental group 4 has a Nash score of 0.26, meaning that the population was starting to reach equilibrium, but the subsequent experimental groups 5 and 6 did not (Figure 9B). For the rattlesnake population, the total number of strategy flips (Figure 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 7H) decreases from experimental group 4 to 5, indicating that there is more fluctuations in microhabitat usage strategies over time as the total number of rattlesnakes in the population decreases (Table 4).

Modelling microhabitat preference as a mixed strategy trait yields similar results to the pure owl experiment as when owls are the more abundant predator this causes a significant preference toward utilizing 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 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 group 4, 5, and 6 are not significantly different in microhabitat preference (Figure 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 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 actually an increase in strategy flips when comparing experimental group 4 and 5 (Figure 8G) and a slight increase in the mean magnitude of strategy flips from experimental group 4 to 5 and 5 to 6 (Figure 8I), indicating that rattlesnakes become more unpredictable in landscape usage at these higher experimental groups.

4 DISCUSSION

4.1 The Nash Score and Expanding Agent Based Modelling Methodology

One of our primary modelling objectives was to integrate 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, and categorizing traits as being either pure or mixed strategies are all concepts developed for game theory that we integrated as inputs into our 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.

The Nash score conceptually 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 Scharf (2021) and is due to adaptation of two trophic levels interacting and coevolving with one another. This is also known as an evolutionary ”chase” Abrams (2007), 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 employing genetic algorithms are applied. 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 unistable 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. This novel modelling framework gives researchers a new computational tool to assess the implications of how changes in ecological conditions impact overall community dynamics.

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

The primary objective of our case study was to experimentally determine the ecological factors that most influence shifts and stability in the microhabitat preferences of a predator-prey system. A long-standing debate revolves around whether the microhabitat preferences of prey are primarily driven by risk aversion

Brown et al. (1999), or by decisions made by prey to maximize foraging yields Tutterow et al. (2021). In order to shed light on this conundrum, we present three distinct case studies, each offering a unique perspective on the matter with a different ecological lens.

The first case study of increased energy gain in one microhabitat does contradict or add nuance to the general principle that predator microhabitat preferences track prey preferences, and prey balance predaton risk with energy gain. When modelling microhabitat preference as a pure trait, as the disparity of energy gain in one microhabitat versus the other grows large enough (experimental groups 4, 5, and 6 Table 2) and one of the microhabitats can no longer provide enough energy to sustain the metabolic costs (Table 1), then prey preference shift completely toward the habitat with greater resources (Figure 5A). However, before this tipping point (experimental groups 2,3 Table 2), the resource disparity has no effect kangaroo rat microhabitat preference (Figure 4A), likely because the increased predation risk in the more valuable habitat balances the potential benefit from foraging there (Figure 5B). This phenomenon is consistent across simulations, such that in experimental groups 4, 5, and 6 rattlesnake microhabitat preference begins approaching an equilibrium and is almost an evolutionarily stable, as the Nash score in these experimental groups is greater than 0.5 (Figure 9B).

The simulations modeling microhabitat preference as a mixed trait underscore the importance of prey to be able to use microhabitats that may provide temporary spatial refuge from predators even at the cost of less energy gain. In experimental groups 3-6 (Table 2), kangaroo rats retain more preference for the bush habitat than in the pure strategy simulations (Figure 5A, B, 6A, B). Additionally, mean number of generations before a strategy flip for the kangaroo rats (Figure 8B) is lower compared to the mean generations before a strategy flip of the other case studies (Figure 8E, H) and the mean magnitude of the strategy flip (Figure 8C) is low in these experimental groups. This indicates that the kangaroo rat population is not altering microhabitat preference over time as drastically, primarily using the open (Figure 6A). but also unpredictably using lower quality bush microhabitats. For the rattlesnakes, it is optimal to partake in some degree of prey behavioral management as seen in the slight preference toward the bush (Figure 6B).

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

The simulations altering snake strike success (Table 3) support the general principle that predators act to diffuse the fear of prey across a landscape as a form of prey behavioral management through evolutionary "chase" dynamics Abrams (2007). Increasing the probability of a rattlesnake strike success in bush microhabitats had little effect on increasing preference toward the bush of the rattlesnake population in the pure experiment (Figure 5D). There is even a direct conflicting affect in the mixed experiment as rattlesnakes have to adopt an open preference (Figure 6D) and have to switch microhabitat usage strategies often through evolutionary time (Figure 8E) despite the being at a disadvantage in this microhabitat. Rattlesnakes must prefer the open microhabitat at high rates because their increased killing efficiency in the bush drives kangaroo rats to the open (Figure 5C-6C). Thus without some outside ecological pressure such as owls in the open or an increased foraging gain for kangaroo rats in the bush, rattlesnakes have to spend more time in the open to partake in behavioral management. An aspect of our experimental design that may change our results for this set of simulations is that each experimental group only has a small change in the strike success probability of rattlesnakes.

4.4 Case Study 3: Introducing Owls

The model also indicates that the introduction of a predator specializing in foraging in open microhabitats (owls) will cause a shift in preference toward using the bush. However, empirical studies have only found

minimal microhabitat preference shifts in natural systems when owls are present (Bouskila (1995), Embar et al. (2014)). This discrepancy could be because our model finds that more substantial preference changes caused by owls only occur when they are very abundant; thus, real world conditions may be more similar to experimental groups 2 or 3 (Figure 5-6 E,F).

Our results also imply that there can be a microhabitat preference state shift when the number of owls exceeds that of rattlesnakes. If the trait is a pure strategy, then preference for bush microhabitats becomes an ESS (Figure 5E, Figure 9A). The snakes adopt the same strategy (Figure 5F), 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. This is similar to findings from the Bouskila (2001) 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 capture by a snake in the bush. 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 9B) with a Nash score of 0.26 but subsequent experimental groups have a Nash score of 0. When the population size is low, even one member of the population having a different microhabitat preference will have a larger affect on the populations mean microhabitat preference due to a low sample size, thus making equilibrium harder to reach. This is one advantage of using agent based models over a mathematical framework where populations are assumed to be infinite in size as our model explicitly parameterized population size which provides researchers an avenue for understanding how population size influences optimal strategies and ESS dynamics.

When microhabitat preference is modelled as a mixed trait, the owl simulations suggests there is a non-zero limit for the rattlesnake population bush preference regardless of the number of owls present (Figure 6). These results critique the idea that rattlesnakes and owls work synergistically Embar et al. (2014) and supports the idea that it is optimal for rattlesnakes to distribute selection pressure in the open a minority of the time to monopolize prey in the bush. This supports the idea that predators work to distribute ”fear” across a landscape Brown et al. (1999), Hugie and Lawrence (1994), Kotler (1984), 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 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 (Figure 9A). 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. The assumptions are model takes that may complicate this finding is that we assume owls are incapable of catching kangaroo rats under bushes which may not be ecologically true as some bush microhabitats may not provide the perfect canopy protection Embar et al. (2014). Other assumptions of our model that may change its findings are that interspecific competition behaviors between owls and rattlesnake have been found where some owls may predate rattlesnakes which would have an impact on their microhabitat preference Rowe et al. (1986). One aspect of our experimental design that may shift results is that in experimental groups 5 and 6 the rattlesnake population is low which lessens statistical impact of our findings.

5 CONCLUSION AND FUTURE WORK

Across all of our case studies, our study supports the hypothesis that, without outside ecological pressures sustaining certain microhabitat preferences, predators will exhibit foraging behaviors that diffuse the probability of predation across a landscape Brown et al. (1999) and predators and prey will display chase dynamics over evolutionary time Abrams (2007). Predator microhabitat preferences diffuse risk across the landscape even when predators are directly disadvantage 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 modelling approach provides a more nuanced understanding of how these dynamics are dependent on ecological circumstances. Our modelling approach also allowed us to develop metrics that illustrate how these preferences shift through evolutionary time via metrics we developed 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 biological systems, and other types of traits in order to develop a deeper understanding of predator-prey dynamics over evolutionary time.

Future work could develop several complementary extensions of our modelling approach. For example, our modelling framework would allow for randomly setting parameters in order to apply a regression based approach to understanding how these ecological forces interact with one another and impact microhabitat preference. Some of the our case studies showed non-linear trends in microhabitat preference shifts across the experimental groups due to trade offs between predation risks and foraging gain. Some of these limits may be shifted or overcome when introducing multiple 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.

Another potential ecologically relevant extension would be to include within-generation behavioral learning of predator and prey in order to model the impact of behavioral experience in these populations. This has been successfully accomplished in other models such as William A (2009) and would better incorporate how ontogeny effects landscape usage over evolutionary time. 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 taking an agent based modelling 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 on how microhabitat preferences of predator and prey population shift as a result of ecological complexity. Our approach allows us to measure the magnitude 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 most other biological systems.

6 FIGURES

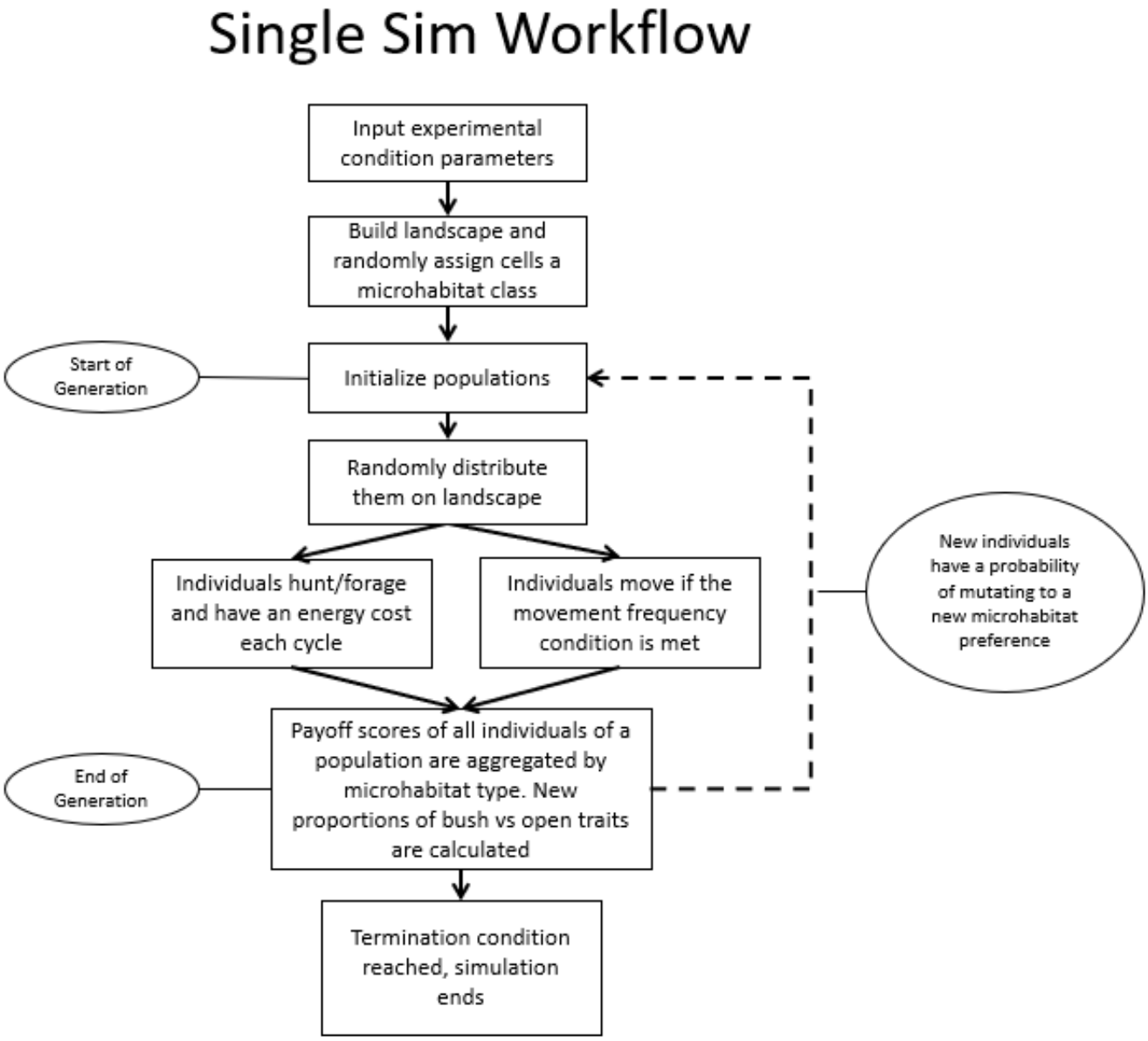

Figure 1. Conceptual diagram showcasing the logic of an individual simulation. This logic is applied to both the kangaroo rat population and the rattlesnake population of all simulations.

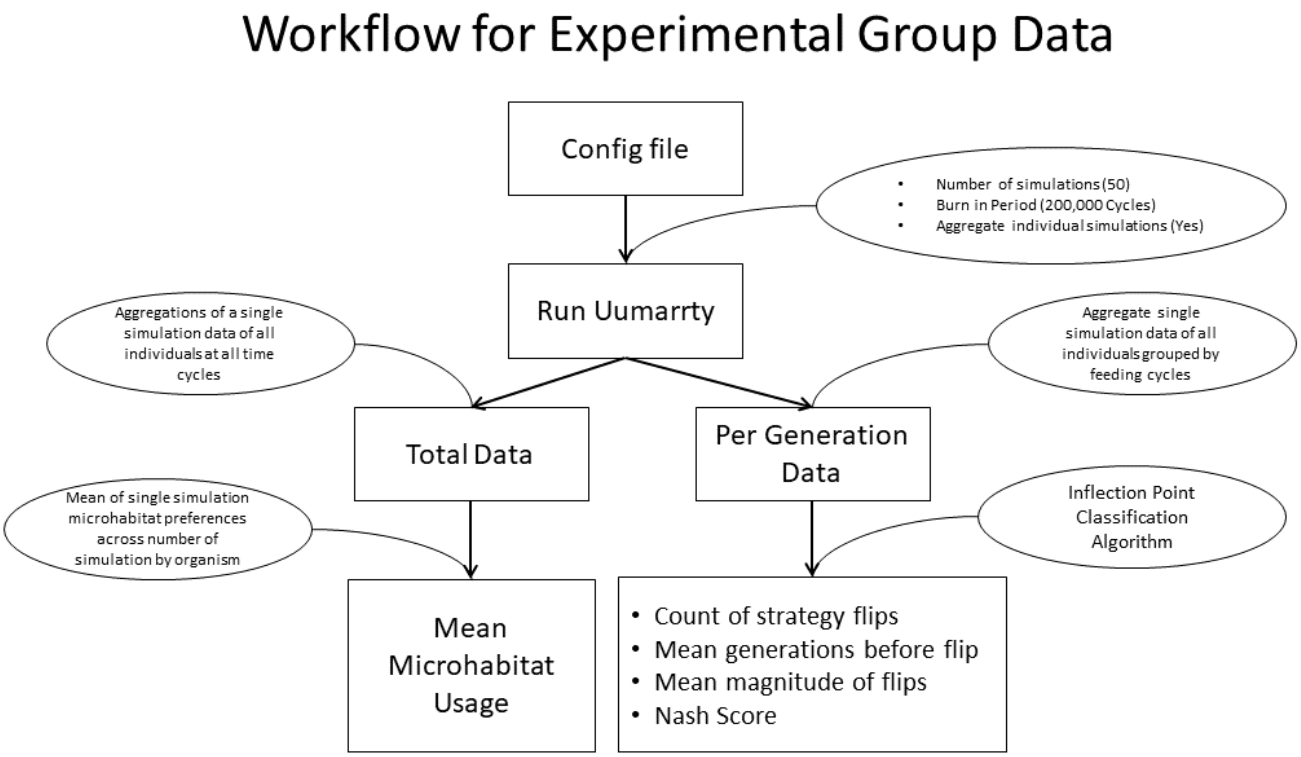

Figure 2. Conceptual diagram of the simulation workflow for how to generate the results of one experimental group of a case study. This work flow was applied to all 6 experimental groups of all 3 case studies.

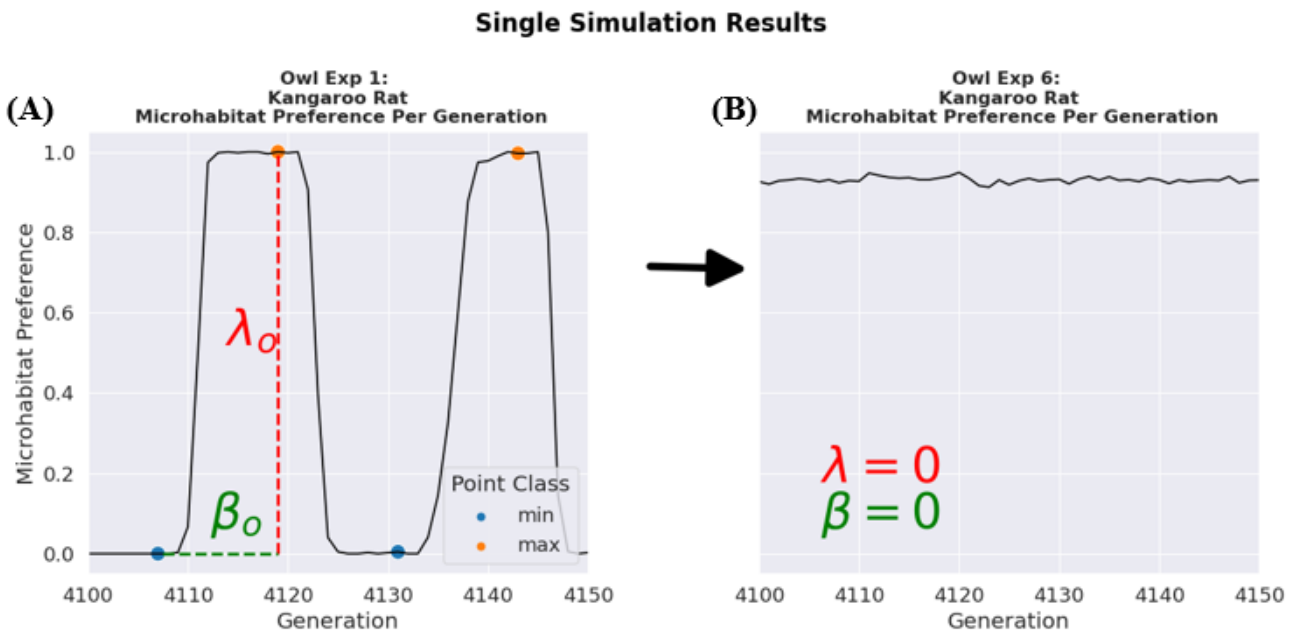

Figure 3. Both graphs are the mean microhabitat preference for the kangaroo rat population per generation during an individual simulation. (A) is a single simulation for the owl experiment from experimental group one. (B) is a single simulation for experimental group 6. The metric λ_o is the difference between the microhabitat preference of an optimal point and the previous optimal point in time, shown by the red dotted line. The metric β_o 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 mirohabitat preference of the population is in equilibrium which can be seen in (B). Point class represents whether an optimality 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.

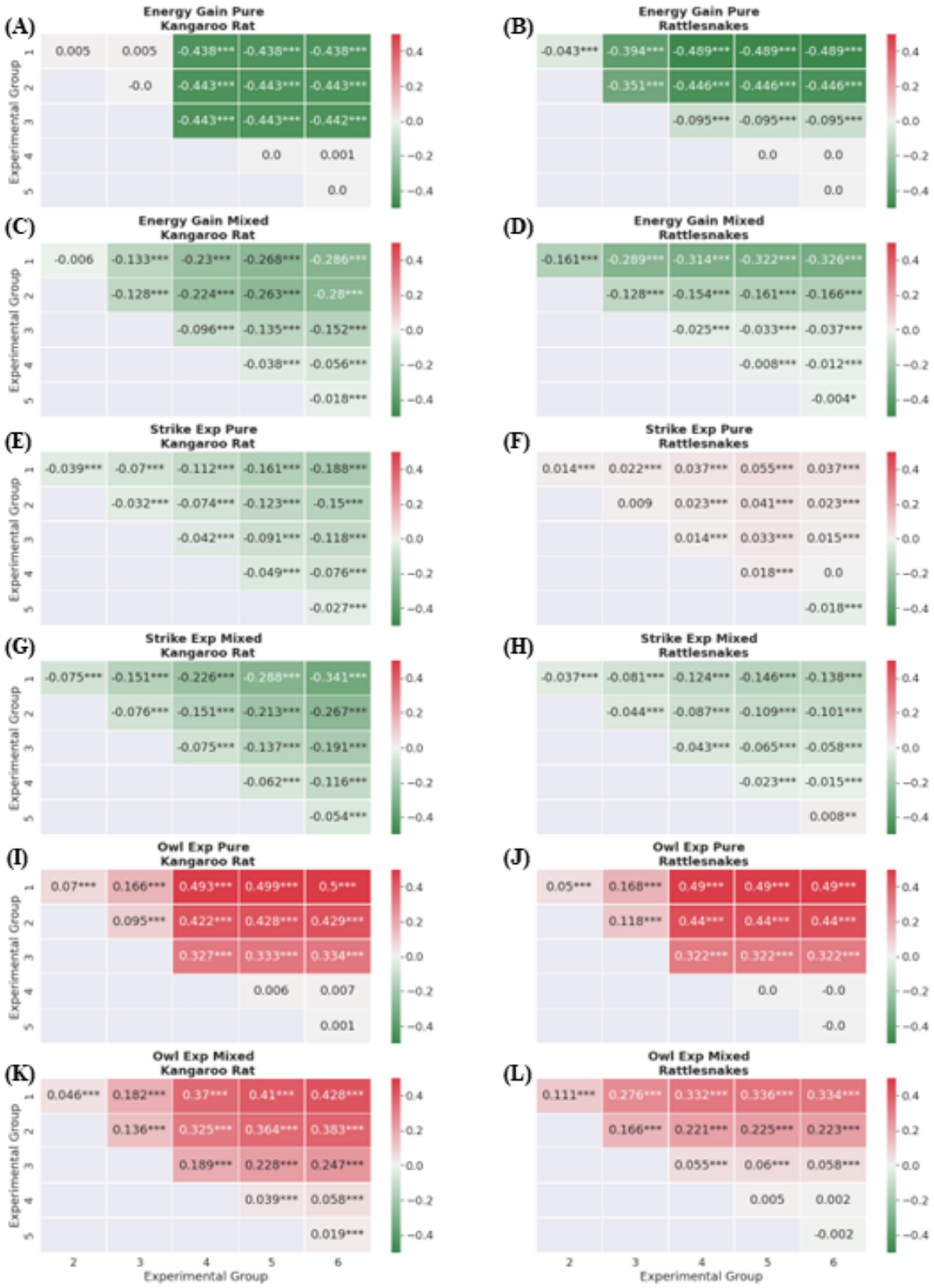

Figure 4. Results of the tukey post hoc anova test. Values in each cell are the differences of the means between experimental groups. A positive increase (red) demonstrates an increased preference to the bush, while a negative mean difference indicates an increased preference for the open. Stars represent whether the experimental groups have statistically significantly different means. *** represents a p-value less than 0.001, ** represents a p-value less than 0.01, finally a p-value less than 0.05 is represented by a single *.

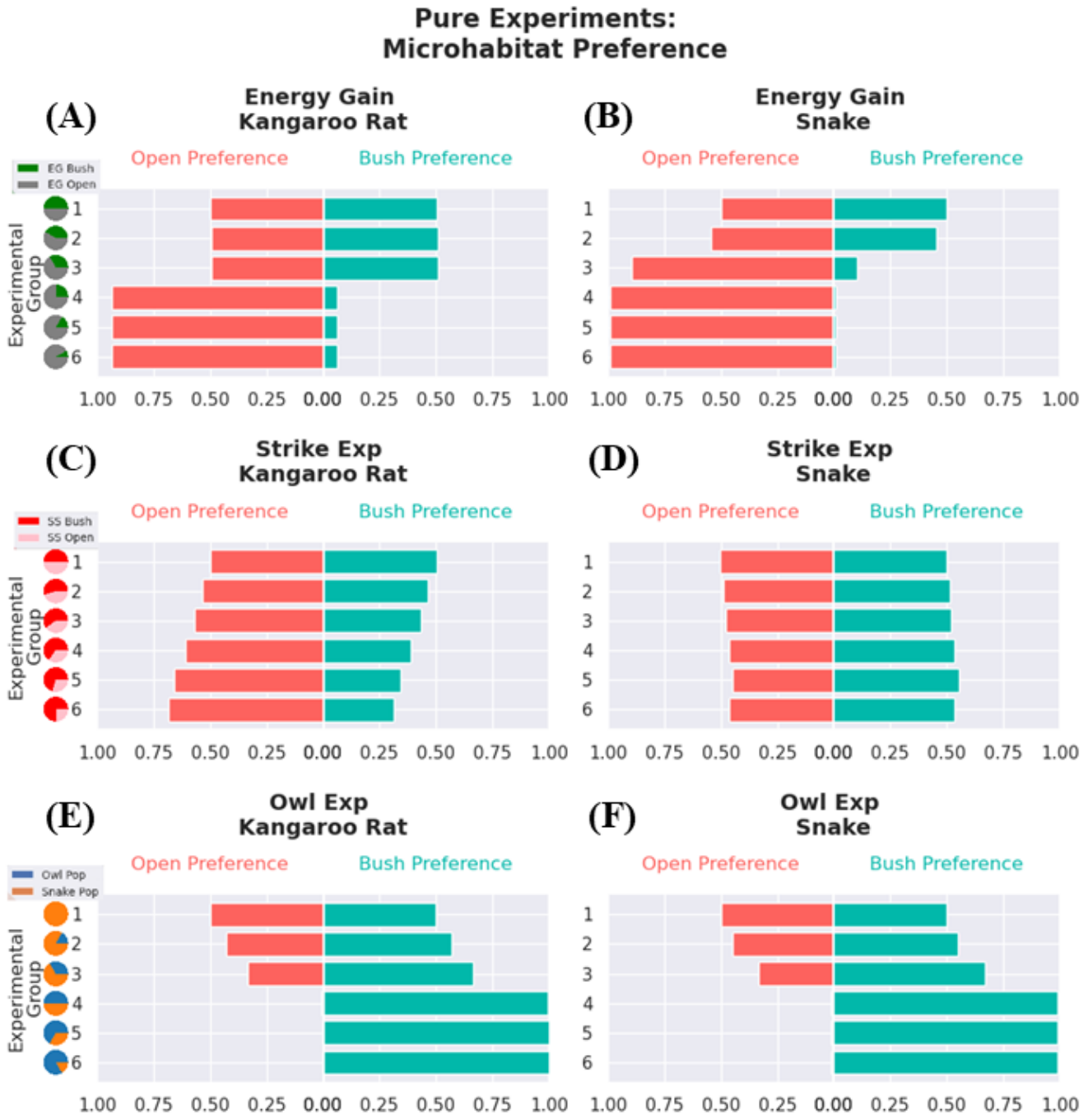

Figure 5. Mean microhabitat preference of the populations for all experiments with pure microhabitat usage strategies. The y-axis shows the experimental groups with pie charts representing how the experimental parameter of interest is being changed. The x-axis is the mean microhabitat preference of the 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 rats population. (B) is the same as (A) but for the rattlesnake population. (C) is the microhabitat preferences of kangaroo rats in the rattlesnake strike probability experiment. (D) is the same as (C) but for the rattlesnake population. (E) is the microhabitat preferences of the kangaroo rat population under different experimental designs for the owl experiment. (F) is the same as (E) but for the snake population.

Figure 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. (A) shows the microhabitat preferences of kangaroo rats for the differing foraging gains for kangaroo rats in the two microhabitats. (B) is the same as (A) but for the rattlesnake population. (C) The microhabitat preferences of kangaroo rats in the rattlesnake strike probability experiment. (D) is the same as (C) but for the rattlesnake population. (E) is the microhabitat preferences of the kangaroo rat population under different experimental designs for the owl experiment. (F) is the same as (E) but for the snake population.

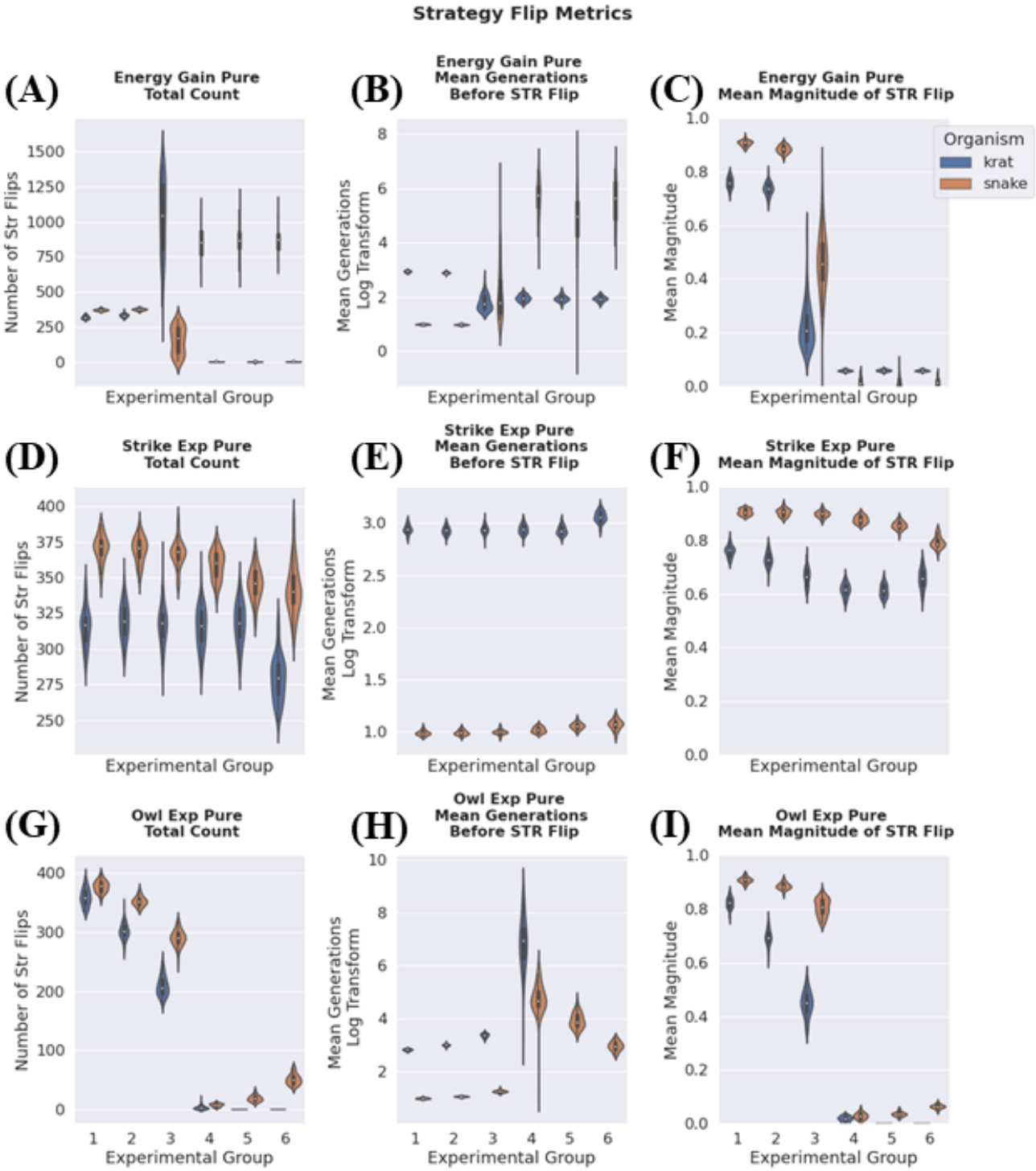

Figure 7. Analysis of metrics produced by the point classification algorithm such as total number of strategy flips, the mean number of generations before a strategy flip, and the mean magnitude of a strategy flip. All of these figures are for the pure microhabitat usage trait.

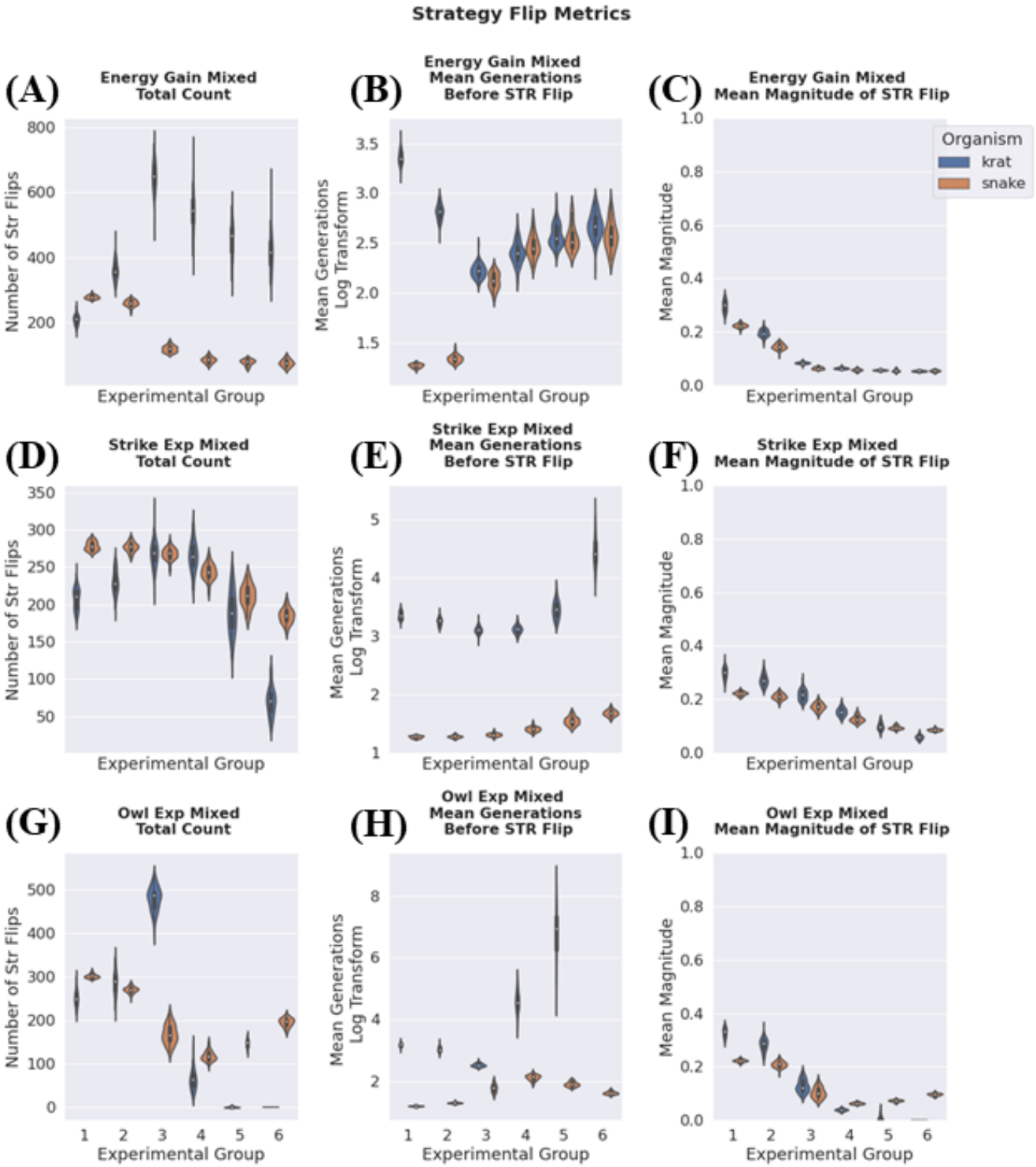

Figure 8. Analysis of metrics produced by the point classification algorithm such as total number of strategy flips, the mean number of generations before a strategy flip, and the mean magnitude of a strategy flip. All of these figures are for the mixed microhabitat usage trait.

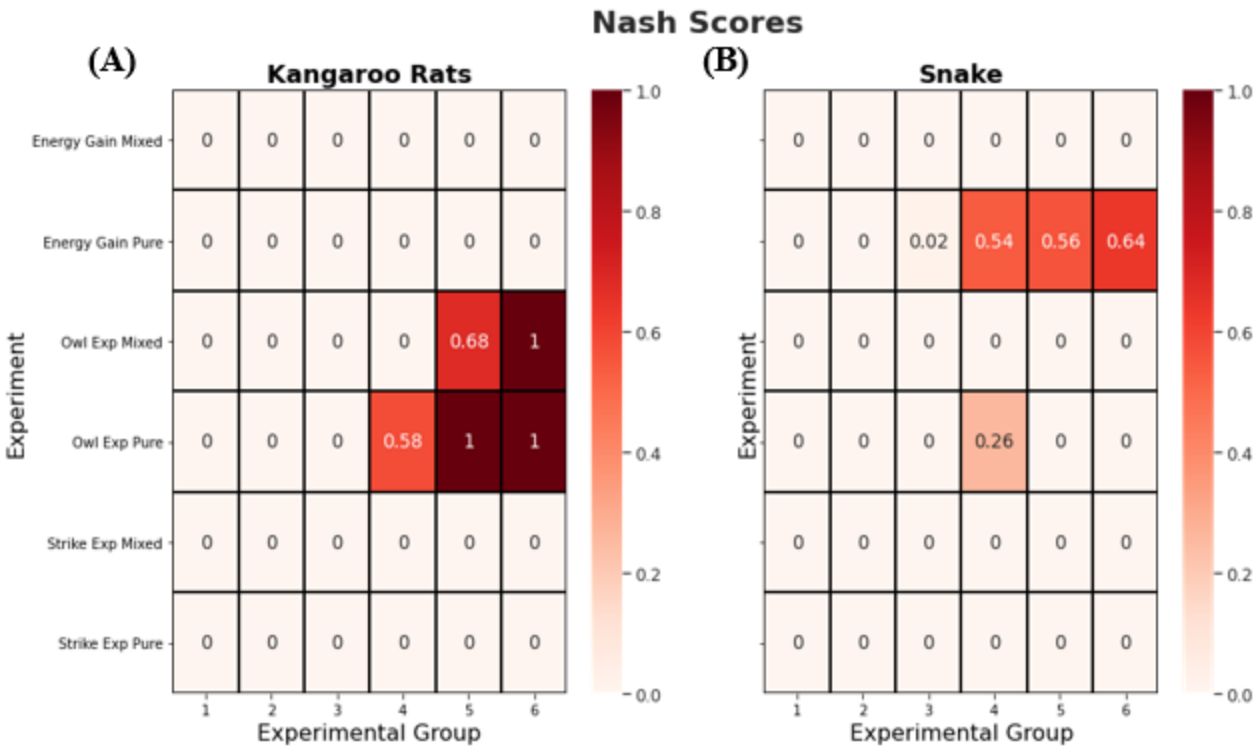

Figure 9. Results of the Nash score analysis where each cell represents the Nash score for that specific experimental group associated with the experimental design. The Nash score is the ratio of simulations that reached equilibrium over the total number of simulations run for a given experimental design. A Nash score of 1 means that 100% simulations completely reached equilibrium and the associated microhabitat preference strategy is an evolutionary stable strategy and can't be invaded by other strategies throughout evolutionary time. (A) shows Nash scores for the kangaroo rat population and (B) shows the same information but for the rattlesnake population.

6.1 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. Constant experimental parameters. Cells titled ”EXP” are parameters that are associated with experimental groups for a given case study.

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 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 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 4. Experimental parameters for the case study of introducing owls into the system experimental groups.

7 ADDITIONAL REQUIREMENTS

For additional requirements for specific article types and further information please refer to the individual Frontiers journal pages

CONFLICT OF INTEREST STATEMENT

The authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

AUTHOR CONTRIBUTIONS

Michael Remington: Conceptualization, Methodology, Software, Validation, Formal analysis, Investigation, Data Curation, Writing - Original Draft, Writing - Review & Editing, Visualization. **Rulon W. Clark**: Conceptualization, Writing - Review & Editing, Supervision, Funding acquisition. **Ryan Hanscom**: Conceptualization, Writing - Review & Editing. **Timothy E. Higham**: Conceptualization, Writing - Review & Editing, Supervision, Funding acquisition. **Jeet Sukumaran**: Conceptualization, Software, Validation, Writing - Review & Editing, Resources, Supervision, Project administration, Funding acquisition.

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A special thanks to Dr. Margaret Field Prof. Emerita, American Indian Studies at San Diego State for recommending the name Uumarrty for our software. Uumarrty is a Kumeyaay word which means ”the gambling game”. We picked this name because the gambling aspect reflects the risk and reward trade off of organisms foraging in a game theory framework. We also wanted to pay homage to the native people of San Diego, the Kumeyaay tribe.

DATA AVAILABILITY STATEMENT

Data available on request from the authors.

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